Literature review:

Impact of Chilean needle grass *Nassella neesiana* on biodiversity in Australian indigenous grasslands

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An Australian Government Initiative
DEFEATING THE WEED MENACE

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CONTENTS

Conventions and standards

Botanical names follow Walsh and Stajsic (2007) or Shepherd *et al*. (2001), where possible, unless outdated. Use has also been made of the International Plant Names Index (2007) [http://www.ipni.org] and 'World Grass Species: Synonymy' (Clayton *et al.* 2002 onwards).

Literature references to *Danthonia* and Australian *Stipa* have generally been altered to *Austrodanthonia* and *Austrostipa*/*Nassella*/*Achnatherum* unless there were clear reasons to retain the historical useages. Similarly, references to exotic stipoids have generally been changed, where necessary, to currently recognised genera, mainly following Barkworth (2006).

Abbreviations

ACT	Australian Capital Territory
c.	circa, approximately
C	carbon
Ca	calcium
cm	centimetre
DSE	dry stock equivalent – the annual energy requirement of an adult merino wether
EVC	Ecological Vegetation Class
gen.	genus
ha	hectare
K	potassium
kybp	thousand years before present
m	metre
mybp	million years before present
N	nitrogen
nov.	new (as in nov. gen.)
NSW	New South Wales
P	phosphorus
Qld	Queensland
S	sulfur
SA	South Australia
sp.	species
spp.	more than one species
t	tonne
Tas	Tasmania
Vic	Victoria
WA	Western Australia
ybp	years before present

INTRODUCTION

Globally and locally, alien invasive plants are one of the most significant causes of degradation of natural ecosystems and amongst the greatest threats to the conservation of biodiversity (Carr 1993, Adair 1995, Vitousek *et al.* 1997, Adair and Groves 1998, Williams and West 2000, Byers *et al.* 2002, Wang *et al.* 2009). Approximately 11% of the Australian vascular plant flora consists of established exotic species (Vitousek *et al.* 1997), a 1990 total of c. 2000 species (Adair and Groves 1998).

The Poaceae (grasses) contains many of the most damaging invasive plants. 22.9% of all grass species are recognised as weeds, the highest proportion of any of the major weedy plant families (Witt and McConnachie 2004). Globally, at least 668 genera and c. 2176 species of grass weeds have been recognised (Randall 2002).

Communities subjected to anthropogenic disturbance and close to human development are more prone to invasion by exotic plants (Fox and Fox 1986, Hobbs 1991, Adair 1995, Adair and Groves 1998). Temperate grasslands worldwide have been conspicuously invaded (Aguiar 2005) and in Australia are one of the ecosystems most severely affected and heavily invaded by a wide range of exotic weeds (McIntyre and Lavorel 1994a, Groves and Whalley 2002). Chilean needlegrass, *Nassella neesiana* (Trinius and Ruprecht) Barkworth (Poaceae: Stipeae) is a relatively new threat.

N. neesiana has many of the characteristics of a successful invasive species. It is a perennial, long-lived (Cook 1999), cool season (winter-spring growing), C_3, South American, monecious, tussock grass, with a high survival rate of all life stages (Gardener *et al.* 1996a 1999 2003a). It is self fertile (Connor *et al.* 1993) but can cross pollinate and has a flexible reproductive strategy involving both chasmogamous and cleistogamous panicle seeds, along with concealed cleistogamous seeds on the stem nodes (Connor *et al.* 1993, Slay 2002c). In Australia it has been identified as an “aggressive” (McDougall and Morgan 2005 p. 35), highly invasive (Morfe *et al.* 2003), high impact (Thorp and Lynch 2000) weed, which is rapidly expanding its range (Lunt and Morgan 2000). It’s rapid inter-regional spread from initial successful population confirms its among a set of the “most worrisome” invaders (Shea and Chesson 2002) and justifies it status as Weed of National Significance (Snell *et al.* 2007). It is both an environmental weed (Carr 1993) and a weed of agriculture (Grech 2007a).

The invasiveness of *N. neesiana* in Australian native vegetation seems to have first come to be widely acknowledged as a result of Carr *et al.* (1992 pp.41, 51) who considered it to be a “very serious threat to one or more vegetation formations in Victoria”. In native ecosystems it is reportedly able to actively invade grasslands (Hocking 1998 2007) and is potentially able to outcompete C_4 (summer growing) grasses such as *Themeda triandra* Forrsk. (Ens 2002a). Along with *Nassella trichotoma* (Nees) Hack. ex Arechavelata, it is rated as the most significant weed threat to temperate grassland biodiversity in Australia (McLaren *et al.* 1998, Groves and Whalley 2002) and “the worst environmental weed threatening native grasslands” (Snell *et al.* 2007).

According to Kirkpatrick (1995 p. 77) *N. neesiana* has “the potential to almost totally displace the native flora” in lowland temperate grasslands. Kirkpatrick *et al.* (1995 p. 35) thought that it seemed to be “capable of dominating grasslands across cool temperate southeastern Australia”. Puhar and Hocking (1996) considered it “a serious emerging weed threat” and Liebert (1996 p. 8) a “major threat” to native vegetation. Morgan (1998d) viewed it as one of the “most potentially threatening species” to *T. triandra* grasslands. Lunt and Morgan (2000 p. 98) rated it as “perhaps the most serious environmental weed in remnant native grasslands in southern Victoria” and Morgan and Rollason (1995) considered it to pose “by far the greatest threat of any potential new invader” at one grassland. Ens (2005) stated that it “swamps all other ground flora and forms expansive monocultures”. According to Beames *et al.* (2005 p. 2) it is “particularly well adapted to the intensively cultivated areas surrounding urban areas and poses a significant threat to mismanaged urban grassland remnants”.

These opinions are based to various extents on supposition, personal observations and scientific study. Gardener and Sindel (1998 pp. 76-77) stated that there is “anecdotal evidence” that *N. neesiana* causes loss of plant biodiversity in grasslands “because litter from the tall tussocks accumulates in the inter-tussock spaces and excludes shade intolerant species”. However *T. triandra*, the major dominant grass of temperate Australian grasslands, has a similar inhibitory effect as the time since fire or thinning increases (Stuwe and Parsons 1977). Diversity of bryophytes (mosses, liverworts) and lichens reportedly shows similar declines following *N. neesiana* invasion “because the mosaic of substrates such as rocks and bare soil becomes covered with litter” (Gardener and Sindel 1998 p. 77, citing V. Stasjic pers. comm.), as also happens in dense *T. triandra* (Scarlett 1994). A single study of *N. neesiana* impact on insects indicated that diversity declines, although some groups benefit (Ens 2002a 2002b).

The success of *N. neesiana* as a weed has been widely attributed to its ability to produce a large, long-lived soil seed bank (e.g. Storrie and Lowien 2003, Gardener 1998) and to the widespread dispersal of seeds by human activities (Bourdôt 1988), particularly by mowing and slashing, and on livestock (Gardener 1998, Grech 2007a). However recent evidence (Hocking 2005b) from southern Australia suggests that the seed bank in native grasslands is much lower and more transient than reported in New Zealand (Bourdôt and Hurrell 1992) and agricultural grassland on the Northern Tablelands of New South Wales (Gardener 1998).

The success of *N. neesiana* is also attributable to the widespread availability of suitable climate and habitat that apparently lacks biotic resistance to it. *N. neesiana* has many of the charactersitics possessed by successful invasive species in general (New 1994, Williamson and Fitter 1996, Cox 2004): a large native range, abundance in its native range, high vagility (via seed), dispersal by abiotic, synanthropic processes, short generation time (reputedly capable of seed production in its first year), high reproductive rate, ecological flexibility, wide climatic and physical tolerances, reproduction via a single parent and a general association with humans. In addition many varieties and forms have been described, suggesting the species has wide genetic variability, at least in South America. Studies of invasive plants in native ecosystems has largely focused on”single-factor explanations” for their success (Callaway and Maron 2006), but it is clear that *N. neesiana* invasion in Australia depends on a complex combination of the plant’s characteristics and the environments invaded.

Williamson and Fitter (1996) stressed the importance of distinguishing between species specific to abundant habitats, and species that are habitat generalists, and note that a unique combination of factors account for each successful invasive species. *N.*

neesiana appears to be a habitat generalist and Australia evidently offers abundant suitable habitat, but the reasons for the success of this species in Australia remain poorly understood.

Management measures for *N. neesiana* in agricultural areas are currently focused on maximising utilisation by livestock and minimising seed production using herbicides or grazing (e.g. Grech 2007a), and in natural areas on control of new outbreaks and some serious infestations with herbicides, managing the rate of mineralisation of nitrogen to favour C_3 grasses (Groves and Whalley 2002, Hocking 2005b 2007).

Carr (1993 p. 278) observed that it is “a general tenet of Australian weed ecology that disturbance is a prerequisite for invasion”. It is also widely suggested that Australia is more subject to invasion than Northern Hemisphere biomes (Crosby 1986, New 1994 citing Di Castri 1990), because of its relative biogeographical isolation over a long period (McIntyre and Lavorel 1994a). Disturbances of various types operate at all spatial and temporal scales and may have individualistic effects on each organism in a community and potential new entrants to that community. A community or ecosystem is the consequence of all disturbances that have acted over the period in which it has been assembled. Natural disturbances are essential to maintain native vegetation (Hobbs 1991). To understand the role of disturbance it is therefore critical to distinguish between perturbations that have been formative factors over evolutionary, biogeographical and ecological time (the endogenous disturbances of Fox and Fox 1986), and those perturbations that are of new types or are extraordinary and contribute to community destruction (usually exogenous, human induced disturbances, but also geological and cosmological) (McIntyre and Lavorel 1994a, Lockwood *et al.* 2007). Distinguishing between such disturbance regimes is difficult in systems, such as Australian temperate grasslands, that are poorly understood historically (Adair 1995). Palaeoecological knowledge of ecosystems has a crucial role in understanding biological invasions (Froyd and Willis 2008), but appears to be fragmentory, at best, for these grasslands. Fire and grazing are two of the most important disturbance factors that have operated both formatively and destructively. Much of the focus of grassland management has consisted of attempts to reinstitute or imitate supposed natural disturbance regimes that are poorly understood, in a new context in which invasive exotic species and exogenous human disturbances (fragmentation, N enrichment, global warming, etc.) have historically had profound influence and continue to have pervasive effects. Thus there is an ongoing requirement to assess contemporary, ‘managed’, disturbance regimes in terms of their new effects.

Disturbance is often necessary in Australian temperate grassland to maintain the canopy gaps between the tussocks of the dominant grasses in which most of the plant diversity of the system exists. But the same sorts of disturbances also promote exotic plants, which comprise the bulk of the soil seed bank (Lunt 1990 etc.). Colonisation by novel plants is itself a disturbance factor. Hobbs (1991) found that disturbances increase invasion if they increase the availability of a resource that limited the invader prior to disturbance and are accompanied by propagule pressure. Identification of the characteristic of disturbance regimes that favour particular weeds and suites of weeds, and the management of these disturbances is one of the most critical tasks in minimising environmental weed impact (Adair 1995).

Gardener and Sindel (1998) advocated quantitative studies to evaluate the biodiversity impacts of *N. neesiana*, compare the impacts resulting from general degradation, and evaluate the effects of *N. neesiana* management techniques on the promotion or inhibition of biodiversity. Grice (2004a) concurred with the need for such studies, noting that monitoring of biodiversity can be an important tool in evaluating a weed management strategy.

The success of a plant invader depends on its biological attributes, the attributes of the communities and ecosytems that are potentially invasible, and the effects of human interference. Bourdôt and Hurrell (1989a p. 415) considered the invasiveness of *N. neesiana* in sheep pastures to be due to “adaptations that enable the plant to survive the hazards of semi-arid, low-fertility environments, rather than to high competitive ability”.

In the review which follows, the invasion of Australian grasslands by *N. neesiana* is first contextualised within the frameworks of current biological invasion theories and hypotheses. The biological and ecological attributes of the plant are then examined in detail, along with its history, impacts and management in Australia. Next, the concept of biodiversity is discussed. The components of biodiversity and the ways they may be assessed are examined, along with the nature of weed impacts on the various components of native ecosystems. In section 4, knowledge of the properties of the invaded grasslands, including their components and dynamics are reviewed. Finally an attempt is made to synthesise this knowledge into a complete picture of what is and is not known about the impact of *N. neesiana* on biodiversity in Australia’s indigenous grasslands.

Theoretical framework

“Apparently the spheres of competitiveness under which the native vegetation had evolved were irreversibly destroyed by alien introduction, or at least by the conditions conducive to the alien introduction.”

Raymond A. Evans and James A. Young (1972), on the success of invasive grasses in the inter-mountain areas of the western USA, in ‘Competition within the Grass Community’, In V.B. Youngner and C.M. McKell (Eds.), *The Biology and Utilization of Grasses*. Academic Press, New York.

A number of competing hypotheses and theories seek to explain exotic plant invasions and their impacts on biodiversity. These concentrate on four elements of the systems: 1. the properties of the invasive plant (‘invasion potential’ or invasiveness) (e.g. Rejmánek and Richardson 1996, Williamson and Fitter 1996), 2. the properties of the system at risk from invasion (its ‘invasibility”) (e.g. Londsdale 1999), 3. the role of disturbance (Hobbs 1991, Hobbs and Heunneke 1992, D’Anotonio *et al.* 1999), and 4. dispersal mechanisms and factors (‘propagule pressure’) (Williamson and Fitter 1996, Levin 2006). Adequate explanation is beset with the same problems faced by ecologists seeking to understand the factors that determine the species composition of any space, in particular the difficulties of distinguishing between causal processes, the environmental conditions that modulate them, and the patterns that result (Leigh 2007).

Residence time, the amount of time that an exotic species has spent in its introduced range, is obviously a major determinant of the extent and impact of an invasion. The longer the residence time, the higher the likelihood that the invader will become widespread (Hamilton *et al.* 2005). For example, the minimum residence time of 116 exotic grasses in Venezuela (time since the first national record of a species) is significantly correlated with the total number of known localities in which each species occurs (Rejmánek 2000). Longer residence time at the patch scale may also be expected to increase impact, due to alterations in the density and age structure of the invader population in the patch, and the accumulation of feedback and indirect effects in the invaded environment.

The ecological mechanisms that enable environmental weed invasions are in general complex and poorly understood (Prieur-Richard and Lavorel 2000, Levine *et al.* 2003, Hayes and Barry 2008). Less than 5% of studies on invasive plant impacts examined by Levine *et al.* (2003) attempted to determine the processes causing the invasion. Disturbance has “unanimously been shown to favour plants invasions” (Prieur-Richard and Lavorel 2000 p. 3) but many species appear to be invasive in the absence of significant anthropogenic disturbance, their success being attributed *inter alia* to inherently faster growth rates, superior competitive abilities related to form, phenology, resource exploitation, etc., and the occupation of unfilled structural niches (Carr *et al.* 1986, Carr 1993).

However, since each succesful invader and invaded system have distinctive characteristics, unique interactions of multiple factors are most likely responsible in each case, and single factor explanations are poorly informative (Callaway and Maron 2006).

Some of these hypotheses and theories are explored in more detail in following sections, commencing with invasiveness, then the enemy release hypothesis and the concept of biotic resistance, the theories of resource enrichment and fluctuating resources with their emphases on the importance of disturbance as a precursor to invasion, theories related to rules of community assembly including the ‘empty niche’ concept and competitive exclusion, an examination of the possibilities that rapid evolution of the invader is a significant contribution to its success, and a discussion of the concept of invasibility of communities and geographical areas. Finally the parameters involved in determination of the impact of an invasive plant are briefly discussed.

Invasive potential of a species

Many attempts have been made to identify characteristics of ‘weediness’ or what makes some plants more invasive than others (Rejmánek 1995, Rejmánek and Richardson 1996, Hayes and Barry 2008) and various suites of charactersitics possessed by successful invasive species have been identified (Table 1).

Each successful invasive species generally possesses a unique subset of these characteristics (Williamson and Fitter 1996). According to LeJeune and Seastedt (2001 p. 1572) a particular species is invasive when it “encounters habitats in which its particular suite of traits confers competitive advantage over the native dominants”. Thus the two best predictors of invasion success are a climate/habitat match of native and exotic range and a history of invasive success elsewhere (Hayes and Barry 2008). Other characteristics significantly associated with invasion success of plants are the date of introduction (residence time), biogeographic origin, brief juvenile period, growth form, asexual or vegetative reproduction, and flowering period and season (Hayes and Barry 2008). Environmental weeds (exotic plants invasive in natural ecosystems) tend to possess similar characteristics, a subset of the following: high input of viable propagules to the envionment, development time <2 years, propagules with >5 year dormancy, high biomass production, dense canopy, efficient long distance (>1 km) dispersal, allelopathic properties, coloniser of disturbed ground, adapted to fire, broad climatic tolerance and resistance to predation (Williams and West 2000, after Adair 1995). A similar set of criteria was used to undertake a rigourous weed risk assessment on *N. neesiana* as part of the Victorian ‘pest plant prioritization process’ (Morfe *et al.* 2003) and *N. neesiana* was classed as highly invasive.

The invasive potential of a species is often compromised by specialised requirements. These may include the need for particular symbionts, pollinaters or scarce, rare habitat features. Invasiveness may also be increased by the possession of special competitive mechanisms, which can include allelopathy or a novel growth form (Newsome and Noble 1986).

R-strategists have a rapid rate of population increase and high mobility, are adapted to unstable environments and early successional stages, and are able to quickly build up their numbers in areas with high levels of unused resources and low population densities of existing species. K-strategists have low mobility and are adapted to late successional stages and stable environments where the carrying capacity is approached and competition is high (Matthews 1976, Rejmánek and Richardson 1996). For perennial plants, the ability to propagate vegetatively has often been considered important (Newsome and Noble 1986).

Table 1. General characteristics of successful vs. unsuccessful invasive organisms. Sources: Newsome and Noble 1986, New 1994, Adair 1995, Rejmánek and Richardson 1996, Williamson and Fitter 1996, Cox 2004, Whitney and Gabler 2008.

Successful invaders	**Unsuccessful invaders**
large native range	small native range
wide climatic tolerance	narrow climate tolerance
abundant in native range	rare in native range
high vagility	low vagility
high reproductive rate	low reproductive rate
short generation time	long generation time
reproduction requiring a single parent	reproduction requiring two parents
small propagule size	large propagule size
high ecological flexibility	low ecological flexibility
wide physical tolerance	narrow physical tolerance
wide genetic variability	narrow genetic variability
larger than related taxa	smaller than related taxa
rapid growth	slow growth
absence of specialised requirements	specialised requirements
low susceptibility to attack by other organisms	high susceptibility to attack by other organisms
special competitive mechanisms	no special competitive mechanisms
r strategists	*K* strategists
association with humans (commensal)	not associated with humans (not commensal)

Subsets of inasive characteristics can be combined to define particular ‘strategies’ possessed by invasive plants. Newsome and Noble (1986) identified four such strategies, based on the suites of ecophysiological characters possessed by different types of weeds:

1. Gap-grabbers – early germinators with fast initial growth enabling preoccupation of ecological space.
2. Competitors - taller growing (light) or with deeper or more extensive roots (water and nutrients).
3. Survivors – longevity due to resistance to mortality factors or clonal growth.
4. Swampers – mass germinators.

Rejmánek (2000) found that Eurasian and North African grass species adventive in eastern and western North America are more often those with large rather than small native latitudinal ranges and that the latitudinal size of the native range is highly correlated with the size of the introduced range. Species with larger ranges may be more successful because of the larger absolute size of the propagule pool and because they are more likely to interact with long distance dispersers (Levin 2006).

Schmidt *et al.* (2008) highlighted a particular character suite for invasive grasses: 1. smaller seed size than the native species; 2. plastic morphological traits that enable the invader to adjust to water and N deficiencies; 3. faster growth to sexual maturity than the native species; and 4. ready stem dehiscence at the lower node (i.e. stoloniferous growth form). However Lonsdale (1994) found no relationship between weediness and height growth, relative growth rate, time to maturity (annual or perennial) or seed weight of exotic grasses introduced into northern Australia. Instead the successful weeds were most likely to be species judged to be useful, high performing or persistent in experimental agronomic field trials.

Numerous studies have investigated particular biological traits and their relationships with the success of invasive plants. Hamilton *et al.* (2005) investigated specific leaf area (the ratio of the light-capturing area per unit dry mass), plant height and seed mass and found significant correlations between invasion success and small seed mass at regional and continental scales, and between high specific leaf area at the continental scale. Greater environmental heterogeneity at regional levels, with consequent increased biotic resistance, was invoked as one cause of the differences across spatial scales. Rejmánek (1995) found that invasiveness of *Pinus* species correlated with small seed weight, short juvenile period, short mean intervals between large seed crops and vertebrate dispersal.

Various attempts have been made to assess the most important invasiveness characters by analysing subsets of regional weed floras. For example, Gassó *et al.* (2009) assessed invasive success on the basis of area occupied in mainland Spain and found that wind dispersed species were the most invasive, followed by animal dispersed species, and that residence time, when <100 years, was significantly predictive. Other studies have applied multivariate statistical approaches to attempt to identify invasive traits.

Although many studies have sought to determine the generalised features of successful invasive plants, the project has resulted in failure: the outcome of invasion is usually “highly idiosyncratic” (Gassó *et al.* 2009 p. 55), depending on the unique taxon involved, and the ecological attributes of successful invasion are habitat dependent or even site-specific (Hayes and Barry 2008, Gassó *et al.* 2009). ‘Inherent’ invasive characteristics can only be expressed if the environment allows. The corollary for success is always the availability of suitable receptor habitats (Newsome and Noble 1986). Thus the best predictors for invasiveness of a non-woody plant species appears to be similarility of native latitudinal range with the latitude of introduction (Rejmánek 1995 1996, Rejmánek and Richardson 1996 citing Forcella *et al.* 1986), or a match of climate and habitat (Hayes and Barry 2008).

The suitability of a new habitat for a particular invader is known as the ‘invasibility’ of the habitat: “the properties of the region of introduction that facilitate the survival of non-indigenous species” (Gassó *et al.* 2009 p. 51).

Enemy release and biotic resistance

‘Enemy release’ theory postulates that an exotic plant becomes a successful invader because it lacks co-evolved natural enemies and plant competitors in its introduced range: it is ‘released’ from the effects of specialist predators, parasites and plant antagonists of its native environment, and is much less subject to herbivory in the introduced range, the native generalist predators being better adapted to, and preferentially consuming native plants (Keane and Crawley 2002, Levine *et al.* 2004, Parker *et al.* 2006a). Reduced control by natural enemies in the invaded areas is believed to enable the plant to be more productive and more reproductively successful, and for its populations to expand.

‘Biotic resistance’ or ‘diversity-resistance’ theory posits that some combination of biological effects of the native organisms regulate the success of the exotic plant, although they seldom prevent invasions (Levine *et al.* 2004). The original idea is attributed to Elton (1958) who proposed that the greater the species-richness of a community, the more resistant to invasion it should be. More intense competion for resources and consequent fuller resource sequestration in more diverse communities is the explanation usually invoked, either due to a combined effect of all the species, or the greater likelihood that a species or functional group competitive with the invader is present in diverse communities (Symstad 2000, Dukes 2002, Stohlgren 2007). Early attempts to test the theory through analysis of plant diversity at a mix of spatial scales (e.g. the meta-analysis by Lonsdale 1999) provided a confused picture and mostly showed correlations of high native plant species richness with high exotic richness. But recent consensus is that biotic resistance functions very differently at different spatial scales. A majority of plant diversity studies and experiments at small spatial scales (patch, plant association) and some modelling support the theory (Prieur-Richard and Lavorel 2000, Symstad 2000, Dunstan and Johnson 2006) but at larger spatial scales there is generally a marked positive correlation between plant species richness and invasibility that corresponds to increased environmental (landscape, regional, continental) heterogeneity (Knight and Reich 2005, Dunstan and Johnson 2006). However Stohlgren (2007) argued that even at the small scale (1 m^2) contradictory results have been found, suggesting that environmental factors other than the plant diversity of an invaded area may frequently be of greater importance in determining invasibility.

Enemy release theory is focused on plant diseases and the invertebrate consumers of plants, more or less ignoring the possibility that native plants in the invader’s area of origin may have similar negative impacts. In that context, to explain a particular successful plant invasion, the enemy release hypothesis requires that the plant’s specialist natural enemies in the native range are absent from the introduced range, that specialist enemies in the introduced range do not shift onto the potential new host, and that the generalist enemies in the introduced range have less impact on the plant than on native plants in the introduced range (Keane and Crawley 2002). The hypothesis is supported by numerous studies comparing the invertebrate predators and diseases of plants in their native and exotic ranges (e.g. Memmott *et al.* 2000). Such studies have often been undertaken preparatory to classical biological control programs.

Enemy release theory has been the “conceptual underpinning” of classical biological control since its inception (Callaway and Maron 2006 p. 371).The numerous examples of pest suppression resulting from practical biological control (Julien and Griffiths 1998) and the very limited non-target impacts of these programs (Waterhouse 1998, Wajnberg *et al.* 2001) provide strong evidence that enemy release is an important cause of plant invasions: deliberately introduced parasites and predators directly control population growth of some invaders and may have indirect effects on their performance (Prieur-Richard and Lavorel 2000). However, to prevent damage to non-target species, classical biological control is constrained to concentrate on specialist enemies with narrow host ranges. The full trophic complexity of the system in the plant’s native range is extremely difficult to assess and highly variable. Furthermore, succesful biological control of a weed does not necessarily demonstrate that the weed became a problem because of natural enemy release, since the biological control agent itself has been released from its natural enemies.

A meta-analysis of 13 studies that quantified the impact of native natural enemies on invasive exotic plants (Keane and Crawley 2002) partially supported the enemy release hypothesis, finding that in every case where native specialist insects were differentiated, they attacked the exotic, however their impact was usually negligible. Native generalist enemies were found to have greater impact on the exotic in only two cases. More recent and comprehensive meta-analyses contradict the suppositions of the enemy release hypothesis (Cox 2004): native generalist predators or “evolutionarily novel enemies” (Parker *et al.* 2006a) preferentially attack exotic prey, which are poorly adapted to resist them or “defensively naive” (Parker and Hay 2005 p. 965), having had limited coevolutionary history of association with the predators. The“evolutionary naïveté” of the invasive species in the invaded system places it at greater risk of attack by newly encountered generalist herbivores (Parker *et al.* 2006b). Furthermore, generalist herbivores commonly have greater impact on plant community structure in terrestrial ecosystems than specialists (Parker and Hay 2005 citing Crawley 1989).

Parker and Hay (2005) found that native generalist herbivores offered food choices of congeneric or confamilial exotic and native species, significantly preferred, with some exceptions, the exotic plants. Following on from this work, Parker *et al.* (2006a) reviewed a large number of manipulative field studies involving over 100 exotic plant species and found that native generalist herbivores suppress exotic plants more than native plants, and that exotic herbivores facilitate the abundance and species diversity of exotic plants by preferentially consuming native plants. Invertebrate herbivores were found to have only one third to one fifth the impact of vertebrate herbivores on survival of exotic plants (Parker *et al.* 2006a). However in the studies examined, the native range of a high proportion of the exotic plants was the same region as that of the exotic herbivore (Parker *et al.* 2006a), suggesting that exotic plants without a common evolutionary history with the exotic predator, and therefore lacking defenses against them, may be as susceptible to predation as native plants. The effect of native generalist predators on exotic plants is reduced if the plant is closely related (in the same genus) to plants in the introduced range, and six times as strong on genera new to the invaded region (Ricciardi and Ward 2006, Parker *et al.* 2006b). Invertebrate herbivores are usually specialised to feed on particular plant parts and to particular plant species, groups of related species, or wide ranges of species, whereas vertebrate herbivores are generally adapted to consume plants of a particular life form or plant product (Cox 2004). Closely related plants have similar defences against herbivores (see references in Ricciardi and Ward 2006) and are likely to share traits that confer resistance to attack, or have similar physiological adaptations that lessen stress and better enable the operation of their defences (Parker *et al.* 2006b). Exotic predators which share little evolutionary history with either the native or exotic plants show no feeding preference for native species (Parker and Hay 2005).

Most studies framed within biotic resistance and/or enemy release hypotheses have largely ignored the role of plant interactions with soil microbes and the acceleration of knowledge of soil microecology. There is good evidence that invasive plants in North America have escaped from the host-specific soil microbes of their homelands and also formed new relationships with non-specific microbial mutualists in the invaded territory (Callaway and Maron 2006).

Mack's (1989) generalisations about the role of exotic livestock in destruction of native caespitose grasslands in western USA, the South American pampas and Australia, their facilitation of invasion by exotic grasses with which they coevolved and the history of native grassland degradation in Australia (Moore 1973 1993, Groves and Whalley 2002) mesh neatly with the biotic resistance hypothesis. In a sense "exotic plants may thrive not by escaping their native enemies, but by following them" (Parker *et al.* 1996a p. 1460).

N. neesiana may possess pre-adaptations that minimise predation by Australian native herbivores (suggested perhaps by the general presence of native Stipeae in invaded areas in Australia), or the native ecosystems invaded now lack their natural herbivore assemblage (e.g. kangaroos generally absent, extinct macropods and marsupial megafauna). The exotic herbivore assemblage that has invaded native grassland (including an array of invertebrates as well as mammals) may differentially attack the native plants (Parker *et al.* 2006a), or the ecosystem has been otherwise anthropogenically disturbed, or *N. neesiana* has other attributes (fecundity, high growth rate etc.) that enable it to overcome the effects of native generalist herbivores (Parker and Hay 2005).

The biotic resistance hypothesis,as it relates to plants, is not challenged by evidence that landscape scale areas with high plant species diversity also tend to have higher numbers of exotic plant species. Lonsdale (1999) compared exotic and native plant species richness at 184 landscape-scale sites of wide variation in size and found that the number of exotic plant species, but not their proportion of the flora, increased with native plant species richness. Similar analyses at large landscape scales show similar trends, however the areas invaded are not plant communities - the ecological units that are expected to show biotic resistance - and such trends are at best weak in small areas (Cox 2004).

The biotic resistance hypothesis has been further elaborated under the moniker of functional group theory: the idea that the diversity of functional groups rather than species enables resistance (Prieur-Richard and Lavorel 2000). Absence of a particular functional group (e.g. grass seed predators) eases constraints on an invasive plant. The presence of a larger number of functional groups of plants suggests that a larger proportion of available resources are already efficiently captured, so there should be greater resistance to invasion.

If there is reduced predator pressure in the new environment, a plant has a lesser requirement for defence and an evolutionary trade-off may occur in which the 'freed up' resources are allocated to other purposes, inclduing reproduction. Trade-offs resulting in growth increases and higher investment in reproduction are believed to be common in invasive plants (Cox 2004).

The rate at which invasive plants acquire new natural enemies is highly variable, but is generally rapid at first, the diversity of generalist herbivores reaching a maximum in as little as 100 years, then slows, with host shifting by and evolution of specialist herbivores gradually occurring over longer periods, up to 10,000 years (Cox 2004). Major factors influencing these rates are the diversity of the native herbivore and pathogen pools and the extent of their adaptation to phylogenetically related native plants, the phenological availabilityof the invasive plant to the potential native utilisers, and the innate defences of the plant (Cox 2004). The abundance or total area occupied by the invasive plant also appears to be important, e.g. as found in a global study of the arthropod pests of *Saccharum officinale*, which found that the number of pest species had a linear relationship to the area of sugar cane under cultivation (Cox 2004 citing Strong *et al.* 1977).

It can therefore be hypothesised that *N. neesiana* is preferentially consumed by native generalist species compared with dominant native grasses, and that exotic generalist plant predators will preferentially consume the dominant native grasses. If this is the case, grasslands with diverse and abundant populations of exotic plant predators should be more susceptible to invasion and more highly invaded by *N. neesiana*. Grasslands that have inherent biotic resistance should be occupied by native generalist mammalian herbivores including kangaroos, and have a greater diversity of native generalist phytophagous invertebrates. Grasslands without biotic resistance should lack large native mammal herbivores, have a depauperate guild of native generalist grass-feeding invertebrates, and an increased complement of exotic grass-feeding mammals Manipulative field experiments involving predator removal or paired feeding assays (e.g. Parker and Hay 2005) are needed to demonstrate such effects.

Resource-enrichment and fluctuating resources

A successful invasive plant may simply be a superior competitor for basic resources such as light, water and nutrients. Many biological attributes that engender such superior ability have been identified, for example plants with C_3 and C_4 photosynthetic pathways are superior convertors of sunlight to sugars in different environments, and any one plant may have higher fecundity or a faster growth rate than another. But because resources are 'locked up' variably in space and time by the plants in the pre-existing community, disturbance that kills or inhibits them and frees up resources is generally required for a successful invasion, or their must be extrinsic addition of resources at a rate faster than the native plants can use (Herbold and Moyle 1986, Hobbs 1991, Burke and Grime 1996, Cox 2004).

The tenet that disturbance is a prerequisite for invasion is implicity based on the notion that in undisturbed, successionally mature vegetation, surplus resources are absent (Carr 1993) or minimised or unobtainable by the existing flora. The fluctuating resources theory posits that a "plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources" (Davis *et al*. 2000). The community becomes more susceptible to invasion by a particular exotic plant if the particular resource was previously limiting the growth or survival of that plant (Hobbs 1991). Continuity of the invasion requires that gains the invader makes are not lost when resource supply contracts (Melbourne *et al.* 2007).

Disturbance, defined as any process that creates open ground, changed habitat or altered resource availability (Hobbs 1989 1991, Mack and D'Antonio 1998, Lockwood *et al.* 2007) is universal at a range of spatial and temporal scales, so gaps in vegetation and fluctuating resource pools are always available. Under this definition, disturbance includes reduction or lack of normal disturbance to which the community is adapted, e.g. reduced fire frequency, removal of grazing, or loss of burrowing mammals, can provide fluctuating resources, as native plants senesce or seed banks decay without replacement. Elimination of perturbation in disturbance-dependent systems is one of the most serious 'disturbances' they can suffer (MacDougall and Turkington 2007). Many plant communities and species require disturbance, particularly for regeneration (Hobbs and Huenneke 1992). Whether or not the gaps or unused resources created by disturbance can be taken up by an exotic species therefore depends on their size, their spatial and temporal availability, the pool of available species and the requirements of the particular species (Prieur-Richard and Lavorel 2000). Whether or not a particular species invades is dependent on the disturbance characteristics: its mgnitude and severity,duration, predictability,distribution in space and time and synergistic effects on other disturbances (Lockwood *et al.* 2007). When the parameters of the disturbance are suitable, exotic species that possess resource utilisation traits not present in the native flora often seize the advantage (McIntyre *et al.* 1995). Invasions of exotic plants can be greatly increased by combinations of disturbance such as nutrient addition and soil disturbance (Cale and Hobbs 1991).

Early successional stages have greater pools of unused resources and less competition, so are more susceptible to invasion (Davis *et al.* 2000). Resource poor environments are not invaded by many exotic species (Cox 2004). Greater species diversity generally corresponds with more complete resource usage, so diversity theoretically confers invasion resistance by limiting resource fluctuation.

Weed invasions are commonly associated with extreme resource fluctuations. One example is the invasion of Buffel Grass *Cenchrus ciliaris* L. in arid Australia. Prior to 1974 it was apparently naturalised in a few small areas in the semi-arid inland, but in the unusually wet season of 1974-5 it spread along flood plains and "run-on areas" across large areas of the arid zone (Moore 1993 p. 316).

Nutrient enrichment is often a significant contributory cause of invasions (Milton 2004). For example, King and Buckney (2002) compared total N and P, and concentration of Na, K, Ca and Mg cations in soils of 16 urban bushlands and 8 national parks in Sydney and the proportion of exotic plant species present in the vegetation. All soil nutrients were significantly higher in urban areas, and gradients from low to high invasion, and low to high concentrations, were correlated. The correlations were best explained by a combination of nutrients rather than any single nutrient. Direct manipulative studies have demonstrated that nutrient addition without other disturbance can cause weed invasion.

Other studies show that both nutrient enrichment and other disturbance are required to alter community composition. Hobbs (1989) experimented in a range of heathland, shrublands and woodlands by digging the soil, adding fertiliser, both digging and fertilising, and adding seeds of *Avena fatua* L. and *Ursinia anthemoides* (L.) Poir. Very similar results were obtained in all communities. *Avena* responded to digging with little fertiliser effect. *Ursinia* showed little response to any treatment. Digging or fertiliser alone had little effect on resultant weed biomass, but a strong effect together. These results were attributed to better seed survival and more safe germination sites in the dug areas, a probable small increase in nutrient availability in dug treatments and extreme nutrient limitation for the weeds. Hobbs (1989) therefore argued that certain types of disturbance do not significantly increase resource availability and do not make a community more invasible. In a long-running experiment Davis *et al.* (2000) demonstrated a strong relationship between the levels of disturbance and nutrient enrichment and the mean aggregate cover of 54 plant species deliberately sown into a Derbyshire, UK, grassland.

Fluctuating resources theory posits that resource removal or impoverishment will not cause an invasion. This was tested by Kreyling *et al.* (2008) who examined the effects of drought and heavy rainfall on simple experimental plant communities by counting individual plants that invaded from the matrix vegetation. Heavy rainfall increased invasibility while drought decreased invasibility. Higher diversity in the experimental plots (4 spp. vs. 2 spp.) decreased invasibility, and the two effects acted independently and were additive. Furthermore, several species that invaded were dependent on the functional groups present in the artificial communities or the nature of the particular weather event. Thus the predictions of both niche theory and fluctuating resources theory were supported.

Enrichment or limitation of any resource including available space, soil nutrients, water and light may facilitate invasion. However the basic ecological processes that enable invasion are no different to those that enable native plants to regenerate or occupy new areas (Davis *et al.* 2000). In ecological time, an organism that is unable to change its distribution in response to environmental change must either evolve or become extinct.

The theory of fluctuating resources predits that greater susceptibility to invasion occurs: 1. immediately after resource enrichment or following a decline in rate of resoure usage; 2. when a disturbance increases resource supply or reduces resident vegetation sequestration of resources; 3. when the interval between resource enrichment and resident vegetation sequestration is long; 4. when grazing is introduced, paticularly in high-nutrient areas; 5. that there is no necessary relationship between community plant diversity and invasion resistance and 6. that there is no general relationship between average community productivity and invasion resistance (Davis *et al.* 2000).

In temperate Australian native grasslands the theory therefore predicts that: 1. areas subject to more intense or frequent resource enrichment are more prone to invasion (e.g. areas with soil disturbance, areas where the existing vegetation has died or been killed, floodplain areas, areas subject to fertiliser drift, areas more subject to anthropogenic N enrichment such as roadsides, urban areas, etc.); 2. fires in autumn create greater susceptibility to invasion than fires in spring, since autumn fires mean a longer interval between the growth period of the dominant grass *Themeda triandra* and the resource enrichment, providing the opportunity for winter growing *N. neesiana* to sequester more nutrients, light and space; 3. more intense fires intensify invasion because they create a greater increase in nutrient supply and a longer period of reduced resource capture by native plants; 4. drought will facilitate invasion, especially if it breaks in the period preceding the main *N. neesiana* seedling establishment and growth periods; 5. grazing of long-ungrazed areas will facilitate invasion since it makes available nutrients that were previously locked up by the native plants, and 6. grasslands with greater native species richness will be more resistant to invasion only if they are characterised by more complete and total resource utilisation.

For invasion to occur there must be not only fluctuating resources or resource enrichment, but propagule pressure (Davis *et al.* 2000). Disturbance (including the absence of particular disturbances), resource enrichment and propagule dispersal events are often correlated and can occur as part of the same event (e.g. intensive grazing by a flock of sheep contaminated with *N. neesiana* seed). Determining the proximate cause of invasions is thus complicated, but it is necessary to investigate the contribution of each of these factors to succesful invasions in order to devise optimal management practices.

Propagule pressure

Propagule pressure is the number of propagules dispersed into a given area and may be more important than any other factor in determining the success of a potential invader (Williamson and Fitter 1996, Lonsdale 1999, Levin 2006). Propagule pressure is equivalent to the factorial combination of the number of introduction events and the number of individuals per event (Lockwood *et al.* 2009). Where the availability of propagules is low, recruitment is always limited (Levin 2006) and when populations are small, there is a reduced likelihood that they will survive (Lockwood *et al.* 2009). Rejmánek (2000 p. 498) examined various proxy measures for propagule pressure and concluded that, as a general rule, initial population size and the number of introduction attempts determined the success of an invasion: the "most robust but ... trivial, generalization in invasion ecology". However a recent metaanalysis (Hayes and Barry 2008) found a significant association between the number of released or arriving individuals or the number of release/arrival attempts and establishment success only for animals, and considered the proposition to be 'untested' for plants.

Propagule pressure is a complex function, based on fecudity, dependent on propagule dispersal mechanisms and the availability and incidence of dispersal agents, and ultimately determined by the ability of the propagules to find suitable habitat and establish new populations (Williamson and Fitter 1996). In situations where an invasive species is already present and reproducing, use of the term "propagule rain" may be preferable (Lockwood *et al.* 2009). Where more than one potential invader is being considered, e.g. with community-level processes, the combination of propagule pressures is better termed 'colonisation pressure' (Lockwood *et al.* 2009).

Plant taxa that achieved successful ancient long distance (transcontinental) dispersal have similar characteristics to modern invasive plants: high propagule dispersability, large propagule production by multiple, large populations, wide geographical range and major presence in their communities (Levin 2006). Species with large native ranges tend to be more abundant and produce more propagules per unit area so have a greater chance of becoming invasive elsewhere, purely based on the propagule pressure they exert (Levin 2006). Substantial propagule pressure is required to overcome the genetic and demographic liabilities of small populations (Levin 2006).

Vacant niches and competitive exclusion

Under the theory of competitive exclusion and niche displacement, a more competitive invader can occupy the niche previously occupied by a native species, and an empty niche is open to invasion. The theoretical underpinnings of this approach are derived from community assembly theory, based on island biogeography (Woods 1997, Seabloom *et al.* 2003, Cox 2004). Shea and Chesson (2002) reframed the theory in the context of community ecology. Niche theory and dispersal assembly theories may be contrasted with 'neutral community assembly', which predicts that the characteristics of a potential entrant to a community have a neutral effect on the possibility of it becoming a part of that community, in particular, each species is equally likely to reproduce (Leigh 2007).

The 'storage effect' is a related concept that incorporates the temporal and spatial variation of niche elements. "The invader must be able to take advantage of times or locations in the landscape where the environment favours its population growth over that of the resident species, and store those gains in time or space in such a way that they are not eroded too much in unfavourable times or locations" (Melbourne *et al.* 2007 p. 84). 'Storage' can consist of a seed bank, a population of adult plants or a dormant tuber.

Richer communities supposedly have more niches, both filled and vacant (Prieur-Richard and Lavorel 2000). Resources that are unsequestered by existing native species represent elements that could contribute to an 'empty niche'. An invader might use resources in a different way to the native species or at different times, without interfering with other species, and so could theoretically occupy a previously empty niche. Or it might, through competitve processes, sequester resources that would otherwise by used by the resident species.

Species that are ecologically similar to an invader are often lacking in successfully invaded communities (Mooney and Drake 1989, Systad 2000), suggesting that vacant niches are often present and that competitive exclusion often repels invasions. However various authors have argued that there is little evidence for the existence of vacant niches (Newsome and Noble 1986, Prieur-Richard and Lavorel 2000) and that the competitive superiority of plant invaders to native species has "rarely been tested experimentally" (Seabloom *et al.* 2003 p. 13384).

Invasive plants that establish in dense populations must displace other plants and alter community composition, unless they occupy an unfilled niche, but if the niche was unfilled there should be no displacement, the invader is not a problem, and it successfully integrates into the existing community. The invasive species may displace another plant with a similar niche, or may be widely competitive and have the potential to completely restructure or replace a community, alter its successional dynamics or directly interact with disturbance regimes (Woods 1997, Mack and D'Antonio 1998), and thus alter the niche space of many community components. A community or one of its members may repel even a superior invasive competitor "because of the priority effect that established residents have over invaders" (Systad 2000 citing Case 1990 1991). Alternatively a native species may persist on sites where they have unusual competitive advantages, e.g. native grasses persist on sites with serpentine soils, but have been largely replaced by exotic grasses in California (Melbourne *et al.* 2007 citing Harrison 1999).

Other author have argued that the niche concept itself is "a circular argument empty of mechanism and process" (Wedin 1999 p. 193). Niche theory is largely contradictory, since niches are multidimensional hyperspaces *defined* by their occupation by a species population in relationship with *all* the other organisms in the community (Herbold and Moyle 1986, my emphasis). A niche cannot be defined if it is infinitely malleable: if the niche is an autecological attribute of a species, the niche moves with the species and there are never empty niches, if it is a synecological attribute, the invasive organism must modify the niches of other organisms to sequester niche hyperspace, so again there is no preformed or definable vacant niche (Herbold and Moyle 1986). An invasive species must rearrange the community and sequester flows or resources previously used by other organisms, and therefore must effect them negatively. In general all invasive species which have been investigated have some negative effects (Herbold and Moyle 1986). The mechanisms by which this happens, what resources are diverted, etc., is the real question of interest (Seabloom *et al.* 2003), and is dependent on particular circumstances.

Current consensus, at least in some schools, appears to be that niche theory is a sterile framework, lacking explanatory and predictive power. However this non-mechanistic approach, seemingly based on the tenet that ‘diversity confers stability’ and the false but “commonly accepted ecological truism” that richer communities are less invasible (Lonsdale 1999 p. 1533) continues under a new guise, with ‘functional groups’ replacing niches as a focus of investigation. Functional diversity, “the number of functional groups with different behaviours for a particular process”, rather than species diversity, supposedly determines “major thresholds in ecosystem processes” and the properties of systems that control their invasibility (Prieur-Richard and Lavorel 2000 p. 5). At least, if the composition of functional groups is based on similarity of resource use, the processes and mechanisms that could cause displacement or facilitiate invasion are more explicit and accessible in these functional group approches than in simple diversity-resistance approaches.

Many mechanisms might be involved in competitive superiority and these are mostly addressed in this essay within the frameworks of the main theories. Competive superiority could result from possession of a particular unique characteristic (“novel weapons” below), general superior adaptation evolved in the native environment (superior ‘invasive potential’, see above), release from natural enemies (above) or the ability to better exploit disturbance (‘resource enrichment and fluctuating resources’, above). Dominance by the invader in some but not other areas, suggestive of competitive superiority, may actually be just a priority effect (Seabloom *et al.* 2003): the exotic cannot outcompete an equilibrium population of competitors, but is the first to invade after strong disturbance, and establishes dominance, leading to “multiple stable equilibria” (Seabloom *et al.* 2003 p. 13384).

‘Novel weapons’

Successful invaders may possess ‘novel weapons’ that enable them to kill, suppress or outcompete native species. Novel weapons possessed by invasive plants may include the ability to produce chemicals that are toxic to native herbivores (see for example McBarron 1976) or to native plants. More broadly, they may consist of “competitively unique traits” (Seabloom *et al.* 2003) or functional attributes, not possessed by the native species, that enable access to unexploited resources (Callaway and Maron 2006).

Grasses have many adaptations that deter predation. These include anatomical structures such as narrow leaves, mechanical structures such as leaf phytoliths, and chemical toxins. In many cases involving grass poisoning it is not the grass but it’s parasites (usually fungi) that are the source of the toxin. If these adaptations are possessed by an exotic species but not the native species, and are effective against predators in the invaded system, then the invader has a novel weapon that facilitates its invasion.

Allelopathy

Chemicals produced by invasive plants while growing or decomposing may also have detrimental effects on other plants – the plant possesses allelolpathic properties (Gill and Davidson 2000). The study of chemical interactions between organisms is still in its infancy, as has been amply demonstrated by recent major advances in the study of tri-trophic interactions between predators, their herbivores and host plants, and chemical communication between individuals within a plant population (Baldwin *et al.* 2002, Reddy and Guerrero 2004). Plants release a complex range of complex organic compounds into both the soil and the air that enable above- and below-ground communication between individual plants in a population and probably between populations, and that influence a range of other plants and animals in the environment.

Simple allelopathy between plant species is known to be widespread, but in most cases the precise chemicals are unknown and the effects have been determined using plant extracts or residues (Gill and Davidson 2000). Probably all plants are more or less allelopathic (Gill and Davidson 2000), and possibly all plants also release chemicals that are beneficial to other plants. *Centaurea maculosa* Lam. (Asteraceae) in North America is probably the best studied example of allelopathy (Ridenour and Callaway 2001). *C. maculosa* root exudates reduce the plant size and root elongation rates of a native tussock grass of invaded areas, *Festuca idahoensis* Elmer by half, and allelopathy accounts for the major proportion of the total interference of *C. maculosa* with the grass. The allelopathic activity of the litter of *Vulpia* spp. (Poaceae) against crop and pasture plants has been demonstrated in laboratory and glasshouse experiments in Australia (Gill and Davidson 2000). Shoot extracts of different cultivars of wheat *Triticum aestivum* L. have been found to have startlingly different impacts on radicle elongation of another grass *Lolium rigidum* Gaud., that is a major weed of wheat crops in Australia (Lemerle and Murphy 2000). The rapid spread of the African grass *Eragrostis plana* Nees in southern Brazil is due in part to its allelopathic effects (Overbeck *et al.* 2007). Similarly, aqueous leachates of seeds, roots and leaves of the African grass *Brachiaria decumbens* Stapf, invasive in Brazilian cerrado, have been found to reduce germination of potentially competing plants (Barbosa *et al.* 2008). Allelopathic activity of *Sorghum halepense* (L.) Pers. partly explains its success as an invader in the USA (Rout and Chrzanowski 2009). Invasive European plants present in North America have greater allelopathic effects on North American native plants than European natives, and on the continental scale chemical co-adaptation amongst members of native plant communities may possibly be commonly disrupted by alien invaders (Callaway and Maron 2006).

Allelopathic effects of species in the Stipeae appear to have rarely been investigated. Ruprecht *et al.* (2008) found that leaf leachate of *Stipa pulcherrima* C. Koch, a dominant species in abandoned continental European grasslands, reduced seed germination, radicle elongation and delayed germination of co-occurring species.

As yet there appears to be no evidence that *N. neesiana* possesses allelopathic properties. However *N. neesiana* does have a unique phytolith profile (see below) that may confer more robust resistance to herbivory.

Rapid evolution

Evolutionary aspects of invasive species have been poorly explored and are little understood (Lee 2002, Callaway and Maron 2006, Whitney and Gabler 2008). Removed from the environment in which they evolved, new immigrant plant populations are subject to new selection regimes, founder effects, genetic drift and new hybridisation possibilities, so should be "prime candidates for ... evolutionary changes", and there is now substantial evidence of rapid evolution in populations of a diverse array of invasive plants (Whitney and Gabler 2008 p. 570). Many grasses set seed in their first year, and most are capable of reproducing when two years old, so invasive grasses are capable of more rapid evolution than many other plants.

Strong new selection effects have demonstrably led to rapid evolution of weeds (Callaway and Maron 2006). Herbicide resistance is one of the most troublesome recent manifestations, and has developed in a large number of grass species (Preston 2000). Similarly genetically based "adaptive breakthroughs" (Cox 2004 p. 61) have sometimes been responsible for relatively inocuous exotic species becoming serious inavaders. Some species have become invasive after rapid evolution of new genotypes with altered seed dormancy or earlier reproduction (Cox 2004), by hybridisation and other mechanisms. Apart from alterations due to deliberately imposed anthropic selection (weed management, including herbicides and biological control), evolved trait changes within 20 or fewer years are documented for several species (Whitney and Gabler 2008).

Plant invasions typically result from one or few founder events, so the genetic variance of the invasive populations is usually surmised to be much reduced compared to populations in the native range. If the population remains small over several generations, genetic drift can result in loss of further variation (allelic diversity and heterozygosity), and the population is said to pass through a genetic bottleneck. Inbreeding species are likely to lose more genetic variation during a population bottleneck than outbreeding species. Inbreeding depression is uncommon in Poacaeae (Groves and Whalley 2002) so genetic bottlenecking may rarely have any impact on their invasions. But genetic bottlenecks also may reduce the potential benefits of genetic outcrossing and favour self-fertilisation (Cox 2004). Combined with strong selection, the surviving population may become highly adapted to the new environment and can strongly differ, genetically and phenotypically, from the conspecific native population (Callaway and Maron 2006). Superior competitive abilities, such as larger stature or greater vigour, may be acquired via evolutionary 'trade-offs' involving the loss of traits, such as predator defences, that no longer provide an advantage (Callaway and Maron 2006).

Characters that increase dispersal ability are likely to be favoured at the expanding periphery of the invaded range (Cox 2004). Thus the evolution of higher levels of self-fertilisation, apomixis and vegetative reproduction are frequent in invasive species, partly because their small initial populations restrict opportunity for out-breeding (Cox 2004). *Watsonia meriana* (L.) Mill., var. *bulbillifera* (J.W. Matthews and L. Bolus) D.A. Cooke is rare in its native South Africa, but is by far the dominant form of the plant in its introduced range in Australia (Cooke 1998), where the main means of dispersal appears to be movement of the vegetative cormils, produced in clusters on culm nodes, along roadsides by graders and other machinery (Parsons and Cuthbertson 1992). In this case, a rare native form with high vegetative dispersal ability has become the dominant form in the invaded range. In contrast, if the invaded system is severely geographically constrained, an invasive species may evolve reduced dispersal ability that minimises the loss of propagules in sink areas (Whitney and Gabler 2008).

Increased levels of out-breeding are also recorded in invasive species, possibly because selection regimes in the new environment favour some of the recombinant genotypes (Cox 2004). Outbreeding species have high levels of cross fertilisation between individuals, so have a more diverse array of phenotypes, theoretically capable of occupying a wider range of habitats. Invasion by obligatory outbreeder is constrained, however, because a breeding population requires multiple individuals.

It is widely recognised that invasion success may depend on the genetic substrate of the source populations. Single source introductions of a limited number of individuals are often assumed, so founder populations are thought to have passed through genetic bottlenecks, but multiple introductions from multiple source populations may be more usual (Petit 2004). For example *Echium plantagineum* L. populations in Australia seem to be the result of the mixing of genetic material from different European sources (Petit 2004). Genetic drift acting alone on the founder population can result in successful invasion, but this is probably exceptional.

Broad environmental tolerance and genetic plasticity in the founder populations are often invoked as the mechanisms behind successful invasions, but do not stand up to examination, although possession of high levels of additive genetic variance (i.e. variance related to phenotype) for invasive traits in source populations has been demonstrated in a number of studies (Lee 2002). Simple directional selection on such traits is likely to explain many successful invasions, with genotype x environment interactions in the invaded resulting in diversification of the available phenotypes (Lee 2002). Lag phases, which precede the expansion phase of a new invasive organism (Shigesada and Kawasaki 1997), are associated with so-called 'sleeper weeds' in Australia (Groves 1999, Grice and Ainsworth 2003) and may be attributable to the slow accumulation of such variance (new mutations, etc.). Epistatic genetic variance (involving interaction between genes) could also generate new phenotypes on which selection could act (Lee 2002).

There is strong evidence that polyploidy increases the colonising ability of plants (De Wet 1986). Many invasive plants are allopolyploid (hybrids retaining chromosomes of both parent species), and hybridisation (inter- or intra-specific) can generate more highly invasive genotypes (Lee 2002). Grasses in particular display high levels of hybrid and polyploid speciation. The invasive grasses *Sorghum halepense* (L.) and *Bromus hordeaceus* L. are both the result of hybridisation, the latter with later chromosome doubling (Cox 2004). *Spartina anglica* C.E. Hubbard, a sterile amphidiploid (tetraploid) evolved by chromosome doubling from *S.* X *townsendii* H. and J. Groves (Cox 2004), and is a more vigourous species that apparently displaces it in Victoria (Walsh 1994), as well as native *Spartina* spp. in many areas of the Northern Hemisphere (Cox 2004, Petit 2004). *S. anglica* is extremely geneticallydepauperate, unlike most allopolyploids which have large diversity because of the multiple origins of their parents (Petit 2004). The normally strongly outcrossing *S. alterniflora* Loisel., introduced from the east coast of North America to San Francisco, rapidly evolved high rates of self-fertilisation in its new evironment (Cox 2004). Stebbins (1972) recorded the invasive nature of an artificial *Ehrharta erecta* Lam. autopolyploid he created by colchicine treatment and released on the Berkeley campus of the Universityof Califorina. Stipeae as a whole apparently consists largely of species resulting from frequent and widespread hybridisation of divergent elements (Johnson 1972, Tsvelev 1977).

Single genes or a few genes might effect invasiveness or weediness traits. *Sorghum halepense*, one of the world's worst weeds (Parsons and Cuthbertson 1992), has few genes affecting weediness that distinguish it from non-invasive grain *Sorghum* spp. (Lee 2002). When *S. halepense* (tetraploid) pollinates the diploid Grain Sorghum, *S. bicolor* (L.) Moench, sterile triploids are produced that are weedy in successive crops (Parsons and Cuthbertson 1992).

Selection pressure after naturalisation can produce phenotypes with altered morphology, physiology and phenology, or with greater plasticity in response to environmental variables (Lee 2002) and these changes can occur within periods as short as a few plant generations (Cox 2004). For example invasive populations of *Echinochloa crus-galli* (L.) P. Beauv. in Canada have evolved greater catalytic efficiency of some enzymes, which compensates for the poor adaptation of their C_4 photosynthetic system to the cold climate (Lee 2002, see her references). Selection can occur in response to environmental gradients, the resident biota and control activities (Lee 2002). Weed mimicry of crop species e.g. by *E. crus-galli* (Lee 2002), is another example of relatively rapid evolutionary adaptation, well known in grasses (Barrett 1983).

Release from predation and competition in the invaded environment removes some selection pressures on the invading plant and may release characters associated with defense mechanisms from evolutionary canalisation (phenotype limitation due to the constraints imposed by developmental pathways) and result in rapid evolution (Lee 2002). This has occurred with *Silene latifolia* Poir. in North America which has apparently allocated resources, previously used in defence, to enhanced reproduction (Whitney and Gabler 2008). Rapid evolution can also occur if plant predators and specialist herbivores expand or shift their host preferences to consume invasive plants (Cox 2004).

Complex patterns of evolutionary change should be expected in each particular invasion, with particular traits favoured at different stages of the invasion, and possible reversals of trait changes (Whitney and Gabler 2008).

Complementary evolutionary changes may also be expected in the invaded community – the more serious the invader, the greater the selective pressure it imposes – and those that have been investigated can also occur rapidly, on timescales of <10-140 years (Whitney and Gabler 2008). To give one example, the 'novel weapon' of *Centauria maculosa* allelopathy has resulted in a period of <30 years in genotypic changes in at least 3 native grasses that confer decreased susceptibility to the invader (Whitney and Gabler 2008).

Introduction to Australia of a range of *Nassella* species has created unique opportunites for intra-specific gene flow that could speed up adaptation and accelerate rates of invasion. From the genetic perspective, Australian *N. neesiana* may already be a markedly different entity to its South American parents. One frightening possibly arises from the fact that *N. neesiana* frequently escapes control in Australia because of its resemblance to native *Austrostipa* species. Inconsistent and partially ineffective control activities might therefore select for even closer resemblance.

Invasibility of grassland communities

The 'intermediate disturbance hypothesis' proposes that species diversity is greatest at moderate (intermediate) levels of disturbance, with only ruderals persisting under frequent, intense disturbance and only a few species able to reproduce in the absence of disturbance, but disturbance also increases invasions, suggesting an insoluble dilemma for conservation management (Hobbs and Heunneke 1992). Invasibility (Lonsdale 1999) is the intrinsic susceptibility of an area to invasion. As discussed above, the concept was initially applied to natural communities (Fox and Fox 1986), which have properties that are presumed to provide resistance to potentially invasive exotics. Communities are sets of co-existing species assembled in evolutionary and ecological time, that are more or less integrated and stable under prevailing endogenous disturbance regimes, and which are presumed to more or less fully utilise available resources (Fox and Fox 1986). Thus invasibility is dependent on both intrinsic (community) properties and extrinsic (environmental and disturbance) factors.

Invasibility is an emergent property related to "climate, level of disturbance, ecosystem resistance to invasion, and native species' competitive ability and resistance to disturbance" (Lonsdale 1999 p. 1524). Lonsdale (1999) acknowledged that his attempt to evaluate it was flawed because the raw data consisted of static historical species counts. Invasibility cannot be an intrinsic property of an area or community, because it is dynamic, changing over time (Davis *et al.* 2000), and is largely a notional property, because it assumes that a community is uniform in composition and can be invaded in any part with equal probability. Furthermore the concept does not discriminate between different invaders (Prieur-Richard and Lavorel 2000), with their different requirements and attributes. A system is invasible by a species only when the system meets that species' particular requirements. Thus a match between the climate and habitat of the native and invaded ranges has been found to be one of the most consistent predictors of invasion success (Hayes and Barry 2008). Another major problem with the concept of invasibility is that the succesful invaders for a particular area can generally be determined, but the species that disperse to it but fail to establish cannot (Lonsdale 1999). A more fundamental difficulty in assessment of invasibility is the requirement to consider highly variable pools of potential or locally present invasive species which may consist of very large numbers of taxa, so it is not possible to standardise the measurements, unless consideration is restricted to one or a small set of potentially invasive species in deliberately assembled, experimental systems.

Lonsdale (1999) found a weak positive relationship between invasibility and vascular plant species richness at the geographical scale, and proposed that both exotic and native richness respond to increased habitat diversity. In other observational studies, both negative and positive correlations between native and exotic species diversity have frequently been reported, with opposite patterns found at local and regional scales in different studies (Prieur-Richard and Lavorel 2000, Dukes 2002, Melbourne *et al.* 2007, Kreyling *et al.* 2008). Attempts to understand the invasibility of areas and communities by subjecting them to experimental manipulation of species diversity, or by assembling simple experimental communities, have given conflicting results (Prieur-Richard and Lavorel 2000). Dukes (2002) assembled combinations of native and naturalised species from four functional groups (annual grasses, perennial grasses, early season forbs, late season forbs) in grassland microcosms and seeded them with the invasive *Centaurea solstitialis*. He tested single species, 2 combinations of 4 spp., and one combination each of 8 and 16 spp., with all combinations containing an equal number of species from each functional group. Above-ground biomass of *C. solstitialis* decreased rapidly with increasing diversity but reached an asymptote of c. 100 g m^{-2} with only c. 4 species. *C. solstitialis* allocated significantly more of its biomass to reproduction in 1 year-old communities than in newly established communities. The resident species produced less biomass in the 1 year old compared to the newly established microcosms, corresponding with increased dominance of *C. solstitialis*. This was contrary to the expectation that the increased resource availability due to disturbance in the newly established microcom would favour the weed. The species most effective in suppressing *C. solstitialis* growth was, like the weed, an annual late-season forb. These findings suggest that at the community scale, diversity reduces invasibility by increasing competition for limited resources, either because of the presence of individual competitive species or as a collective response of the resident species. Dukes calculated "impactibility", as the percentage change in biomass of resident species divided by invader biomass and found that as species richness increased communities became more impactible but less invasible.

More recent investigations of invasibility have usually explicity incorporated extrinsic properties that relate to human environmental impact. Gassó *et al.* (2009) found that invasive plant richness in mainland Spain was significantly positively correlated with the proportion of built-up land and the length of roads and railways in an area, and negatively correlated with distance from the coast, altitude and annual rainfall. The factors negatively correlated with invasibility reflect in part the level of anthropogenic disturbance. Thus land that has been impacted by human activities is generally more highly invaded and more invasible than semi-natural or natural areas.

Melbourne *et al.* (2007) proposed that invasibility of a community is dependent on its temporal, spatial and invader-driven environmental heterogeneity, 'invader-driven' heterogeneity encompassing the effects of the invader itself on the environment. Thus small, relatively homogeneous areas are more 'species saturated' and have lower invasibility than large, more heterogeneous areas, which are able to accomodate more invasive species without losses of natives; and a successful invader can modify the invaded environment, altering its invasibility by other species. Environmental heterogeneity theory can be viewed as a broadening of the theory of fluctuating resources (Kreyling *et al.* 2008).

Dunstan and Johnson (2006) argued convincingly that the spatial scale of a community is a critical variable in determining its invasion resistance. Where a community occupies a small area, the variability within the area decreases with increasing species richness, but when the area of a community exceeds a critical size, increasing richness increases variability. This pattern results from the well-known vulnerability of small populations to extinction through stochastic factors. The invasibility of the system is strongly dependent on its variability – less variable communities being more invasion resistant. Their approach partially reconciles a number of competing theories but also presages "a much larger continuum of possible relationships between richness, stability (both persistence and resilience), invasion resistance, species invasion/extinction, and area than have previously been explored" (*op. cit.* p. 2849)

Nevertheless the invasibility of an area in relation to a particular invasive plant depends on proximity to invasion sources, the availability of dispersal mechanisms or vectors that can deliver propagules into the community, and the existence of suitably-resourced patches or openings in which the organism can establish, survive and reproduce (Hobbs 1989). Thus invasibility has been demonstrated to be influenced by factors such as landscape situation, edge effects and the size and type of community (Morgan 1998d), and is increased by disturbance and high resource availability (Hobbs and Heunneke 1992, Levine *et al.* 2003). For example, in studies of urban open forest and woodland in Sydney, King and Buckney (2001) found the highest number of exotic species in the soil seed bank and the above-ground vegetation was at the edges, that the vegetation was a very poor indicator of seed bank contents, 84% of the exotic species not being present in it, and that lack of suitable conditions (nutrient enrichment or other disturbance), rather than lack of propagules, was probably restricting the establishment of the exotics in areas away from edges. Structure and density of vegetation may restrict propagule entry, and integrity of the soil crust may restrict invasion, despite nutrient addition (Hobbs 1989). Predators, pathogens and competitors in the community may confer invasion-resistance, rather than plant species or the vegetation community, while symbionts and mutualists may act as invasion faciltators (Davis *et al.* 2000).

Increased susceptibility to invasion in general has been found in areas with strong, temporally-varying change that creates abundant under-utilised resources, or to which such resources are anthropogenically supplied in short-term fluxes (Rejmánek 1989, Davis *et al.* 2000, Cox 2004). Areas without such fluxes appear to be generally less invasible the greater their plant species or functional group richness at small spatial scales (Cox 2004, Melbourne *et al.* 2007). The environments with greatest plant diversity are generally the most nutrient impoverished, and may therefore be the most susceptible to anthropogenic nutrient enrichment and consequent increase in invasibility: this may in part explain Lonsdale's (1999) findings that high plant diversity is associated with greater invasibility (Davis *et al.* 2000). Increased plant diversity may confer invasion resistance only in highly stable environments subject to very limited disturbance.

In Australia as elsewhere in the world, temperate native grasslands communities that lacked co-evolved large, herding ungulate graziers have proved to be highly invasible by exotic plants when subjected to continuous grazing by introduced livestock (Crosby 1986, Mack 1989). The effects of livestock movement and on nitrogen cycling are important factors (Milton 2004). In the temperate grasslands of south-eastern Australia, both physical and chemical soil disturbance, and particularly nutrient enrichment, can increase invasibility at patch, community and landscape scales (Morgan 1998d). When not overgrazed, species-rich, high quality grassland is in general less weed-invasible (Beames *et al.*(2005 citing Hector *et al.* 2001). Appropriately managed (frequently burnt or conservation grazed) *Themeda triandra* grasslands are more resistant to *N. neesiana* invasion than those that are poorly managed or where the dominant *Themeda triandra* is allowed senesce (Hocking 1998). When *T. triandra* dies, "areas of dead grass are quickly occupied by exotic species, against which a healthy *T. triandra* sward provides considerable defence" (Lunt and Morgan 2002 p. 183). At the patch scale, resistant grasslands tend to have high cover of healthy *T. triandra*. In a *T. triandra* grassland at Evans St., Sunbury, burnt 9 months before surveying, a high cover of weeds (i.e. >40%)

correlated with significant reduction in native plants, but high native cover had no such relationship (Morgan 1998d). However native plant species richness *per se* does not appear to inhibit exotic plant invasion in these grasslands (Morgan 1998d). Damage to the cryptogam crust appears to be one factor that facilitates invasion (Scarlett 1994), presumably because it enables more rapid seed burial and therefore decreases exposure of exotic seeds to fire and predators (Morgan 1998d), but possibly also because of the nutrient fluxes that result.

At the landscape scale, high levels of fragmentation by roads and proximity to agricultural land and urban areas makes native grassland more invasible (Williams 2007).These factors are important drivers of propagule pressure, that increase movement of seeds from established weed infestations into the surrounding landscape (Melbourne *et al.* 2007). Similarly, the factors with the most influence on the extinction of native plants from grassland remnants in the Victorian basalt plains have been found to be the road density of the surrounding landscape, and long intervals between fires, which are general indicators of habitat degradation (Williams *et al.* 2006), and probably represent good indicator measures of the invasibility for such grasslands.

Apart from factors that affect colonisation pressure, the extent and nature of resource fluctuation is probably the main determinant of what species invade (Morgan 1998d). In effect, exogenous disturbance is “a special case” of environmental heterogenity (Melbourne *et al.* 2007 p. 78) – the greater the severity and range of such disturbances, the greater the invasibility of the area.

Impact

Impact has been defined as the effect that an invader has on the invaded system once established (Melbourne *et al.* 2007), however this approach ignores effects associated with the establishment phase, and longer term effects post-establishment. Immediate impacts during the establishment phase might be substantial (e.g. lethal toxicity to animals) and long-term effects might include changes to the abiotic environment (e.g. changes to soil pH). The approach also distances any analysis from whatever management is targetted at the invader, and ignores effects that persist after its eradication or removal (Mgobozi *et al.* 2008). Furthermore such an approach glosses over the complexities of evolutionary change that are likely to occur in the invader and the invaded system as they interact (Whitney and Gabler 2008). Since very few plant invaders are ever eradicated, ultimately both the invader and the invaded system adapt to accomodate each other, and since there is more adaptive potential in the community that the single invader, the impact will eventually decay, or, if these adaptive changes are themselves considered to be impacts, may continue to slowly increase (Fig. 1).

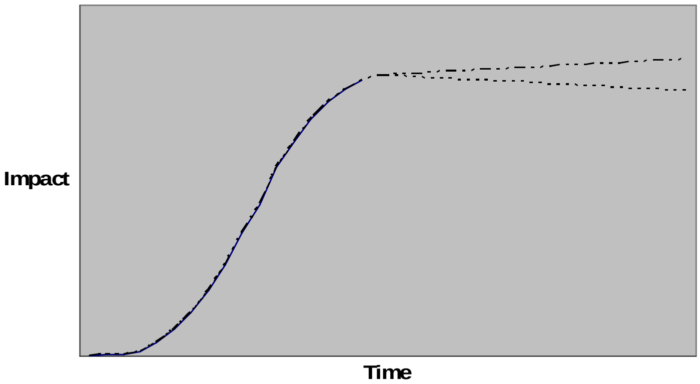

Figure 1. Hypothetical impact of an invasive species on the invaded community over time. Overall impact rises at some rate during the establishment and spread phases, then the rate of increase of impact declines as the invader occupies all suitable habitat and areas. Impact reaches a plateau after which it either slowly declines, as previously hidden effects of adaptation and evolutionary compensation in the invaded community gradually reduce the effects, or continues to slowly increase if these compensatory changes are themselves considered to be components of impact.

Impacts of invasive plants can be negative, positive or neutral, and in a particular invasion are typically composed of a mixture of such effects on different system components; so perceived impact on biodiversity is highly dependent on the measures of biodiversity that are assessed (Groves 2002). Effects can be identified at hierarchical levels from genetic, through individual to community and ecosystem, and can include extinction of other species, reduced abundance of native species and facilitation of other species. At one extreme, mere presence of an alien plant in a natural ecosystem may not be tolerated by humans (Groves 2002), even if the plant is accomodated in the system without other apparent negative effects.

Transformer species

Plants that cause major and permanent (or difficult to reverse) changes in invaded communities have been called “transformers” (Henderson 2001) or “ecosystem engineers” (Byers *et al.* 2002), although the latter term is usually applied to animals (Cox 2004). Transformer species often have a habit, life form or phenology not present in the invaded community (Woods 1997). Henderson (2001 p. 253) defined a transformer as a plant which can “as monospecies dominate or replace any canopy or subcanopy layer of a natural or semi-natural ecosystem, thereby altering its structure, integrity and functioning”. The definition is that of Swarbrick (1991), but not the terminology.

Henderson (2001) contrasted ‘ruderal’ and ‘agrestal’ weeds, which “invade mainly sites of severe human disturbance”, with other invasive plant species – the implication being that invasion by transformers does not require such disturbance. Rather, such species tend to be those which transform the system invaded by rapidly modifying the prevailing disturbance regime (Richardson and van Wilgen 2004). Transformer species often have disproportionately large effects compared to other weeds because they become numerically dominant in the invaded area or dominate the biomass. Good examples of transformer species are *Mimosa pigra* L. in *Melaleuca* woodlands in northern Australia (Braithwaite *et al.* 1989), *Tradescantia* in New Zealand forests (Kelly and Skipworth 1984) and *Pinus* and *Acacia* species in South Africa (Versfeld and van Wilgen 1986). Transformer grasses include 'land builders' such as *Spartina* (Gray *et al.* 1997), and *Andropogon gayanus* (Kunth) in northern Australia, which has massive stature in comparison to native grasses and greatly enhances the intensity and frequency of fires (Rossiter *et al.* 2003, Ferdinands *et al.* 2006).

Impact of *N. neesiana*

N. neesiana does not neatly fit the definition of transformer species in Australian native grasslands. It dominates the canopy in many invaded native grasslands, although its morphology, biomass and phenology is similar to some of the major native grasses that it replaces. The invaded systems remain as grasslands, and other effects it may cause are poorly known.

The biodiversity impacts of *N. neesiana* in temperate Australian natural grasslands is probably critically determined by its presence and impact in the cultural steppe that surrounds and fragments the remaining indigenous remnants. The success of *N. neesiana* in the cultural steppe drives propagule pressure, so determines, in part, the susceptibility of grassland remnants to invasion. Their invasibility is also strong influenced by their health or degradation state, which is critically influenced by management. The prevalence of major anthropogenic disturbance and the disruption of 'natural' disturbance patterns appear to be central issues. A range of other factors most likely contribute to the success of *N. neesiana* in native grasslands and its biodiversity impact, including release from natural enemies.

Nassella neesiana

"Over the past few years is has become increasingly clear that the introduced grass *Stipa neesiana* is a serious threat to remnant stands of native grassland ... and can almost completely displace perennial native grasses, including the dominant *Themeda triandra* ... Prior disturbance does not appear to be necessary for invasion ... We request that urgent attention be given to control of the plant ..."

M.J. Bartley, R.F. Parsons and N.H. Scarlett of the Botany Department, La Trobe University, in a letter to the Victorian Department of Conservation and Environment, 7 May 1990

Nassella neesiana is a long-lived, perennial, cool season (winter-spring growing), C_3, South American, monecious, tussock-forming grass, with flexible reproductive mechanisms and a high survival rate of all life stages (Cook 1999, Gardener *et al.* 1996a 1999, 2003a, Storrie and Lowien 2003, Benson and McDougall 2005). In Australia it is both a serious enivornmental weed (Carr *et al.* 1992, McLaren *et al.* 1998) and a problem weed of agriculture (Grech 2007a).

N. neesiana is a widely recognised threat to Australian temperate native grasslands. One of the earliest reports was that of McDougall (1987) who recorded it as a weed in native tussock grassland and *Eucalyptus camaldulensis* woodland in the western region of Melbourne. Carr *et al.* (1992 pp. 41, 51) considered it to be a "very serious threat to one or more vegetation formations in Victoria". It has rapidly expanded its range (Lunt and Morgan 2000), is able to actively invade grasslands (Hocking 1998), reportedly without prior disturbance (Bartley *et al.* 1990), is allegedly potentially able to outcompete C_4 (summer growing) grasses such as *T. triandra* (Ens 2002a), and is rated, along with *Nassella trichotoma*, as the most significant weed threat to grassland biodiversity (McLaren *et al.* 1998, Groves and Whalley 2002). Trengrove (1997) considered it to be "much more invasive" in *T. triandra* remnants than *N. trichotoma*. Morgan and Rollason (1995) considered it to pose "by far the greatest threat of any potential new invader" at one grassland, Kirkpatrick *et al.* (1995 p. 36) classed it as "a major threat to one or more grassland communities", Morgan (1998d) called it one of the "most potentially threatening species" to *T. triandra* grasslands and Lunt and Morgan (2000 p. 98) rated it as "perhaps the most serious environmental weed in remnant native grasslands in southern Victoria". Humphries and Webster (1992 and 2003 p. 2) and Webster *et al.* (2003 p. 3) wrote that "the aggressive invasion" of *N. neesiana* at Derrimut and Laverton North Grasslands in Victoria needed "immediate attention if the values of these grasslands [were] to be preserved". Ens (2005) stated that it "swamps all other ground flora and forms expansive monocultures". According to Beames *et al.* (2005 p. 2) it is "particularly well adapted to the intensively cultivated areas surrounding urban areas and poses a signficant threat to mismanaged urban grassland remnants".

N. neesiana is a successful invader because of it wide ecological flexibility, synanthropic dispersal mechanisms, the availability of suitable habitats in a suitable climate, and limited biotic resistance in the invaded communities. It has many of the general charactersitics possessed by successful invasive species (Cox 2004): a large native range, abundance and sometimes dominance in its native range, high vagility (via seed), dispersal by abiotic processes, short generation time, high reproductive rate, ecological flexibility, wide climatic and physical tolerances, reproduction involving a single parent individual and association with humans. In addition many varieties and forms have been described, suggesting that the species has wide genetic variability, at least in South America. Bourdôt and Hurrell (1989a p. 415) attributed its invasiveness in New Zealand sheep pastures not to "high competitive ability" but rather to "adaptations that enable the plant to survive the hazards of semi-arid, low-fertility environments".

It is often generally contended that invasion only occurs as a result of disturbance and that Australia is more subject to invasion than northern hemisphere biomes (e.g. New 1994 p. citing Di Castri 1990). Exotic stipoid grasses in Australia "generally invade plant communities which are already highly degraded and have a history of disturbance" (Gardener and Sindel 1998 p. 76 citing G. Carr pers. comm.), along with "lands with higher fertility soil often previously used for grazing or farming" (*op. cit.*). Since temperate native grasslands often occupy highly fertile soils, and are communities dependent on disturbance for the maintenance of their natural diversity, this appears to create a significant dilemma. The disturbance necessary to create gaps in the dominant grass canopy, in which most of the native vascular plant diversity can flourish, simultaneously promotes exotic plants, which comprise the bulk of the seed bank at least at some sites (Lunt 1990b, Morgan 1998c).

Gardener and Sindel (1998) advocated quantitative studies to evaluate the biodiversity changes associated with invasion by exotic *Nassella* species, to determine if any of these changes result from general degradation and to evaluate the impact of *Nassella* management techniques on the promotion or inhibition of biodiversity. To date, only a single study of *N. neesiana,* with a narrow focus, has been undertaken, that of Ens (2002a). She found that diversity of insects declined in areas occupied by the plant in Sydney woodlands, although some groups benefited. Monitoring of biodiversity is necessary to provide a sound basis for evaluating the techniques and strategies used to manage *N. neesiana* as a weed (Grice 2004a). Mangement measures are currently focused on minimising seed production using herbicides or grazing in agricultural (Grech 2007a) and natural areas, and managing the rate of mineralisation of nitrogen to favour C_3 grasses in natural ecosystems (Craigie and Hocking 1998, Hocking 2002 2005b, Groves and Whalley 2002). However there are concerns that some current approaches may be counterproductive, producing grasslands that are more impoverished, and more highly invasible.

The success of a plant invader depends on its biological attributes, the attributes of the community or ecosystem invaded and the effects of human activities. These factors are examined in detail in the review below.

Taxonomy and nomenclature

Stipeae

Nassella neesiana is a member of the Poaceae: Stipeae, "a cosmopolitan tribe ... widely distributed" with "major centres of diversity in South and North America, Australia and Eurasia", "primarily in temperate or warm-temperate regions" and "dominant in many of the arid grasslands of southern Australia, South America and Asia at varying elevations (0-5000 m)" (Arriaga and Jacobs 2006). The tribe contains "approximately 500" (Vásquez and Barkworth 2004 p. 484) or "c. 450" (Arriaga and Jacobs 2006) species. Simon (1993) erected a new subfamily Stipoideae for the tribe, a classification adopted by Watson and Dallwitz (2005), but not followed by others (e.g. Briese and Evans 1998).

In the past Stipeae has been included with Poeae in a festucoid group, close to Miliceae, Diarrheneae and Nardeae (Tsvelev 1984). The tribe was sometimes assigned to subfamily Arundinoideae (e.g. Barkworth and Everett 1986), and sometimes to Pooidae (Wapshere 1990) e.g. by Edgar *et al.* (1991), but molecular evidence indicated that it did "not sit comfortably in either subfamily" (Briese and Evans 1998 p. 94) and was not clearly delimited (Barkworth and Torres 2001). Zucol (1996) argued that phytolith leaf assemblages in *Nassella* species indicated an affinity with Arundinoideae, while Honaine *et al.* (2006) considered their phytolith study of *Nassella* and *Piptochaetium* spp. supported the assignment to Stipoideae. Molecular data currently indicates that Stipeae is monophyletic (Jacobs and Everett 1996) and it is now often considered a basal lineage within Pooidae (GPWG 2001, Arriaga and Jacobs 2006, USDA ARS 2006), or the largest of six tribes in Stipoideae, along with the monogeneric Nardeae, Lygeae, Ampelodesmae, Anisopogoneae and doubtfully Brachyelytreae (Watson and Dallwitz 2005).

The tribe is best defined by characters of the embryo (Jacobs and Everett 1996) which are correlated with a set of characters not exclusive to the tribe: florets with a single spikelet, a coriaceous or firmer lemma with comparatively large unicellular macrohairs (Arriaga and Jacobs 2006), disarticulation of the seed above the glumes and absence of a rachilla extension (Jacobs and Everett 1996) (i.e. the rachilla is not prolonged (Jacobs *et al.* 1989)), a well-developed callus, and a terminal, usually articulated awn (Barkworth 1993). Stipoids are commonly wiry, "bamboo-like" perennial grasses (Jacobs *et al.* 1989 p. 570) and generally have a leafless, paniculate infloresence and a lemma that is tougher than the glumes (Barkworth and Everett 1986).

For many years a large proportion of Stipeae were considered to be included in a broadly defined genus *Stipa*. From the late 1970s taxonomic work led to the resurrection of old names and reassignment of species to other genera, some of very long standing (Barkworth and Everett 1986, Barkworth 1993, Jacobs *et al.* 2000, Barkworth and Torres 2001, Vásquez and Barkworth 2004). The concept of *Nassella* (Trinius) E.Desvaux was expanded to include species with long florets, formerly in *Stipa sens. lat.* Barkworth (1990) recognised nine genera in Stipeae: *Achnatherum*, *Anemanthele*, *Hesperostipa*, *Nassella*, *Oryzopsis*, *Piptatherum*, *Piptochaetium*, *Ptilagrostis* and *Stipa*. Several additional genera are now recognised in the tribe: Jacobs and Everett (1996) assigned all Australian native species formerly included in *Stipa* to the new genus *Austrostipa* and provided a key to the then ten genera of Stipeae; Peñailillo (1996) described a new genus *Anatherostipa*; Jacobs and Everett (1997) resurrected *Jarava*; Torres (1997) described *Nicoraella*; Vásquez and Barkworth (2004) defined a new genus *Celtica* for *Stipa gigantea* Link and resurrected the genus *Macrochloa* Kunth for *Stipa tenacissima* (Loefl. ex L.) Kunth. Barkworth (2006) included the small or monotypic genera *Aciachne*, *Lorenzochloa*, *Macrochloa*, *Ortachne*, *Psammochloa* and *Trikeraia* in her world list of Stipeae. Watson and Dallwitz (2005) included these 15 genera plus, tentatively, *Danthoniastrum* (possibly Aveneae). Tsvelev's (1977) concept of Stipeae also included *Orthoraphium* Nees, *Eriocoma* Rydb., *Streptachne* R.Br., *Stephanacne* Keng and *Pappagrostis* Roshev.

Barkworth (1990) reviewed the complex taxonomic history of *Nassella*. The name was first used by Trinius 1830 at subgeneric rank. Barkworth (1990) expanded *Nassella* from c. 9 spp. to include 79 species, with most of the additions, including *N. neesiana*, being from *Stipa sens. lat.* Watson and Dallwitz (2005) probably relied on Barkworth (1990), giving a total of "about 80" spp. for the genus. According to Barkworth and Torres (2001) *Nassella* included at least 116 spp., but Barkworth (2006) listed only 110. Quattrocchi (2006) gave an upper limit of 116.

Barkworth (1990) considered *Nassella* to be most closely related to *Piptochaetium* and *Hesperostipa*. Analysis of morphological and anatomical characters placed *Austrostipa* close to *Achnatherum* and *Ptilagrostis*, but study of rDNA indicated a closer relationship to *Nassella* than to *Achnatherum* (Jacobs and Everett 1996). Detailed molecular and morphological examination (Jacobs *et al.* 2000) found *Nassella* and *Piptochaetium* to be sister groups; likewise for *Austrostipa* and *Achnatherum*. *Austrostipa* appears to be the most recently evolved genus in the tribe (Jacobs *et al.* 2000).

Nassella is distinguished from other stipoid genera by having 3 stamens (1-3: Quattrocchi 2006); a tough lemma with three or more nerves and strongly and tightly overlapping margins, the outer margin extending 1/3 to 2/3 (25-50% Barkworth and Torres 2001) of the way around the inner, an unridged surface, heavily silicified with round or oval silica bodies in the epidermis, the fundamental cells of the epidermis being extremely short and much shorter than wide, a solid apex often developed into a corona (crown) at the summit of the lemma, with cilia that often appear to be fused at the base; and a flat, veinless, usually glabrous, short, rudimentary palea, less than 30% as long as the lemma, and completely concealed by the lemma (Barkworth 1990, Barkworth 1993, Jacobs and Everett 1996, Barkworth and Torres 2001, Watson and Dallwitz 2005, Barkworth 2006; *contra* Stace 1997 p. 840: "palea <3x (not >3x) as long as lemma").

Other common characters in the genus are the presence of both short and long anthers in a species or on the same plant or floret, tuberculate lemma, and abundant apical cilia on the long anthers (Barkworth 1990, Barkworth 2006). A many-noded culm with frequent branching is usual, but also occurs in *Achnatherum* and some *Austrostipa* spp. (Barkworth 1990). All *Nassella* species are caespitose perennials, the glumes are often strongly anthocyanic (anthocyanins = the water soluble glucoside compounds forming colouring matter in many flowers and other plant parts). No vegetative characters that distinguish the genus have been identified (Barkworth 2006). *Nassella* species are bisexual, mostly perennial, rarely annual, have hollow internodes and open sheaths and "readily deciduous" awns (Quattrocchi 2006 p. 1361).

In the Americas *Nassella* species are found from southern South America to southern Canada at altitudes from 0-5,000 m. Two areas have particularly high diversity: the altiplano of the central Andes, and the pampas of Uruguay, southern Brazil and eastern Argentina (Barkworth and Torres 2001).

The *Nassella* lineage has diverged to form two morphologically distinct groups (Barkworth 1990): one, to which *N. neesiana* belongs, with long symmetrical florets, long, sharp calluses and long, persistent awns, the other, to which *N. trichotoma* belongs, with short, eccentric florets, short, relatively blunt calluses, and relatively short, deciduous awns. Quattrocchi (2006 p. 1361) incorrectly attributed "readily deciduous" awns to the whole genus.

The assignment of species present in Victoria to *Nassella* on the basis of three character states - lemma margins strongly overlapping, palea membranous and not more than one third the length of the lemma - was questioned by Walsh (1994) who considered these characters to be present in some *Stipa sensu stricto* (in which he included the native Australian stipoids) and not present in other species assigned to *Nassella* by Barkworth (1990). *Austrostipa* is the only other stipoid genus with strongly convolute, coriaceous lemmas (in some spp.), but the palea is not reduced, glabrous and unveined (Barkworth and Torres 2001).

Six *Nassella* species are naturalised in Australia: Lobed Needle-grass *N. charruana* (Arechav.) Barkworth, Cane Needle-grass *N. hyalina* (Nees) Barkworth, Texas Needlegrass *N. leucotricha* (Trin. and Rupr.) Poly, Short-spined Needle-grass *N. megapotamia* (Spreng. ex Trin.) Barkworth, Serrated Tussock *N. trichotoma*, and *N. neesiana* (Jacobs and Everett 1996; McLaren, Stajsic and Iaconis 2004). Mexican Feather-grass *N. tenuissima* (Trinius) Barkworth, an ornamental grass, is present in the nursery trade and gardens, and is possibly incipiently naturalised (Jacobs *et al.* 1998, McLaren *et al.* 1999, Maguire 2005).

The name *Nassella* is derived from the Latin *nassa* meaning "a fish basket" or "a basket for catching fish" (Quattrocchi 2006).

The basionym: *Stipa neesiana* Trinius and Ruprecht 1842 has been variously cited as appearing in:

Mem. Acad. St. Petersb. Ser. 6 Sc. Nat 5: 27 (Caro 1966);
Mém. Acad. Imp. Sci. Saint-Pétersbourg, ser. 6, Sci., Math., Seconde Pt. Sci. Nat. 5:17 (Vickery *et al.* 1986);
Mém. Acad. Imp. Sci. St. Pétersbourg, sér. 6, Sci. Nat. 5: 27 (Torres 1997);
Mém. Acad. Sci. St. Pétersb., sér. 6, Sci. math. phys. and nat. 7^2: Bot. 27 (Willis 1970);
Mém. Acad. Imp. Sci. St-Petersb., ser. 6, 5: 17 (1842) (Jessop *et al.* 2006).

Synonyms

The taxonomic synonyms of *N. neesiana* are numerous. The following synyonyms have been listed by Caro (1966), Torres (1993), Zuloaga *et al.* (1994) Barkworth and Torres (2001), Quattrocchi (2006), Barkworth (2006) and Barkworth *et al.* (2007):

Stipa barbinodis Philippi (1896) = *S. neesiana* var. *barbinodis* (Philippi) Caro (1966)
Stipa contracta Phil.
Stipa eminens Nees *in* Mart. (1829) nom. illeg. *non S. eminens* Cavanilles (1799)
S. fernandeziana Phil. (1873) *non S. fernandeziana* (Trin. and Rupr.) Steudel (1854)
S. hackeli Arechavelata
S. hispida Phil. (1896)
S. longiflora Steudel (1854)
S. neesiana Trinius and Ruprecht (1842)
S. neesiana var. *chilensis* Trin. and Rupr. (1842)
S. neesiana var. *fernandeziana* Trin. and Rupr. = *S. skottsbergii* Pilger (1916)
S. neesiana var. *glabrata* Arechavaleta (1896) = *S. setigera* forma *glabrata* (Arechav.) Speg. (1901)
S. neesiana var. *hirsuta* Arechavaleta (1896) = *S. setigera* forma *hispidula* Speg. (1901) = *S. neesiana* var. *hispidula* (Speg.) Hackel (1911)
S. neesiana var. *hispidula* (Spegazzini) Hackel (1911)
S. neesiana var. *longiaristata* Arechavaleta (1896)
S. neesiana var. sublaevis (Spegazzini) Speg. ex Caro
S. neesiana var. sublaevis (Spegazzini) Speg. (1925)
S. neesiana var. *virescens* Hackel (1904)
S. neesiana forma *contorta* Hackel (1904)
S. neesiana forma *depauperata* Hackel
S. setigera auct. non. J. Presl
S. setigerna sensus Spegazzini non Presl var. *glabrata* (Arechavaleta) Spagazzini
S. setigera Presl var. *glabrata* Arechavaleta *ex* Spegazzini (1901)
S. setigera forma *glabrata* (Arechavaleta) Spegazzini
S. setigera Presl var. *hispidula* Spegazzini (1901)
S. setigera forma *hispidula* Spegazzini
S. setigera var. *hispidula* forma *pallida* Spegazzini (1901)
S. setigera var. *hispidula* forma *purpurascens* Spegazzini (1901)
S. setigera var. *hispidula* forma *versicolor* Spegazzini (1901).
S. sublaevis Spegazzini (1901) = *S. neesiana* var. *sublaevis* (Speg.) Speg. *ex* Caro (1966)
S. skottsbergii Pilger
S. trachysperma Phil. (1864)
Urachne longiflora Steudel

Additional infraspecific taxa synonymous with currently recognised varieties are listed below.

Ens (2005 under "Notes") erroneously stated that *Nassella tenuissima* was previously known as *Stipa neesiana*.

Many South American authors continue to use "*Stipa*" (sens. lat.) for most *Nassella* species (e.g. Honaine *et al.* 2006, Iriarte 2006).

Vernacular names

'Needlegrass' is a name that has been used for the genus *Stipa sens. lat*. in North America (Hitchcock and Chase 1971). The single word form of the name, the hyphenated form and the two-word form are all used in Australia. Shepherd *et al.* (2001), perhaps the best standardised source for vernacular plant names in Australia, uses "needlegrass". "Spear grass" and "corkscrew grass" are also applied as broad names for stipoids (Bourdôt and Hurrell 1989b). The term "arrow-grasses" has been applied to species of *Stipa sens. lat*., *Piptochaetium* and *Aristida* in Uruguay (Rosengurtt 1946).

The name "flechilla" (Hayward and Druce 1919, Bourdôt and Ryde 1986, Soriano *et al.* 1992, Martín Osorio *et al.* 2000) (wrongly "fletchilla" (Slay 2002a)), meaning 'little arrow' (Gardener 1998) or 'little dart' (Hayward and Druce 1919, Bourdôt and Ryde 1986, Soriano *et al.* 1992), in reference to the characteristics of the seed, is used in Argentina, but also applies to other *Nassella*, *Stipa*, *Piptochaetium* and *Aristida* spp. with piercing seeds (Soriano *et al.* 1992).

Additional vernacular names used for *S. neesiana* include American Needle-grass in the UK (Stace 1997), Uruguayan Tussockgrass in the USA (Randall 2002, Quattrocchi 2006, Barkworth 2006, ITIS 2006) and, not in common parlance, Chilean Spear-grass, in Victoria (Carr *et al.* 1992). Spanish names include "Aguja chilena" and "Hierba chilena de agujas" (Martín Osorio *et al.* 2000).

Infraspecific Taxa

Some infraspecific names have already been mentioned. A number of varieties have been recognised but their validity and usefulness is unclear:

var. *barbinodis* (Philippi) Caro (1966); recognised by Caro (1966) and equivalent to
    Stipa barbinodis Philippi
var. *chilensis* Trin. and Rupr. (1842)
var. *fernandeziana* Trin. and Rupr. (1842)
var. *formicarioides* Burkart (1969); recognised by Zuloaga *et al.* (1994) and Verloove (2005)
var. *glabrata* Arechav. (1896)
var. *gracilior* Burkart (1969); recognised by Zuloaga *et al.* (1994) and Verloove (2005)
var. *hirsuta* Arechavaleta; recognised by Zuloaga *et al.* (1994), and Caro (1966) who included within it
    S. setigera sensu Spegazzini non Presl var. *hispidula* Spegazzini
    S. neesiana forma *contorta* Hackel
    S. neesiana var. *hispidula* (Spegazzini) Hackel
var. *longiaristata* Arechavaleta (1896), recognised by Burkart (1969), Rosengurtt *et al.* (1970), Moraldo (1986), Torres (1993) and Zuloaga *et al.* (1994) and synonymous with
    S. sublaevis Spegazzini (1901), and
    S. *neesiana* var *sublaevis* (Spegazzini) Spegazinni, comb. superfl.
    S. neesiana var. *sublaevis* (Speg.) Spegazzini *ex* Caro (1966)
var. *neesiana*; also recognised by Caro (1966) and Zuloaga *et al.* (1994), and including:
    var. *glabrata* Arechavaleta
    f. *contorta* Hackel
    f. *depauperata* Hackel
var. *sublaevis* (Spegazzini) Spegazzini; recognised by Caro (1966) and including:
    S. hackeli Arechavelata
    S. sublaevis Spegazzini
var. *virescens* Hackel; recognised by Caro (1966) and Zuloaga *et al.* (1994), considered to be a synonym of *N. argentinensis* by Barkworth and Torres (2001) but recognised as part of *S. neesiana* by Barkworth et al. (2007).

Torres (1993 p. 19) discussed var. *hirsuta* and was unable confirm it as a variety of *N. neesiana*, but the synonymy was accepted by Barkworth et al. (2007).

An additional taxon, *S. neesiana* var. *ligularis* Grisebach, is considered equivalent to *S. ligularis* (Griseb.) Speg. (1901) (Torres 1993, Zuloaga *et al.* 1994, Barkworth and Torres 2001), while *S. neesiana* Kuntze is an illegal name for *S. tenuis* Phil. (*Zuloaga et al.* 1994).

Variety determination is sometimes difficult (Anderson 2002b) and the varieties may have little or no validity, merely representing extreme individuals within variable populations,clinal variation, or the output of taxonomists working with limited specimen material. Verloove (2005) considered the infraspecific variability to be of little taxonomic value and noted that some supposedly distinguishing subspecific characters varied between leaf surfaces or with age on the same plant.

Caro (1966) provided a key for the separation of vars. *neesiana*, *hirsuta*, *virescens* and *sublaevis*. Torres (1993) provided a key for vars. *neesiana*, *gracilior* and *longiaristata*. Moraldo (1986) provided a very brief description of var. *longiaristata* that does not enable it to be distinguished from other varieties. The varieties have sometimes been called subspecies in Australia (e.g. Britt *et al*. 2002, Jessop *et al.* 2006), without justification.

Variety *neesiana* is found in Argentina, Bolivia, Brazil, Chile, Ecuador, Peru (Rosengurtt *et al.* 1970) and New Zealand (Jacobs *et al.* 1989). Variety *longiaristata* is found in Argentina and Uruguay (Rosengurtt *et al.* 1970, Torres 1993, Barkworth *et al.* 2007) and according to Moraldo (1986) in Italy. Variety *gracilior* is found in Argentina (Torres 1993), as are vars. *hirsuta*, *virescens* and *sublaevis* (Caro 1966). The type of var. *chilensis* is from Chile, that of var. *fernandeziana* from the Juan Fernandez Islands (Chile), and those of vars. *hirsuta* and *sublaevis* from Uruguay (Barkworth *et al.* 2007). Var. *glabrata* is based on Uruguayan material (Barkworth *et al.* 2007). Var. *barbinodis* is found in Chile (Caro 1966).

Caro (1966) illustrated a plant, ligule, glumes and seed of var. *hirsuta*. Burkart (1969) illustrated a whole plant and seed of var. *neesiana*, seed of var. *longiaristata* and the caryopsis of var. *neesiana*. Torres (1993) illustrated seeds of vars. *neesiana*, *longiaristata* and *gracilior*.

Hocking (2002) suggested that more than one "type" of *N. neesiana* may be present in Australia. All the Australian specimens examined by Vickery *et al.* (1986) 'seemed' to be *N. neesiana* var. *neesiana*. Walsh (1994), who examined Victorian material, did not contradict this. Britt (2001) and Britt *et al.* (2002) stated that the varieties present in Australia were "unknown". Gardener *et al.* (2005) considered the plants they studied on the Northern Tablelands of NSW were var. *neesiana* and stated that it appeared to be the only variety present in Australia. Jessop *et al.* (2006) classed all South Australian material as subsp. *neesiana*.

Nevertheless, the large number of varieties and forms recognised by American taxonomists indicates the existence of considerable infraspecific phenotypic variation. Information at hand is inusufficient to indicate whether this variation is merely phenotypic plasticity in response to environmental variation or represents distinct genotypes.

Misapplied names

In Europe the name *Stipa setigera* (= *Nassella mucronta*) has been widely misapplied to *N. neesiana* and all verifiable records of these taxa in Europe are *N. neesiana* (Verloove 2005). *N. neesiana* and *N. mucronata* are easily confused (Vàzquez and Devesa 1996). Zanin *et al.* (1992, cited by Gardener 1998) used the name *Nassella setigera* var. *setigera* for *N. neesiana* vars. *gracilior*, *virescens* and *hirsuta* in Brazil. Overbeck *et al.* (2007) also used the name *S. setigera* for what is apparently *N. neesiana*. Longhi-Wagner and Zanin (1998) used the name *Stipa setigera* for *N. neesiana* and recorded it from Paraguay.

Hybridisation etc.

Many groups of grasses arose by intergeneric hybidisation (Tsvelev 1984) and interspecific hybridisation is very common in Poaceae (Wheeler *et al.* 1990) and in Stipeae. According to Tsvelev (1977) all extant Stipeae are of hybrid origin and the tribe itself may have arisen this way. Grasses in general are highly dispersable and fecund, a characteristic of higher taxa with high speciation rates (Levin 2006). Wind pollination and simultaneous flowering of grass species provides much opportunity for cross-fertilsation (Groves and Whalley 2002).

Sterile intergeneric stipoid hybrids are very common (Johnson 1972). *Oryzopsis caduca* Beal (?name: not in Barkworth 2006) is a hybrid between *Achnatherum hymenoides* (Roem. and Schult.) Barkworth and *Nassella viridula* (Trin.) Barkworth, and *A. hymenoides* crosses spontaneously with 11 stipoid species in the USA, including *Nassella pulchra* (Hitchc.) Barkworth, *N. cernua* (Stebbins and Love) Barkworth and species of *Stipa*, *Achnatherum*, and *Heterostipa*, producing plants that have all been classified as *Oryzopsis bloomeri* (Boland) Ricker (Johnson 1972). "In favorable years and under advantageous conditions of habitat disurbance hundres [sic] of individuals have been observed in some hybrid swarms" (Johnson 1972 p. 25). Barkworth (1990 2006) and Barkworth and Torres (2001) considered *N. viridula* itself to be most probably an alloploid, with *Achnatherum* and *Nassella* progenitors, or possibly an autoploid derivative of a common ancestor of *Achnatherum* and *Nassella*. According to USDA FEIS (2006), the occasional hybrids of *N. viridula* with *A. hymenoides* produce the sterile *Achnella caduca* (Beal) Barkworth. Watson and Dallwitz (2005) listed such hybrids as X *Stiporyzopsis* B.L. Johnson and Rogler and X *Achnella* Barkworth.

Tsvelev (1984 p. 903) considered intra-sectional hybrids in *Stipa* to be "probably ... not so rare", but inter-sectional hybrids to be "rarer". Examples of the latter include *S. gregarkunii* P. Smirnov, reportedly a result of crossing between *S. pulcherrima* C. Koch (section *Stipa*) and *S. caucasica* Schmalh. (Section *Smirnovia*), and *S. kopetdaghensis* Czopan. (section *Smirnovia*), possibly a cross between *S. caucasica* Schmalh. (section *Smirnovia*) and *S. zalesskii* Walensky subsp. *turcomania* (P. Smirn.) Tzvel. (section *Stipa*). The presence of hybrids in *S.* aggr. *capillata* L. and in section *Stipa* was undoubted, and in section Barbatae a hybrid *S. arabica* Trin. and Rupr. subsp. *arabica* X *S. hohenacheriana* Trin. and Rupr. subsp. *nachiczevanica* Tzvel. (*S. hohenackerana* according to Barkworth 2006) had been recorded (Tsvelev 1984).

Hybridisation of *N. neesiana* does not appear to have been reported. However Verloove (2005) examined specimens from South America and France with characters intermediate between *N. neesiana*, *N. mucronata* (H.B.Kunth) R.W.Pohl and/or *N. poeppigiana* (Trin. and Rupr.) Barkworth. Barkworth and Torres (2001) considered *N. mucronata*, *N. mexicana* (Hitchock) R.W. Pohl and *N. leucotricha* (Trin. and Rupr.) R.W. Pohl to comprise a species complex, with intergrades of the former two species in northern South America and of *N. mucronata* with *N. leucotricha* in northern Mexico. Data in Britt *et al.* (2002) suggest the possibility of some gene flow between *N. neesiana* and *N. leucotricha* at Melton, Victoria.

The new combinations of exotic and native stipoids now occurring in south-eastern Australia would appear to create new possibilities for hybridisation. It should be kept in mind that hybrid individuals might be found in Australia, and any suspected examples should be collected. Hybrids between *N. neesiana* races or regional populations may occur as a result of pollen flow, as may hybrids with other *Nassella* spp., or possibly with other introduced Stipeae and native *Austrodanthonia* spp.

Evolutionary origin

The evolutionary origin of the Poaceae is obscure. Grasses are presumed to have existed since the Mid-Cretaceous (c. 120 mybp, Mesozoic Era) on the basis of fossil leaves (Tsvelev 1984). Stebbins (1986) suggested their first appearance in the Late-Cretaceous, but molecular clock estimates suggest an origin about 83 mybp (Prasad *et al.* 2005). A minimum age of 90 mybp (Cretaceous) for the crown group of Poaceae has recently been suggested (Bouchenak-Khelladi *et al.* 2009). Thomasson (1986) found that the oldest definite grass fossils were from the Oligocene (c. 36-24 mybp, Tertiary Era) of North America, that fossils of probable grasses were also known from the Oligocene of Germany, and that Mesozoic leaf impression fossils from Europe, North America and Mongolia were only "possible" grasses. Jones (1999a) stated that grass fossils occur in the Eocene (45 mybp) in the Americas and Africa. Currently the oldest unequivocal grass macrofossils are recorded from the Paleocene-Eocene boundary c. 56 mybp (Piperno and Sues 2005). Bouchenak-Khelladi *et al.* (2009) considered a spikelet with a minimum age of 55 mybp to represent a crown node for almost all recognised grass genera. However grass phytoliths representative of a diverse range of taxa have been found in 70 mybp (late Cretaceous) fossilised dinosaur dung (Prasad *et al.* 2005) (65-67 mybp according to Bouchenak-Khelladi *et al.* 2009). The earliest fossil grass pollen has been found in the early Tertiary, with doubtful earlier records from the Cretaceous (Thomasson 1986), and presumed records (*Monoporites*) from 70-60 mybp (Prasad *et al.* 2005). Grass pollen first appears in the Australian record in the Paleocene (Macphail *et al.* 1994), at the end of the Paleocene (c. 58 mybp) (Keith 2004), or about 50 mybp (Keith 2004).

Undoubted fossils, with seeds very similar to modern *Stipa*, *Piptochaetium* and *Phalaris*, occur in rocks dated to the mid-Tertiary (c. 35 mybp) long after the family first evolved (Stebbins 1972). Bouchenak-Khelladi *et al.* (2009) indicate that the BEP clade (Bambusoideae, Ehrhartoideae and Pooideae), which includes Stipeae, originated in the Paleocene (57 mypb), while the other major clade, including most C_4 species, is younger, originating in the late Eocene (40 mybp). C_4 physiology was probably well developed by the Miocene (Thomasson 1986), the oldest origin in grasses being approximately 30.9 mybp (Christin *et al.* 2009, Bouchenak-Khelladi *et al.* 2009).

Tsvelev (1977 1984) convincingly argued that Poaceae first evolved in response to colder and drier conditions in mountainous areas with an increasingly continental climate. Stebbins (1986) argued a probable origin from *Joinvillea*-like ancestors (Joinvilleaceae) and differentiation into major families in lowland, open tropical savannahs with seasonal droughts; the *non sequitur* of a grass-less savannah going unremarked. A South American (Gondwanan) origin for the family has been suggested on the basis of the distribution of extant taxa, with diversification of subclades in Gondwana by the late Cretaceous (Prasad *et al.* 2005). Although considerable diversification within the family took place in the mid-Miocene (Piperno and Sues 2005), most modern tribes probably existed by the Paleocene (early Tertiary, c. 50 mybp), probably along with many modern genera (Tsvelev 1984, Jones 1999a). The Stipeae probably arose from primitive Pooideae (Stebbins 1986) which existed at least as early as 70 mybp (Prasad *et al.* 2005).

Jones (1999a) cited authors who argued the tropical origin of grasslands in areas that were cooling and developing seasonal aridity, in forest-savannah ecotone. Poaceae are uncommon in the fossil record until the mid-Miocene (16-11 mybp) (Piperno and Sues 2005) and "only became widespread 25 to 15 million years ago when cool, dry conditions kicked in" (O'Donoghue 2008 p. 39). The unimportance of mammals, except for South American gonwanatherians, with typical grazing adaptations such as hypsodont teeth until the Oligocene and Miocene also indicates that grasses were a minor component of vegetation before this time (Prasad *et al.* 2005).

Barkworth and Everett (1986 p. 261) noted that the character sets that define non-Australian supra-specific stipoid taxa do not occur in Australian taxa, even though Australian stipoids in aggregate possess almost all of these characters. They believed that Stipeae originated in Gondwana, suggesting a late Jurassic or Cretaceous (c. 135 mybp) origin for the tribe (Jones 1999a). Tsvelev (1977) more or less agreed, noting that the impoverished stipoid flora of Africa (excluding the Mediterranean areas) probably resulted from repeated long dry periods and the absence of high mountain refugia. Africa began to split from the South American section of Gondwana in the mid to late Mesozoic (c. 165-70 mybp) leaving Australia and South America still linked through Antarctica by the early Tertiary (c. 65 mybp) (Barlow 1981). Separation of Antarctica and Australia occurred in the Paleocene (53-50 mybp) and accelerated in the middle-late Eocene (c. 43-36 mybp) (McGowran *et al.* 2000). Several authors have favoured the Gondwanan centre of origin of *Stipa* (*sens. lat.*) including Moraldo (1986 p. 205) who placed it in the 'suture zones between South American, Antarctica and Australia'.

South America has a very rich stipoid flora, paralleled only by that of Eurasia (Tsvelev 1977). The current centre of diversity of *Nassella* is Argentina with c. 72 species, with greatest diversity in the north west, and 26 indigenous species. Uruguay has 23+ spp., and the greatest diversity in Bolivia and Chile is in the central Andes, adjacent to Argentina (Reyna and Barkworth 1994, Barkworth and Torres 2001, Barkworth 2006). The pampas or Rio de la Plata grasslands have 25 *Nassella* species (Gardener *et al.* 1996b).

Whether the genus evolved in the Pampas region is not known. There are no macrofossil Stipeae known from South America (Barkworth 2006). Tsvelev (1977) considered Oligocene (36-25 mybp) fossil panicles from Colorado to be *Stipa florissanti* (Knowlt.) MacGinitie, and noted that the American grass specialist Agnes Chase considered them identical with the extant species *Stipa mucronata* (now *Nassella mucronata* (Kunth) R.W. Pohl. Barkworth). Everett (1986) accept the Miocene North American *Berriochloa primaeva* Thomasson to be the earliest stipoid fossil. According to Barkworth (1990) "nasselloid" fossils are present in Late Miocene-Early Pliocene (c. 13-5 mybp) deposits in the USA. These have *Nassella*-like lemma epidermal patterns, and were considered to be *Nassella* by Thomasson (1986). Other described fossil stipoids from the USA include Oligocene and Miocene *Stipidium* and *Stipa* and Oligocene *Piptochaetium* (Thomasson 1986). Barkworth and Torres (2001) appeared to accept four North American fossil *Nassella* species, but point out that only a single *Nassella* sp. is today present in the areas of Colorado, Kansas and Nebraska where the fossils were found. Tsvelev (1977) accepted lower Miocene fossils as *Nassella* and *Piptochaetium* spp. along with other grasses, indicating that prairie grasslands existed at that time. Johnson (1972) prematurely considered this fossil record provided geological evidence of a stipoid evolutionary 'hot-spot' in the high plains of Nebraska during the Tertiary and argued for a North American focal point of polyploidisation.

Barkworth and Everett (1986) considered that American stipoids consisted of groups derived directly from Gondwana, such as *Nassella* (in the narrow sense) and *Piptochaetium*, and from a separate independent group that initially occupied Eurasia, notably *Achnatherum*. According to Barkworth (1990) citing Tsvelev (1977), the North American *Stipa sens. lat.* evolved from South American taxa, and European taxa from North American, however this is not evident in my reading of Tselev (1977), who argued that stipoids in South America evolved in parallel with those in North America and Eurasia over a very long period prior to the Pliocene, and that they first evolved around the Tethys sea between Africa and Eurasia when all the continental masses were joined in Pangaea (i.e. in the Triassic period c. 200 mybp). Tsvelev (1977) thought that evolution of the Stipeae in all areas simultaneously involved elongation of the spikelet and all its parts, and the lengthening of the awns, usually correlated with elongation of the glume apices to prevent premature shedding of the floret. Based on anatomical and distributional data, he had no doubt that *Stipa sens. lat.* evolved before the formation of lowland grasslands and considered *Achnatherum* to be the most primitive stipoid genus.

The extant Stipeae are believed to be products of widespread hybridisation and subsequent stabilisation (Tsvelev 1977). There is “little doubt that the recombination of genetically divergent evolutionary lines in the Stipeae has been a factor in colonization of diverse habitat” (Johnson 1972 p. 26).

Reconstruction of the eco-geological history of the Pampean stipoid areas of South America is at an early stage but some patterns are apparent. Since the mid Tertiary (c. 35 mybp) the Mesopotamian region of Argentina has been subjected to a marine transgression that flooded Pampasia, separating the Andean margin from the Brazilian-Uruguayan region, followed by a Pliocene (late Tertiary, 2-10 mybp) regression which allowed the development of fluvial plains with a diverse biota, then during the Quaternary (c. 2 mybp – 10 kybp), cooling and aridification alternated with warm to temperate humid periods, and finally in the Holocene (recent) there was another marine transgression (Aceñolaza 2004). In south-eastern Uruguay the Late Pleistocene (c 10-15 kybp) sediments show high concentrations of C_3 pooid Poaceae and Asteraceae indicating cool, dry grasslands, similar to those at the time in southern Brazil and on the Great Plains of North America; the Early Holocene (c. 7-10 kybp) shows a marked transistion to C_4 panicoid grasses with wetlands, indicating warmer and wetter conditions; the Mid Holocene (c. 4-6 kybp) showed dynamic climate oscillations from wet to dry with freshwater wetlands predominating; the Late Holocene (4 kybp to present) showed major increase in wetlands, and panicoid grasses, similar to southern Brazel but unlike conditions in the Argentine pampas which became more arid (Iriarte 2006). The cool arid periods in the Tertiary may have favoured stipoid speciation, while the cooler times throughout the Caionozoic have probably favoured the proliferation of stipoid dominated grasslands.

The pattern of evolution of the Australian Stipeae is largely unknown. The Australian fossil record of all terrestrial plant taxa is absent or very poor over long periods of the Quaternary, although this period probably saw little speciation (McGowran *et al.* 2000). Poaceae taxa are difficult to distinguish palynologically, the fossil pollen record is generally poor in Australia (Kershaw *et al.* 2000) and grass macrofossils are rare, although a potential *Bambusites* has been described from Tertiary stem impressions (Thomasson 1986). Phytolith analysis (see below) has potential for greater resolution, but has been little used in Australia (Kershaw *et al.* 2000).

Morphology and anatomy

A detailed description of *N. neesiana* extracted from published works has been compiled. Some descriptions of *N. neesiana* in monographs, floras and other publications are clearly stated to be of material found in the region of naturalisation (e.g. Burbidge and Gray 1970, Jacobs *et al.* 1989, Walsh 1994, Verloove 2005), while others are of material from the native range (e.g. Burkart 1969). Original or revisionary taxonomic papers generally provide details of the material described and examined. In some other descriptions, particularly non-taxonomic and informal publications, it is unclear what material is being described: these often cite dimensions, etc. that are clearly derivative of a single earlier author. Often one anatomical description clearly contradicts another (notably in dimensions) and it is not clear whether this is due to errors, inherent variation in the plant material or to selective assessment of character states within individual specimens and within populations. Where possible, errors have been noted.

Form and habit: “Erect, strongly caespitose with shoots swollen and close-set at base” (Jacobs *et al.* 1989, Edgar and Connor 2000); lightly geniculate (Martín Osorio *et al.* 2000); but lacking the dense tussock form when growing in association with other grasses (Champion 1995). Branching intravaginal (Burkart 1969, Jacobs *et al.* 1989); short-leaved (Burbidge and Gray 1970); a robust tussock when established, “not as clumpy as *Poa* or *Eragrostis*” (Duncan 1993), consisting of “a number of independent tufts” (ACT Weeds Working Group 2002). Tillers profusely when grazed, forming dense (Bourdôt and Ryde 1986), wide clumps (Liebert 1996), that may “form a matt” (Slay 2002c p. 5); grazed tussocks are not large and resemble *Festuca arundinacea* Schreb. (Duncan 1993, Slay 2002c), *Austrostipa* spp. (Slay 2002c), or in New Zealand at any time of year *Rytidosperma* spp., in winter under hard grazing *Sporobolus africanus* (Poir.) Robyns and Tournay, and in the flowering and fruiting stage *Bromus diandrus* Roth (Slay 2002c). Areas of mature tussocks in New England Tablelands pastures have basal ground cover of c. 20% (Gardener *et al.* 2003b). Tussocks have an overall “yellowish-green” colour that contrasts with surrounding pasture (Bourdôt and Ryde 1986, Liebert 1996), although Snell *et al.* (2007 p. 10) stated that it “becomes yellow or straw like” in winter in colder regions, and “can be a darker green compared to most other pasture species” during early growth stages, and Slay (2002c) stated that in continuous pasture it may have narrower leaves and by lighter green in colour, possibly due to soil fertility and management practices. Mature tussocks typically have masses of dead leaves in the center and green leaves around the margin (Gaur *et al*. 2005). Heavily grazed tussocks in winter, according to Slay (2002c p. 11) “are ‘mushroom’ shaped ... with’flaggy’ 20 cms+ long leaves extending horizontally beyond the perimeter ... of the tussock”. The flowering heads are open with drooping branches (Weber 2003). Masses of maturing seed heads in dense infestations are “dark green-brown” in colour (Slay 2002c p. 12). After seed is shed, the stems change to “light green-silver” in colour (Slay 2002c p. 12), but remain green into late summer (p.22 and Slay 2001). The green slowly fades, and by autumn the stems are “light brown” (Slay 2002c) or straw-coloured and are easily dislodged from the plant (Slay 2002c).

Like other grasses, the buds (apical meristems) are at or close to ground level and are protected under tightly enclosed leaf sheaths, so are more likely to survive fire and mammalian grazing (Wheeler *et al.* 1999). Young shoots are intravaginal (Watson and Dallwitz 2005), a condition that gives rise to the tussock form. In grazed situations in short pastures in the non-reproductive phase plants have a rather flat, almost rosette-like form. In the reproductive phase, plants are strongly upright, and consist almost totally of reproductive tillers, largely stalks with panicles, dead leaves and a few small living leaves. The contrast between these phases is extremely pronounced, and they can easily mistaken for different species. The flat, rosette-like growth stage, with smaller leaves, has been called the “sward form” and may be induced by slashing (Bedggood and Moerkerk 2002) and heavy grazing.

Height: culm to 2 m (Jacobs *et al.* 1989, Edgar and Connor 2000, Slay 2002a), 30-100 cm (Hayward and Druce 1919), 60-200 (Weber 2003), 30-140 cm (Barkworth 2006), to 140 cm (Moraldo 1986), 40-90 (Baeza *et al.* 2007), 1 m or more in the absence of grazing (Bourdôt and Ryde 1986), up to 1 m (Martín Osorio *et al.* 2000, Germishuizen and Meyer 2003, Snell *et al.* 2007), to c.

1 m (Walsh 1994), ca. 90 cm (Verloove 2005); to 90 cm (Zanin 1998); 80 cm (Carolin and Tindale 1994), 60 cm (Stace 1997), 30-100 cm (Burkart 1969, Barkworth and Torres 2001), 50-120 cm (Muyt 2001).

Leaves: As with other grasses, the leaves mature and senesce progressively from the tip to the base (Wheeler *et al.* 1999). Lamina mid to dark green (Muyt 2001), flat or loosely inrolled (Jessop *et al.* 2006), inrolling occurring under stress including drought (Snell *et al.* 2007); flat to convolute (Barkworth 2006, Zanin 2008), or somewhat inrolled (Walsh 1994), plane or involute (Verloove 2005), rolled when the plant is under moisture stress (Bourdôt and Ryde 1986), sometimes tightly (Slay 2002a); sharp pointed (Martín Osorio *et al.* 2000); basal leaves up to 40 cm long cauline leaves 20 cm long and 3 mm wide (Martín Osorio *et al.* 2000); leaves in general to 30 cm long (Walsh 1994, Slay 2002c), mostly <10 cm long (Burbidge and Gray 1970), 10-30 cm long (Muyt 2001, Weber 2003), to 40 cm (Jacobs *et al.* 1989), 5-50 cm long, 0.6-5 mm (Jessop *et al.* 2006), 1-5 mm (Bourdôt and Ryde 1986, Slay 2002c, Weber 2003), 1.5-7 mm (Baeza *et al.* 2007), 2-2.5 mm (Carolin and Tindale 1994), up to 5 mm (Walsh 1994, Jacobs *et al.* 1989), 4-5.5 mm (Burkart 1969). 2.5-8 mm (Barkworth and Torres 2001) or 2-8 mm (Barkworth 2006); 2 mm (Zanin 2008) wide; finely veined (Muyt 2001), canaliculate (Hayward and Druce 1919), upper side strongly ribbed (Bourdôt and Ryde 1986, Slay 2002c), the ribs adaxial; lacking cross-venation; midrib not readily distinguishable except by position, containing a single vascular bundle; lamina symmetrical on either side of the midrib (Watson and Dallwitz 2005); often (Muyt 2001) glabrous or sparsely pubescent (Walsh 1994), ciliolate (Hayward and Druce 1919) with spreading stiff hairs (Burbidge and Gray 1970), generally rough and scabrous (Cook 1999); lamina scabrous (Carolin and Tindale 1994), glabrous or with scattered hairs below, hairy above (Jessop *et al.* 2006), with scattered long white hairs especially on lower leaves (Verloove 2005) or abaxially with scattered long hairs, both surfaces scabrous (Jacobs *et al.* 1989), sometimes scabrous sometimes with hairs (Barkworth 2006), scabrous below (Hayward and Druce 1919), may be "shaggy" with hairs on the underside, upper surface with erect hairs (Slay 2002c p. 9); with short erect hairs on the upper side (Snell *et al.* 2007); short marginal hairs ('prickle teeth' – Slay 2002c) creating a rough leaf margin (Bourdôt and Ryde 1986), or margins scabrous (Jacobs *et al.* 1989); marginal hairs evenly spaced, c. 2-3 mm apart (Cook 1999); sheath split almost to the base, without auricles (for Stipeae - Tsvelev 1984); with membranous margin, partly transparent, ciliate (Martín Osorio *et al.* 2000), glabrous (Moraldo 1986), glabrous or slightly hispid (Barkworth 2006) or scabrid or hairy, with glabrous or cilate margins (Jessop *et al.* 2006), 0.2-4 mm long (Moraldo 1986), usually with scattered long white hairs (Verloove 2005), densely pubescent at base, long hairs at apex, hairs sometimes forming an abaxial ligule, elsewhere glabrous (Jacobs *et al.* 1989), smooth (Hayward and Druce 1919); convolute (Burkart 1969, Martín Osorio *et al.* 2000); striate, to 5 cm long (Jacobs *et al.* 1989); ligule a short flap of opaque tissue (Bourdôt and Ryde 1986), smooth and entire (Slay 2002c), short, roundish (Hayward and Druce 1919), extending across the leaf base (Slay 2002a); 0.5 mm or less (Slay 2002c), ±0.5 mm (Jacobs *et al.* 1989), 0.5-1 mm (Zanin 2008), 0.8-1 mm (Baeza *et al.* 2007), 0-3 mm (Jessop *et al.* 2006), 1.5-4 mm (Verloove 2005), 1-4 mm (Barkworth and Torres 2001), to 3 mm (Walsh 1994) or 1-3 mm (Muyt 2001, Weber 2003) long, flat-topped (Jacobs *et al.* 1989), membranous (Liebert 1996, Verloove 2005, Zanin 2008), papery (Weber 2003), sometimes obsolete (Walsh 1994), glabrous (Walsh 1994) or small tufts of erect hairs on either side in the collar region (Bourdôt and Ryde 1986, Muyt 2001, Jessop *et al.* 2006) or finely and shortly ciliolate at apex or shallowly crenate (Jacobs *et al.* 1989) or laciniate (Martín Osorio *et al.* 2000). The lamina anatomy of Stipeae is said to be bambusoid (Tsvelev 1984). The mesophyll of stipoids is "usually unorganised ... with more than three cells between adjacent bundles" (Barkworth and Everett 1986). The abaxial surface of leaves of *Nassella* spp. have long files of regularly alternating silicose and non-silicose cells over the veins, the silica bodies being nodulose to dumbbell-shaped (Barkworth 1990). Watson and Dallwitz (2005) provided more detail but did not examine *N. neesiana*: mid-intercostal long-cells rectangular, microhairs absent, intercostal short-cells common, mostly in cork/silica-cell pairs, costal silica bodies well developed, present througout the costal zones, mesophyll with non-radiate chlorenchyma, without adaxial palisade tissue, all the vascular bundles accompanied by sclerenchyma. Moraldo (1986 p. 214) illustrated the leaf base of *N. neesiana* in transverse section. Stomata of Poaceae normally have two gaurd cells and two parallel subsidiary cells. Arrillaga-Maffei (1966) reported anomalous stomata in material from Uruguay and Argentina. Uruguayan material had approximately 50% normal stomata on the abaxial leaf surface along with anomalous stomata that had four gaurd cells and two normal subsidiary cells or two gaurd cells and various arrangements of three or four subsidiary cells. Plants grown from chasmogamous and cleistogamous seed from the original Uruguayan specimen had the same anomalies. Presumably the increased structural complexity of thse stoma could result in more complex control of gas exchange through the stomatal pore, and thus of metabolic processes. Prophylls (two-keeled, bladeless, modified leaf within the leaf sheaths) membanous, slender, transparent (Connor *et al*. 1993). First seedling leaf with a well-developed, narrow, curved lamina (Watson and Dallwitz 2005).

Culm: erect (Muyt 2001, Verloove 2005) or arching (Muyt 2001) or geniculate (Barkworth 2006), or growing both vertically and horizontally (Slay 2002c); [height: see above]; 1-1.8 mm thick, internodes glabrous (Barkworth 2006) or glabrous except for 'prickle teeth' below the infloresence (Jacobs *et al.* 1989, Slay 2002a); hollow (Watson and Dallwitz 2005); 4 nodes per culm (Slay 2001), nodes mostly 4-6 (Gardener *et al.* 2003a), or usually 2-4, exposed, sericeous (Barkworth 2006), 2-3 nodes (Baeza *et al.* 2007), generally with only 2 nodes (Martín Osorio *et al.* 2000); nodes swollen (Muyt 2001), bifurcate laterally and up to 3 mm in diameter (Martín Osorio *et al.* 2000) or bulging over the concealed spikelets (Bourdôt and Ryde 1986), pilose (Morldo 1986, Verloove 2005), downy (Muyt 2001), pubescent (Hayward and Druce 1919, Walsh 1994) or appressed pilose (Jacobs *et al.* 1989), with hairs to 1 mm (Martín Osorio *et al.* 2000) or 1.2 mm (Barkworth 2006); culm base tissue with abundant starch (Watson and Dallwitz 2005); bearing small numbers of cauline leaves (Martín Osorio *et al.* 2000); wide variation in number of culms per m^2 from 88 to 835 (Gardener *et al.* 2003a), 793± 128 per m^{-2} in pure sward (Slay 2001); first internode can be long or very short and distance between first node and ground surface can be very short (Julio Bonilla pers. comm.); first node at or below ground level, second node 15± 4 mm above ground, third node 110 ±29 mm above ground, fourth node 363 ±77 mm above ground, panicle tip 1160 ±74 mm above ground (Slay 2001); bearing cleistogenes under leaf sheaths at nodes.

Panicle: a complex infloresence, with a prominent 'overt' aerial section (the apical inflorescence, developing beneath the terminal leaf) and axillary inflorescences, subsidiary "clandestine" panicles concealed beneath leaf sheaths of all other culm nodes (Conner *et al.* 1993 p. 301) described by Martín Osorio *et al.* (2000) as an open panicle, open or scarcely enclosed in the base of the upper sheath, with the inferior internode up to 8 cm long and the next one about 4 cm long when fully expanded, each node giving rise to two ramifications that later ramify into irregular single-flowered peduncle spikes (rough translation from Spanish). The developing overt panicle swells the terminal leaf sheath and continues to extend after it emerges (Slay 2002c). The overt panicle is more or less contracted, becoming more effuse with age, up to 25 cm long (Verloove 2005); unilateral (Burkart 1969); 5-40 cm

(Barkworth 2006), 10-25 cm (Barkworth and Torres 2001), 5-30 cm (Burkart 1969), 10-25 cm (Moraldo 1986), 13-28 cm (Baeza *et al.* 2007), 14-35 cm (Zanin 2008) or 20-35 cm long (Martín Osorio *et al.* 2000) or up to 30 cm long, open, branches drooping, flexuous (Jacobs *et al.* 1989, Edgar and Connor 2000) or erect to nodding (Barkworth 2006), up to 40 cm long, "the branches breaking up at maturity" (Carolin and Tindale 1994 p. 772); loose (Walsh 1994, Muyt 2001), lax, nodding (Hayward and Druce 1919), drooping (Muyt 2001), sometimes interrupted, to 40 cm long (Walsh 1994); rachis smooth to slightly scabrous, branches and pedicels with stiff hairs (Jacobs *et al.* 1989); pedicels 1.5-12 mm (Baeza *et al.* 2007); branches thin, angular, scabrid (Hayward and Druce 1919) or pubescent (Martín Osorio *et al.* 2000); overall "very distinctive purplish colour" (Duncan 1993) or "initially ... striking violet ... with ....green awns" (Slay 2002c); branches 2.5-8.5 cm with 2-5 spikelets (Barkworth 2006), 3-5 spikelets (Hayward and Druce 1919), average of c. 15 spikelets in the aerial section and a progressive reduction in length of infloresence sections and number of spikelets at lower nodes (Connor *et al.* 1993), averages of 16 to 27.4 seeds per panicle (Gardener *et al.* 2003a). Disarticulating above the glumes (Verloove 2005). Published descriptions often lack precise descriptions of the subsidiary clandestine panicle sections. According to one description (Jacobs *et al.* 1989, Edgar and Connor 2000): "Occasionally an aerial-type branch may be produced at the uppermost culm node, and so far as can be judged, remains unsheathed". This may be equivalent to what Slay (2002c p. 21) refers to as "another 'emerged seed head' [that] may develop from the top node underneath the terminal leaf sheath" on larger plants (see his Fig. 26). Slay (2002a) noted that such secondary panicles develop in the leaf sheath of all culm nodes, are progressively smaller towards the base of the plant and may occasionally produce exposed, strongly-awned seed. The 'overt' panicle is purplish in the flowering stage, becoming more silver as the seeds ripen (Bourdôt and Ryde 1986). Plants grown from single tillers and from seed produced a mean of 18 and 16 panicles per plant respectively after 6-9 months (Hartley 1994). The potential seed yield per panicle of plants in a dense sward in New Zealand was 38 (Slay 2001). As in other paniculate grasses, the panicle matures basipetally, the uppermost spikelet developing first (Stebbins 1972).

Flowers:

hermaphrodite; pedicels 1-8 mm long, angled, scabrous, pubescent (Barkworth 2006), drooping (Slay 2002c); terminal panicle spikelets – glumes unequal (Hayward and Druce 1919) or subequal (Walsh 1994, Barkworth 2006); 10-22 mm (Barkworth 2006), 16-20 mm (Walsh 1994), 15-25 (Moraldo 1986), 16-25 (Walsh 1998), 14-21 mm (Barkworth and Torres 2001), up to c. 2 cm (Weber 2003), 15-20 mm long (Verloove 2005), shorter than the awn column, the upper to 15 mm, the lower to 20 mm (Jacobs *et al.* 1989) or the lower 17-20 mm long and the upper 2-3 mm shorter (Martín Osorio *et al.* 2000) or the lower 13-15 mm and the upper 12-14 mm (Baeza *et al.* 2007); the lower 15-17 x 0.4-1 mm, the upper 13-15 x 0.5-1 mm (Zanin 2008); 1.8-2.3 mm wide (Barkworth 2006), narrowly lanceolate (Martín Osorio *et al.* 2000, Barkworth 2006), linear lanceolate (Hayward and Druce 1919), acuminate (Hayward and Druce 1919, Walsh 1994), produced into awn-like processes to 3 mm (Jacobs *et al.* 1989); 3-5 veined (Barkworth 2006), 3-nerved (Hayward and Druce 1919, Jacobs *et al.* 1989, Zanin 2008), the lower 3-nerved (Martín Osorio *et al.* 2000), or 5-nerved, the upper 3-nerved, scabrous-pubescent on the nerves and/or margins (Verloove 2005), nerves scabrous (Moraldo 1986, Jacobs *et al.* 1989), central nerve prominent with rigid hairs, lateral nerves with rudimenary hairs and lightly rough (Martín Osorio *et al.* 2000); glabrous (Jacobs *et al.* 1989, Watson and Dallwitz 2005, Barkworth 2006); overall maroon (Cook 1999) or purple (Bourdôt and Ryde 1986), the lower violet, the upper clear to violet at anthesis (Slay 2002c); violet below, hyaline above (Jacobs *et al.* 1989), strongly (Walsh 1994) purplish with hyaline apex and margins (Verloove 2005), hyaline or violet (Moraldo 1986), hyaline and dyed purple in the upper half (Martín Osorio *et al.* 2000), green-violet (Baeza *et al.* 2007), brownish with white margins (Hayward and Druce 1919), losing colour but retained on plant for some time after seed fall (Muyt 2001), retaining a pinkish tinge even after the seeds have dropped (Liebert 1996); florets 6-13 mm long, 1-1.5 mm wide, terete, widest just below the crown (Barkworth 2006); anthoecium (including callus, lemma body and crown, plus the concealed palea) cylindrical, 7.5-9 mm but up to 10 mm long, diameter c. 1.2 mm (Verloove 2005) or ±cylindrical 7-11.5 mm long (Barkworth and Torres 2001) or fusiform 6.3-11.5 mm long, c. 1-1.5 mm wide, white or violet in colour (Burkart 1969), purple (Muyt 2001) or corona purple (Bourdôt and Ryde 1986), lemma white, corona violet, awn light green at anthesis (Slay 2002c); basal spikelets more or less cleistogamous, enclosed by uppermost leaf sheath (Burbidge and Gray 1970), other spikelets chasmogamous. ["In the Australian species [of *Stipa sens. lat.*] there are no externally visible differences between the two, but the cleistogamous spikelets usually have shorter stamens. Both types may be found scattered through a panicle" (Vickery at al. 1986 p. 11)]; lemma and palea – see description below under 'Fruit'; ovary glabrous (Jacobs *et al.* 1989); lodicules (scales below the stamens and ovary, regarded as a reduced perianth): 2, c. 1mm (Jacobs *et al.* 1989), membranous, glabrous (Watson and Dallwitz 2005), hyaline, transparent (Baeza *et al.* 2007), nerveless; styles 2, plumose (Jacobs *et al.* 1989); ovary 1-1.5 mm, glabrous (Baeza *et al.* 2007); stigmas 2 (Watson and Dallwitz 2005), white (Slay 2002c), 2-2.5 mm (Baeza *et al.* 2007); anthers 3, penicillate,3-3.5 (Barkworth 2006) or 4-4.5 mm long (Baeza *et al.* 2007), or up to 3.2 mm long in chasmogamous flowers and in cleistogamous flowers reduced to one fertile 0.5-0.7 mm long and 2 sterile, 0.1-0.2 mm long (Edgar and Connor 2000), yellow (Slay 2002c); pollen grains smaller than in Aveneae, almost spherical (tribal characters, Tsvelev 1977).

axillary cleistogamous spikelets - extremely variable (Gardener and Sindel 1998); the various floral parts are progressively reduced in number and size from the upper to the basal spikelets (Connor *et al.* 1993) i.e. loss of glumes and reduction of awn. See description under "Cleistogenes", below.

Fruit = 'seed' (Fig. 2). Caryopsis "a dry monospermic indehiscent fruit" (Sendulsky et al. 1986);(= grain, includes the hilum and embryo). 3.5-5 x 0.6-1 mm (Zanin 1998), 4.8-5.5 x 0.9-1.2 mm (Baeza *et al.* 2007), 3-5 (Barkworth 2006), 4-5 mm (Verloove 2005) or 6-8 mm (Martín Osorio *et al.* 2000) long; cylindrical (Burkart 1969), obovoid (Baeza *et al.* 2007); tightly enclosed by the lemma (Bourdôt and Ryde 1986); clear-coffee coloured (Baeza *et al.* 2007); hilum (the scar left on the caryopsis at the point of attachment) linear (Jacobs *et al.* 1989), 2 mm long (Baeza *et al.* 2007); embryo small (Jacobs *et al.* 1989), 1.5-1.6 mm (Baeza *et al.* 2007), festucoid, $^{1}/_{6}$ -$^{1}/_{3}$ of the grain (for Stipeae- Tsvelev 1984), with an epiblast and a neglibible mesocotyl internode, without a scuteller tail (Watson and Dallwitz 2005); endosperm hard, without lipid, containing compound starch grains (Watson and Dallwitz 2005).

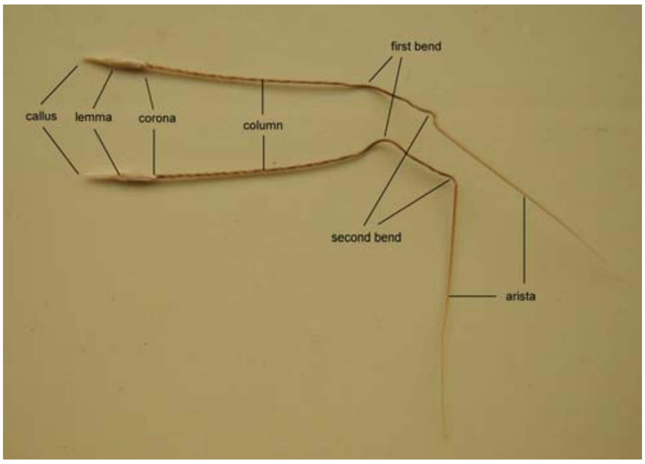

Figure 2. Anatomy of the seed of *N. neesiana.*

Panicle seed: (aerially exserted) consisting of cayopsis, enclosed by the palea and the lemma, the callus (woody pointed extension of the lemma) and the awn; weight c. 6 mg (Gardener *et al.* 1999; this is the fresh green seed). Lemma hardened (Bourdôt and Ryde 1986), conspicuously tuberculate (Verloove 2005), tubercular-scabrous (Jacobs *et al.* 1989), papillose (Barkworth and Torres 2001, Zanin 2008), coriaceous (Martín Osorio *et al.* 2000), or rugose-papillose, especially near the apex (Burkart 1969), or finely rugose-papillose, particularly near the crown (Barkworth 2006), or papillose-scabrid (Walsh 1994), with 5 (Hayward and Druce 1919, Jacobs *et al.* 1989) conspicuous (Walsh 1994) or inconspicuous (Martín Osorio *et al.* 2000) nerves; lemma 6-10 (mostly 8-10) mm long excluding the corona (Walsh 1994), 8-14.5 mm long including callus (Martín Osorio *et al.* 2000), about 8 mm long including callus (Burbidge and Gray 1970), c. 10 mm (Weber 2003), or 7-10-(13) mm (Moraldo 1986), 5.9-10 mm (Zanin 2008), or to 6 mm long (Jacobs *et al.* 1989); constricted below the crown (Barkworth 2006); glabrous except for the lower half on the veins (Verloove 2005), midveins pilose proximally, glabrous between the veins at maturity (Barkworth 2006), median nerve with long hairs (Jacobs *et al.* 1989), glabrous except near the callus and midrib (Walsh 1994), lobes minute (Jacobs *et al.* 1989); often purple (Barkworth 2006), pale brown at maturity (Walsh 1994).

Corona (called a "crown" by Tsvelev 1977, Barkworth 1990 2006 and Barkworth and Torres 2001; a "membranous cupule" by Stace 1997 and a "crowned collar" by Walsh 1998), a fusion of the edges of the lemma at its apex resulting in a solid cylinder (Barkworth 1990), or "a concave platform with the [awn] joint inside" (Tsvelev 1977 p. 8), best developed on mature seed, although apparent on immature (Muyt 2001), a prominent ridge (Jacobs *et al.* 1989), usually wider than long, sides usually flaring somewhat distally (Barkworth 2006), 0.8-1.3 x 0.7-1.1 mm (Zanin 2008), c. 1 mm wide and high (Verloove 2005), 0.6-1.6 mm high (Burkart 1969), 1.5 mm (Baeza *et al.* 2007), c. 0.7 mm (Moraldo 1986), 0.4-1.6 mm (Barkworth 2006), 0.5-1 mm (Barkworth and Torres 2001), or up to 1 mm (Jacobs *et al.* 1989) long, c. 1 mm long excluding the apical spines (Walsh 1994), cupuliform, "bone-like", constricted (Verloove 2005) and narrower (Martín Osorio *et al.* 2000) at the base, glabrous (Jacobs *et al.* 1989), with, at the apex, a conspicuous ring of cilia (Burbidge and Gray 1970) or denticulate hairs with a clearly broadened base (i.e. "conspicuously triangular" (Verloove 2005 p. 107)), or spreading spines 0.2-0.5 (Walsh 1994, 1998), to 0.5 m (Barkworth 2006),0.6-1.6 mm (Martín Osorio *et al.* 2000) or to 1 mm (Jacobs *et al.* 1989, Edgar and Connor 2000) long, the spines elongating as the seed matures (Walsh 1998). Violet or violet-suffused (Jacobs *et al.* 1989) or dark violet (Martín Osorio *et al.* 2000). The corona functions to ensure no backward movement of the seed once it has lodged in fur or penetrated soil or litter, even after the awn becomes detached (Slay 2002a).

Palea oval, much shorter than lemma (Jacobs *et al.* 1989), up to one third of the lemma in length (Martín Osorio *et al.* 2000), 1.5-2 x 0.5-0.7 mm (Baeza *et al.* 2007), 1.2-1.4 mm (Burkart 1969), 1.5 mm (Jacobs *et al.* 1989), 1-2 mm (Walsh 1994, Zanin 2008), 1-2.5 mm long, membranous (Verloove 2005, Baeza *et al.* 2007), transparent (Baeza *et al.* 2007), hyaline (Walsh 1994, Martín Osorio *et al.* 2000, Baeza *et al.* 2007, Zanin 2008), glabrous (Walsh 1994, Martín Osorio *et al.* 2000,Verloove 2005, Baeza *et al.* 2007), nerveless (Jacobs *et al.* 1989) but "internerve" glabrous (Jacobs *et al.* 1989); apex 2-denticulate (Baeza *et al.* 2007).

Awn persistent (Edgar *et al.* 1991); "extremely strong" (Slay 2002c); robust, 60-90 mm (Moraldo 1986, Walsh 1994 1998, McLaren, Stajsic and Iaconis. 2004), 50-90 mm (Weber 2003, Jessop *et al.* 2006), 60-70 mm (Burbidge and Gray 1970), to 70 mm (Jacobs *et al.* 1989), 60-80 mm (Bourdôt and Ryde 1986), 60-90 mm (Zanin 2008), up to 70 mm Slay (2002c), 6-9.5 cm (Barkworth and Torres 2001, Verloove 2005), 5-12 cm (Burkart 1969, Barkworth 2006), 6-12 cm (Martín Osorio *et al.* 2000), 44-70 mm long (Baeza *et al.* 2007) [total range of awn lengths cited = 44-120 mm]; bent above the middle (Hayward and Druce 1919), 15-30 mm to the first bend (Walsh 1994), hygroscopic (Murbach 1900, Bourdôt and Ryde 1986), with 1 (Bourdôt and Ryde 1986, Jacobs *et al.* 1989, Edgar and Connor 2000), 1 or 2 (Slay 2002c), 2 (Burbidge and Gray 1970, Walsh 1994, Barkworth and Torres 2001, Martín Osorio *et al.* 2000, Baeza *et al.* 2007), often 2 (Storrie and Lowien 2003), or 2-3 (Carolin and Tindale 1994) bends ("clearly twice-geniculate" Barkworth 2006); initially violet/green in colour, turning brown as seed matures (Slay 2002a); column stout (Weber 2003), tightly twisted (Jacobs *et al.* 1989, Edgar and Connor 2000), spirally twisted (Weber 2003), appearing like a 'corkscrew' (Slay 2002c), long-hairy (Jacobs *et al.* 1989, Edgar and Connor 2000), pubescent (Baeza *et al.* 2007), or sub-plumose (Burbidge and Gray 1970), or "corto-pilosa" at the base (Zanin 2008 p. 90); 25 mm long, an intermediate section about 15 mm long that is shallowly twisted with short stiff hairs (Jacobs *et al.* 1989, Edgar and Connor 2000) and straight (Barkworth and Torres 2001, Barkworth 2006), the lower section, about one third of the lower half of the awn spiralled and covered with hairs (Martín Osorio *et al.* 2000); and a terminal section, the arista (bristle or seta), scabrid to 35 mm long (Jacobs *et al.* 1989, Edgar and Connor 2000), "usually intertwined with awns of adjacent florets" (Jacobs *et al.* 1989).

The anatomy of the awn of *Stipa sens. lat..* (including *Nassella*) "differs from ... most other grasses ... although there have been attempts to explain the twisting and untwisting motion, more work could be usefully done on the subject. The awn in transection consists mainly of thickened cells (fibres) with two lateral pockets of chlorenchyma. The chlorenchyma breaks down with age and, apparently, the awn does not twist until this breaking-down process has been initiated" (Vickery *et al.* 1986 p. 11). Murbach (1900: studies on the eastern USA sp. *Piptochaetium avenaceum* (L.) Parodi, formerly *Stipa avenacea* L.) found that the awn of panicle seed has an outer layer of sclerenchyma cells with a spiral structure to the cell wall, a central fibro-vascular bundle and a band of chlorphyllous tissue on each side of the bundle. The two outer layers consist of thick-walled mechanical cells with a very small lumen oriented on the inner side of the cell and surrounded by spirally arranged cellulosic material. Wetting and drying of cells on opposite sides of the awn produce forces that act in opposite directions, producing torsion, and both the outer and middle layers are responsible. The awns therefore straighten when wetted and twist as they dry out (Whittet 1969, Groves and Whalley 2002, personal obs.). The awn twists in an anticlockwise direction (Slay 2002a).

The awn columns of adjacent seeds often become intertwined (Connor *et al.* 1993, Edgar and Connor 2000) or twisted together at maturity (Walsh 1994) forming a tangled mass (Liebert 1996), and fall as an aggregate, losing the dispersal ability of lone seeds (Gardener *et al.* 2003a). Such seed masses may be retained by the plant long after the seeds mature (Groves and Whalley 2002), or may be "easily detached en masse attaching themselves to clothes, machinery and animals" (Slay 2002a p. 10).

<u>Callus</u> - an extension of the lemma formed by the oblique articulation of the lemma with the rachilla (Hitchcock and Chase 1971), attaching the seed to the stem (Bourdôt and Ryde 1986); sharp (Walsh 1994, Barkworth 2006), particularly sharply pointed (Bourdôt and Hurrell 1989b), "extremely sharp ... when dry and mature" (Slay 2002c p. 8); approximately one third the length of the seed (Martín Osorio *et al.* 2000); 2-4 mm (Moraldo 1986, Walsh 1994, McLaren, Stajsic and Iaconis. 2004), 2.5-3.5 mm (Jessop *et al.* 2006), 2.8-3.5 mm (Baeza *et al.* 2007), 3-4 mm (Jacobs *et al.* 1989), c. 4 mm (Verloove 2005), 2.5.-3.2 mm (Burkart 1969), 2-4.5 mm (Barkworth 2006), 3-5.5 mm long (Barkworth and Torres 2001), strigose (Barkworth 2006), oblique (Jacobs *et al.* 1989); with silky white hairs 1-2 mm long (Martín Osorio *et al.* 2000), or 1.5 mm long (Baeza *et al.* 2007), bearded (Barkworth and Torres 2001), hairy (Bourdôt and Ryde 1986), covered with white appressed hairs (Hayward and Druce 1919), villous (Burbidge and Gray 1970) or hidden by a tuft of white hairs (Verloove 2005), the hairs antrorse (Gardener *et al.* 2003a) and up to 4 mm long (measured from their lowest position on the callus to their furthest extent) (Jacobs *et al.* 1989).

All the seed hairs are retrorse, i.e. pointed away from the callus tip.

<u>Cleistogenes</u>: "clandestine seeds" (Bourdôt and Hurrell 1992 p. 102), "floreted cleistogenes" on "clandestine axillary spikelets" (Connor *et al.* 1993); formed at nodes "towards the base of flowering culms" (Jacobs *et al.* 1989, Edgar and Connor 2000), on all (Connor *et al.* 1993) or able to be produced on all culm nodes (Gardener *et al.* 2003a); subtended by slender transparent prophylls (Connor *et al*. 1993, Jacobs *et al.* 1989); 1-3 flowered, with 2 awned glumes about half the length of those in panicle florets (Jacobs *et al.* 1989, Connor *et al.* 1993), lower glume 1-3 nerved, upper glume with up to 7 nerves; lemma, corona and palea as in aerial florets (Jacobs *et al.* 1989), except reduced in size, awn to 25 mm, caryopsis to 4 mm, callus about 0.5 mm (Jacobs *et al.* 1989, Edgar and Connor 2000); 2.5 x 1.4 mm (Jacobs *et al.* 1989, Connor *et al.* 1993); anthers reduced to 1 fertile and 2 small sterile anthers, cayopsis round or planoconvex to 4 mm long (Jacobs *et al.* 1989); stem cleistogenes of two types – 4-5 mm, turbinate, long-callused and 1.4-2.5 mm and plump (Slay 2002a); Descriptions rarely have the clarity and detail necessary to appropriately describe the variation in cleistogenes. Cleistogenes in general are more rounded than panicle seed (Bourdôt and Hurrell 1992); lack a large hygroscopic awn (Gardener *et al.* 2003a) and have a less well-developed lemma than panicle seed (Hurrell *et al.* 1994). Upper nodes produce larger numbers, a maximum on the third and fourth nodes and an average of c. 7 per tiller (Gardener *et al.* 2003a); up to 5 "unsheathed" cleistogenes on the second and third nodes (Slay 2001 p. 28); each node above the basal with the potential to produce a few seeds (Gaur *et al.* 2005); a potential total of 13 cleistogenes (including the basal) per culm (Slay 2001). Thin stems may have more cleistogenes than thick ones, possibly indicating a compensatory effect for reduced panicle seed production of thin stems (Julio Bonilla pers. comm.). Mean mass of upper node cleistogenes 2.0 mg, maturity on average 4 weeks after maturation of panicle seed (Gardener *et al.* 2003a). <u>Basal cleistogenes</u> initiated as a bud at the base of the culm, present even in small 3-tillered plants (D. McLaren, 26 October 2006, based on observation of Shiv Gaur); solitary (Burkart 1969, Gaur *et al.* 2005), "always singular" on the Northern Tablelands of NSW but "often in multiples" in Argentina (Gardener *et al.* 1996b), successively develop one on top the other, so accumulate upwards (D. McLaren, 26 October 2006, based on observation of Shiv Gaur); 1-3 (Slay 2001), or 1-2 (Connor *et al.* 1993), less than half the basal nodes producing one cleistogene on average (Gardener *et al.* 2003a); occurring beneath the soil surface (Gaur *et al.* 2005) or often below ground (Gardener *et al.* 2003a); nut-like, 2..5 mm long, 1.5 mm wide, yellow to dark brown depending on age (Slay 2002a), light dull yellow when newly formed, becoming brown and thin as they mature (Gaur *et al.* 2005), lemon to fawn colour, plump, with the top "'Turkish roof' shaped" (Slay 2001 p. 42); mean mass 3.3 mg (Gardener *et al.* 2003a).

<u>Roots</u>: fibrous, crown thickened (Muyt 2001), not rhizomatous (Barkworth 2006).

In the context of the flora of Victoria, identification to species from macroscopic vegetative characters alone is unreliable, but can possibly be achieved by microscopic examination of epidermis morphology and distribution of stomata and silica bodies (Walsh 1998). The detail provided by Watson and Dallwitz (2005) indicate this is possible, at least for distinguishing the *Nassella* species present in Australia. Identification using leaf phytolith character assemblages also appears possible (see below).

Evolved changes, which may be reflected in morphology, and perhaps enhanced growth, can be expected in introduced populations of exotic plants, but these changes can be difficult to distinguish from genotypic plasticity (Cox 2004). There is a need to determine if there are any morphological differences between exotic and native populations and between exotic populations in different areas. Possibly some evidence for differences exists in the morphological descriptions above. No morphological descriptive publications examined provides sample sizes or standard deviations for any measurements, nor any evidence that the material described is truly representative of the populations. Evolved changes are likely to be evident in the diaspore and other reproductive characteristics (Cox 2004). For example populations of *Pinus concorta* ssp. *latifolia* at the exanding edge of their post-glacial invasion front have smaller, better dispersing seed than the core population (Rejmánek and Richardson 1996 see their citation). A comparison of the seed morphology of core and fringe populations would be of interest:

are the seeds larger/smaller, longer/shorter awned, less/more hairy, and how might this relate to increased dispersal efficiency? Is there evidence of higher cleistogene production in Australia, e.g. does Burkart's (1969) 'solitary' indicate a true difference between populations in the core native range and with the Australian and New Zealand populations?

Phytoliths

The epidermis of grasses includes specialised small cells known as silica cells which occur in pairs with cork cells amongst the unspecialised ground cells, and which manufacture variously-shaped silica (SiO_2) bodies (Esau 1977). Silica deposition in these cells was thought to occur "by a passive nonmetabolic mechanism" and the silica cells lose their protoplast (Esau 1977 p. 86). However Si appears to be actively taken up by plant roots as monosilic acid and concentrated in the shoots where it is polymerised (Reynolds *et al.* 2009). The microscopic particles of hydrated silica, deposited in intracellular and/or intercellular spaces are known as opaline phytoliths in the older literature, or simply phytoliths, and are particularly abundant in Poaceae, in which a multiplicity of phytolith forms occur (Gallego and Distel 2004, Parr *et al.* 2009). Phytoliths are found in plants of other familes including Equisetaceae, some gymnosperms and dicotyledons, and other plants in the Poales, but they are most abundant and diverse in Poaceae (Thomasson 1986). Most phytoliths consist of hydrated SiO_2 (Honaine *et al.* 2006), but they also occlude plant carbon at the time of creation (Iriarte 2006, Parr *et al.* 2009). The occluded C is probably derived from internal cytoplasmic material and is highly resistant to decomposition, in some cases for >10,000 years (Parr *et al.* 2009). Higher taxa of grasses can be readily distinguished by the types of leaf phytoliths they produce (Piperno and Sues 2005) and each grass species has a characteristic phytolith assembage, determined by identification of the relative frequency of the phytolith morphotypes (Gallego and Distel 2004). These have so far been classified by shape and size into over 50 forms, including dumb-bells, crosses, elongate types and hairs (trichomes).

Zucol (1996) defined leaf phytolith assemblages in eight Argentinean *Nassella* spp., including *N. neesiana*, using cluster and principal component analyses and 49 morphological characters, and found that *N. neesiana* was grouped with *N. hyalina*. Gallego and Distel (2004) were able to define a group including *N. tenuissima* that contained phytoliths with a high frequency of dumb-bell shapes with a short central portion, straight ends, rectangular, smooth elongate hooks and and a sharp-pointed apex. Species differences within the group could also be identified and the possibility of species level identification. Honaine *et al.* (2006) found that *Nassella* spp. and *Piptochaetium* spp. have "abundant *Stipa*-type dumb-bells" and "great quantities" of rondels (truncated cones), and formed a clear group separate from the other grasses examined. They illustrated typical *N. neesiana* phytoliths: a prickle hair, prickle, dumb-bell with a long central portion and convex ends, simple lobate dumb-bell with a short central portion and convex ends, *Stipa*-type dumb-bell with a short central portion and convex ends, and dumb-bell with a spiny central portion. Honaine *et al.* (2009) illustrated *N. neesiana* rondells. Honaine *et al.* (2006) provided a chart of the relative frequency of phytolith morphotype groups for the species examined. *Inter alia*, *N. neesiana* was found to have an exceptionally high frequency of dumb-bells with a long central portion and convex ends, and of simple lobate dumb-bells, compared with the other stipoids examined. Whether there is a distinctive stipoid phytolith 'profile' has yet to be determined, "*Stipa*-type" dumb-bells also being present in members of Pooideae and Arundinoideae (Honaine *et al.* 2006 pp. 1160-1).

Phytoliths are incorporated into soil after degradation of plant tissue, and because of their resistance to decay can be used to reconstruct former plant communities and ecological history (Honaine *et al.* 2006 2009) and long-term prehistorical grassland dynamics (Iriarte 2006). They also survive and are concentrated by animal digestion, so can be extracted from dung to determine animal diets (Piperno and Sues 2005, Prasad *et al.* 2005). As fossils, they are more resistant to oxidisation than pollen (Iriarte 2006), and more taxonomically informative than grass pollen, which generally has few useful identification characters and is very similar to pollen of some other families, including Restionaceae (Thomassen 1986).

Phytoliths and silica cells undoubtedly play a major role in deterrence of herbivory (Stebbins 1986, Reynolds *et al.* 2009), both vertebrate and invertebrate, and the silica bodies are "among the few substances capable of inducing morphological changes to animal mouthparts" (Piperno and Sues 2005 p. 1128). Silicon defenses reduce the palatability and digestibility of plant tissue and increase its abrasiveness and hardness (Reynolds *et al.* 2009). Soluble Si is also involved in induced chemical defences against insect herbivore attack (Reynolds *et al.* 2009).

The phytolith profile of different plant organs (leaf, culm, root, inflorescence) differs markedly in a species (at least for *Paspalum quadrifarium*) (Honaine *et al.* 2009), suggesting adaptation to defend against the differing ranges of predators to which these organs are susceptible. Since the earliest known grasses contain a range of phytolith morphotypes similar to modern taxa, extant grasses produce much larger quantities of phytoliths than other plant taxa (Prasad et al. 2005) and chemical anti-predator defences are generally uncommon in the family, it is clear that these silica defences have played a very important role in the long history of coevolution of grasses and their predators (Piperno and Sues 2005, Reynolds *et al.* 2009). The relationships between particular plant predators and particular silica-based plant defences have been partially explored (Reynolds *et al.* 2009), with some emphasis on the functioning of trichomes in defence against insects.

Cytology

Chromosome numbers in grasses range from 2n = 4 to 2n = 263-265 (Hunziker and Stebbins 1986, Groves and Whalley 2002), with n = 6 or n = 7 most likely the primitive condition (Stebbins 1972, Tsvelev 1984), probably the former (Hunziker and Stebbins 1986). More than 80% of grasses are polyploid in origin, a larger proportion than any other large plant family, and polyploid series are common within species (Hunziker and Stebbins 1986, Groves and Whalley 2002). Hybidisation resulting in polyploidy has been very important in the diversification of stipoid taxa: Hunziker and Stebbins (1986) calculated that 91% of 250 *Stipa* spp. were polyploid, while Barkworth and Everett (1986) and Vásquez and Barkworth (2004) considered all Stipeae to be probably of polyploid origin.

Chromosomes in Stipeae are reportedly "fairly small" and "usually aneuploid" (Tsvelev 1984 p. 848), i.e. the diploid chromosome number is usually not an exact multiple of the haploid number (Johnson 1972). *N. neesiana* material from Argentina, Bolivia, Chile and Uruguay was found by Bowden and Senn 1962) to have diploid chromosome numbers of 28 and was considered tetraploid, except for one sample from Limache, Chile (Bowden and Senn 1962). The exceptional material, identified as *Stipa. neesiana* by Dr. J.R. Swallen but also referred to also as "*Stipa* sp.?", had 2n = 60. It differed morphologically from the tetraploid specimens, "but it was not possible to clarify the identification" (Bowden and Senn 1962 p. 1122). According to Moraldo (1986) *N. neesiana* is tetraploid with 2n = 44.

The lowest known chromosome count of a stipoid species is n =10 in a *Piptatherum* sp. and the highest are n = 41 and n = 48 (Barkworth and Everett 1986). In *Stipa* (*sens. lat.*) and *Oryzopsis* (*sens. lat.*) the chromosome numbers range from n = 11 to at least n = 41 (including n = 12, 16, 17, 18, 20, 21, 22, 23, 24, 32, 33, 34, 35), a situation that can be explained by recurrent amphiploidy, i.e. combinations of autopolyploidy (simple doubling of the number of chromosomes in an individual) and allopolyploidy (hybridisation of diploid and/or polyploid individuals), begining with n = 6 and n = 5 (Johnson 1972). In most European *Stipa* species that have been studied 2n = 44 (Tsvelev 1977, Moore 1982), derived through aneuploidy from a primary basic number of 2n = 22 (De Wet 1986). Of other European species, *S. capensis* Thunb. 2n = 34, 36, *S. parviflora* Desf. and *S. bromoides* (L.) Dörfler 2n = 28, and *S. gigantea* Link 2n = 96 (Moore 1982, Tsvelev 1984, Moraldo 1986). 2n = 24 in many *Achnatherum* spp. (Tsvelev 1977). Among other South American stipoids, 2n = 40 in *Jarava plumosa* (Spreng.) S.W.L. Jacobs and J. Everett, 2n = 42 and 44 in *J.ichu* Ruiz and Pavon and 2n = 40 and 44 in *Amelichloa brachychaeta* (Godr.) Arriaga and Barkworth (Bowden and Senn 1962). Of the North American species, 2n = 24 in *Piptatherum pungens* (Torrey) Dorn, 2n = 44 in *Heterostipa comata* (Trin. and Rupr.) Barkworth and 2n = 48 in *Oryzopsis asperifolia* Michaux and *Piptatherum racemosa* (Sm.) Barkworth (Barkworth 2006). *Stipa sens. str.* has a base number of 11, while the base number of *Acnatherum* is unclear but frequently cited as 11 or 12 (Vásquez and Barkworth 2004).

Among the North American *Nassella* species, n = 11 in *N. pungens* E.Desv., n = 16 in *N. tenuissima*, n = 17 in *N. lepida* (Hitchc.) Barkworth, n = 23 in *N. tucumana* (Parodi) Torres, n = 32 in *N. pulchra* (Hitchc.) Barkworth, n =35 in *N. cernua* (Stebbins and Love) Barkworth and n = 41 in *N. viridula* (Trin.) Barkworth (Johnson 1972). However *N. tenuissima* material from Argentina examined by Bowden and Senn (1962) had a diploid number of 40, different from that of Texas plants. Of the South American species, 2n = 34 in *N. hyalina*, 2n = 36 in *N. charruana*, 2n = 36 and 38 in *N. trichotoma*, 2n = 42 in *N. chilensis* (Trin.) E. Desv., and *N. exserta* Phil., 2n = 64 in *N. mucronata* (Kunth) R.W. Pohl, 2n = 66 in *N. lachnophylla* (Trin.) Barkworth (Bowden and Senn 1962). But according to Watson and Dallwitz (2005) 2n = 38 in *N. trichotoma*.

Genetic variation

Grass species often possess wide racial or ecoytpic variation within their populations, partial discontinuities of phenotypes resulting from self-fertilisation, hybrid sterility between phenotypically similar populations, and other features, including polyploidy, that tend to obscure species boundaries (Stebbins 1972). Ecotype variation is known for *N. trichotoma* in Australia (Michalk *et al.* 2002) but has not been recorded for *N. neesiana*.

Britt (2001) and Britt *et al.* (2002) sought evidence of genotypic variation in Australian populations. They compared four Victorian (Altona, Melton, Bacchus Marsh and Tarrawingee) and two New South Wales (Armidale and New England Tablelands) populations, using three molecular genetic profiling methods:

1. ITS – RFLP. Internal transcribed spacer - restriction fragment length polymorphism – a method for cutting the DNA at particular short sequences of nucleotides using restriction endonucleases – the polymorphisms in the restriction fragments are RFLPs and variation in the size of the RFLPs is dependent on the particular sequence recognised by each endonuclease. The ITS is a moderately conserved region of nuclear ribosomal DNA, and differences in its length and base pair pattern have revealed taxonomic patterns in grasses and enabled accurate scoring of their genotypes (Britt 2001).
2. ITS – PCR sequencing. Using the polymerase chain reaction (PCR) to generate large quantities of DNA to enable sequencing of the ITS region.
3. RAPD - PCR. Using PCR and random amplified polymorphic DNA (RAPD) analysis on the whole genome. The technique allows differentiation of closely related organisms or even single base changes by display of the DNA banding patterns using gel electrophoresis.

DNA was extracted from between 18 and 10 plants grown from seeds collected in each geographical area (Britt 2001 p. 21), but no indication was provided of the number of individuals sampled from each population, their spatial arrangement in the source area, or the date of sampling (Britt 2001, Britt *et al.* 2002). The plants from which DNA were extracted were grown from seed collected in a particular area, but that seed could have been harvested from a single mother plant, and even if multiple mother plants were sampled a variable proportion of the seed from each would be cleistogamous. Thus all the individuals from which DNA was extracted for a particular area could have been genetically identical because of inadequate population sampling.

No variation was found in the size of the ITS region (650 base pairs) or in the ITS-RFLP patterns tested. ITS sequencing revealed uniformity within the plants analysed from a particular area, but differences between plants from different areas, unrelated to their geographical proximity. All areas had shared homologies above 90%, suggesting conspecificity, except for Bacchus Marsh and Tarrawingee populations, but no one else appear to have suggested these populations are not *N. neesiana*. 98% homology – suggestive of convarietal status – was shared only by Altona and New England samples (Britt 2001). Jacobs *et al.* (2000) also analysed sequence data of the ITS region of nuclear rDNA and found no variation within the species tested, however, again, the number and intra-population source of their samples were not published. Britt's (2001) RAPDs showed inter- but not intra-area variation but no consistent area groupings. Comparison of population differences using the two different methods produced two inconsistent 'distance tree' structures. ITS data indicated that the Melton population was most similar to *N. leucotricha* (Britt *et al.* 2002), suggesting the possibility that some hybridisation may be occurring. Jacobs *et al.* (2000) indicated that they are sister species.

Britt (2001) and Britt *et al.* (2002) concluded that Australian *N. neesiana* possesses large genetic variation between areas (a number of subspecies/varieties – the terms were used interchangably – are present), that this may have arisen locally, and that local populations have no variation, so must have arisen via cleistogenes or seeds fertilised only by local pollen.The latter argument is flawed because Britt (2001) failed to demonstrate that the real population variation in each area was sampled. It is also based on a misunderstanding of the breeding system (see Britt 2001 pp. 86-87): all the panicle seed is not necessarily cross-fertilised (see the observations of floral anatomy by Burbidge and Gray (1970) and Vickery *et al*. (1986) above), the basal spikelets in a panicle are more or less cleistogamous, while cleistogamous spikelets can be found anywhere in the panicle. In order to reach such a concluison a methodology was required that ensured only the sampling of DNA from chasmogamous seeds. The local populations could also be the offspring of separate founder events involving different South American source populations, with the lack of local polymorphism (if it is not an artefact) resulting from genetic bottlenecking.

As with most such studies these appear to be rather random probings of the genome, the genetic material examined is not necessarily expressed in the phenotype, nor is its functional role known. Future molecular genetical work in this area should start with an examination of South American populations ascribed to particular varieties and should also be integrated with a study of morphological variation, as suggested by Britt (2001).

Phenology, growth and productivity

Within the revised Raunkiaer plant life form spectrum (Mueller-Dombois and Ellenberg 1974), *N. neesiana* is classified as a hemicryptophyte (a perennial herb with periodic shoot reduction), subtype ‘caespitose graminoids’ (bunched or circular shoot arrangement with shoots more or less at the soil surface) and probably as 3.103 “sparingly evergreen during unfavourable season”.

N. neesiana grows predominantly over the coooler months (Muyt 2001) with vegetative growth mainly from autumn to spring (Snell *et al.* 2007). Storrie (2006) considered it “one of the few” major weedy grasses in New South Wales “that produces green feed in winter”. In Argentina both agronomists and landholders agreed that it produced a large amount of good livestock feed during winter (Gardener *et al.* 1996b). High rainfall in spring promotes panicle proliferation (Cook 1999). Flowering and fruiting occurs from September to March in South America (Zanin 2008). In south-eastern Australia flowering occurs mainly during spring and early summer (September to December), but can occur at other times of the year when moisture and temperature conditions are suitable (Snell *et al.* 2007).

At Inverleigh, Victoria, Gaur *et al.* (2005) recorded plants in the vegetative phase to 3 October 2003 and 1 October 2004, flag leaf swelling over the developing panicle on 13 October 2003, spiky stems on 18 October 2004 and full panicle emergence on 27 October 2003 and 28 October 2004. Pritchard (2002) recorded that plants at Laverton North had panicles still concealed in the sheath on 3 October 2000 and all the foliage was green, and that on 15 November there was a dense covering of emerged panicles. In Italy *N. neesiana* flowers and fruits from May to July (Moraldo 1986) approximately 6 months out of phase with Australia, where bolting generally begins in mid October and panicle seed drops in mid December (D. McLaren in Iaconis 2006b). Slay (2002c) reported a similar phenology in New Zealand: elongation of reproductive tillers in spring with the main flush of tiller production from mid-September to mid-October, flag leaf swelling in mid-October, then 24 days between the first emergence of the panicle and anthesis. Slay (2001) found the period from the boot stage to anthesis was 36 days and from anthesis to 100% viability of seed was 33 days.

Slay (2001) identified: three phases of seeding: 1. basal cleistogene production during vegetative growth of the tiller, initiated in autumn and completed in spring before anthesis of panicle flowers; 2. cleistogamous and chasmogamous seed production in the panicle; 3. cleistogene production on the stems, initiated before anthesis of panicle flowers and completed after panicle seed maturation.

In Victoria stems are brown and breaking down and cleistogenes form in mid to late summer, and by the end of February most stems have cleistogenes (McLaren in Iaconis 2006b). In New Zealand old culms are easily broken by late March (Slay 2001). The inactive period from mid summer to the time of autumn rain has been inadequately documented and summer dormancy appears to have been widely assumed. However flowering is indeterminate (Grech 2007a) and plants are known to flower in response to summer rain (Bedggood and Moerkerk 2002). Senescence of foliage and cessation of leaf growth occurs in all grasses in response to drought, but truly summer-dormant grasses display these traits despite summer irrigation (Norton *et al.* 2008). Across the range of pasture grass taxa there is a continuum of responses from full dormancy to non-dormancy, and the intensity of summer dormancy can be assessed by simulating a mid summer storm in the midst of drought, and measuring subsequent herbage production or senescence (Norton *et al.* 2008). Full dormancy is supposedly characterised by complete cessation of growth, full herbage senescence and dehydration of young leaf bases, whereas senescence and partial growth cessation may be just a dehydration avoidance strategy which can be expressed in any season under conditions of soil moisture stress. The possession of true summer dormancy is supposedly critical for pasture grass persistence in the drought prevalent pastures of south-eastern Australia, so a number of commonly utilised exotic grass cultivars have been assessed for this characteristic (Norton *et al.* 2008). Assessments of weedy and native Poaceae, including *N. neesiana*, would be informative.

Average production in New England pasture was 2.3 t ha^{-1} y^{-1}(Gardener *et al.* 2005). Slay (2001) recorded production of 5.5±0.5 kg ha^{-1} of dry matter per day during the first 48 days after mowing in November in New Zealand. Grech (2004) found that plants that were regularly clipped to simulate grazing produced more digestible growth (significantly more crude protein, metabolisable energy and digestible dry matter) than unclipped plants. N fertiliser (100 kg ha^{-1} in two applications) increased the feed value only at the seedhead stage.

Crude protein levels of green leaves (in South America) were 6.3-18.3% (Gardener *et al.* 1996b). Crude protein levels of winter foliage regrowth after clipping in Australia were 12.7-16.6% and digestible dry matter of green leaf material was c. 60% (range 58-66%), compared to *Festuca arundinacea* with crude protein of 13.0-18.8% and digestible dry matter 62-69% (Gardener, Storrie and Lowien 2003, Gardener *et al.* 2005). Culm material had a crude protein content of 4.5%. New Zealand data indicates a crude protein level of green leaves of plants in the vegetative phase of 14.5%, while leaves of plants early in the flowering stage had a crude protein level of 6.4%. The metabolisable energy value of vegetative phase leaves was 7.7 in early summer and of 7.5 in early flowering. Comparable crude protein and metabolisable energy (ME) levels were 9.9% and 11 for *Lolium perenne* L., while ME values in summer 1991 for *D. glomerata*, *L. perenne*, *Phalaris aquatica* L. and *Festuca arundinacea* were 8.3, 7.5, 8.4 and 9.3 respectively (Slay 2001, Slay 2002a). The minimum maintenance level of crude protein for livestock is 7% (Slay 2001). Gardener *et al.* (1999 p. 10) compared N. neesiana productivity and feed analysis with *Festuca arundinacea*, and Grech (2007a) compared it with *Dactylis glomerata*.

Flowering and fruiting

According to Barkworth and Torres (2001 p. 462) and Barkworth (2006) Australian populations "do not appear to set seed in the exposed inflorescences". These erroneous statements are possibly based on a few herbarium specimens collected during drought conditions.

Plants in their first year of growth do not flower (Sethu Ramasamy pers. comm. 13 June 2007). Benson and McDougall (2005) provided the primary juvenile periods of many other grasses but failed to provide one for *N. neesiana*. No definitive published information appears to be available on the juvenile period.

The factors that trigger a shift from vegetative to reproductive growth, are partially known. Low winter temperatures are necessary for vernalization (Gardener *et al.* 1996b). (See Sinclair 2002 for the variety of factors involved in floral inducation in grasses). Rainfall appears to play a role. In southern Victoria bolting generally commences in mid October (D. McLaren, 26 October 2006).

According to Gardener *et al.* (2003a) the main 'flowering' period is November to February in Australia and October to January in South America (based on herbrium specimens) with some flowering as late as May. Near Guyra on the Northern Tablelands of NSW 'flowering' commenced between early October and early November and finished between early March and late April (1994 and 1995, Gardener *et al.* 2003a). Two separate flowering periods were observed near Guyra in 1995, but not in 1996 or 1997. However Gardener *et al.* (2003a, etc.) had a very broad, inaccurate definition of 'flowering time' covering the period from the first emergence of the panicle from the leaf sheath to the time when the last mature seeds were dropped.

Burkart (1969) may be more accurate, giving the flowering period in Argentina as October and November. In south western Europe, flowering occurs from May to July (Verloove 2005). Slay (2002c) is pehaps most specific, stating that anthesis (flowering) occurs around mid-November in New Zealand, while Slay (2001) observed flowering over a period of approximately 17 days from mid to late November in an infestation at Waipawa, New Zealand. In Australia, according to Cook (1999), panicle production occurs from late spring to early summer, sometimes with a secondary, much less prolific, flush in autumn. Snell *et al.* (2007 p. 8) noted that there is "a second panicle seeding period during autumn" in northern NSW. Bedggood and Moerkerk (2002) state that flowering occurs from early October through to March or April and that panicle seed are produced in autumn in northern areas. In the ACT *N. neesiana* usually flowers from November to February (ACT Weeds Working Group 2002). In South Australia flowering or fruiting inflorescences are present in November and December (Jessop *et al.* 2006). Flowering in Victoria is mostly October to February (Walsh 1994) and in Australia generally from spring to early summer with occasional plants to April (McLaren, Stajsic and Iaconis**.** 2004).

According to the ACT Weeds Working Group (2002) and Ens (2005 citing Ens 2002a) *N. neesiana* " has the ability to flower all year round" given favourable environmental conditions. Bedggood and Moerkerk (2002) recorded that it will flower in response to summer rain. High density of tiller production (and thus seed production) appears to require consistent rainfall during the reproductive period (Gardener *et al.* 2003a). Slay (2002c) noted that a second flush of panicles can be produced if the normal late spring panicles are removed by mowing or grazing, and that isolated plants are more likely to have a secondary flowering period than plants in dense populations.

The flowering periods recorded mostly appear to apply to large populations in broad areas. No information seems to be available on site specific aspects of flowering, the proportion of the population that has a particular floral phenology, or the individual variation of a single plant. There is no indication of the duration of flowering on a particular panicle or the sequence and timing of individual flower opening and closing on a panicle. The time of day that the flowers open and their period of opening do not appear to have been recorded. Information about the timing of fertilisation, the period of receptivity of the stigma, the period between pollination and fertilisation and between fertilisation and embro development have rarely been determined for any plants (de Tirquell 1986) and are unknown for *N. neesiana*.

The period from flowering to seed maturation is about 7 weeks (Liebert 1996). According to Slay (2002c), seed became viable within 8 days of flowering, 76% of seed was still 'soft' after 14 days, with 60% viable after 22 days. In New Zealand most seed reaches full maturity between late December and early January and is quickly shed, but seed produced on sub-panicles that emerge from stem nodes matures later (Slay 2002c).

The seed is a velate caryopsis, i.e. the caryopsis falls free of other spikelet parts (Sendulsky *et al.* 1986). Panicle seed matures and is shed from mid to late summer (Gaur *et al.* 2005), generally in mid December in southern Victoria (D. McLaren, 26 October 2006). Near Guyra on the Northern Tablelands of NSW most seeds matured between late December and mid-February (1994 and 1995, Gardener *et al.* 2003a), and was generally shed in December-January (Gardener *et al.* 2003ba). Slay (2001) noted that panicle seed at one site was almost all shed simultaneously in early January 2001. Most panicle seed has been shed by late February in NSW (Duncan 1993) and this is the case in Victoria (Liebert 1996). Stem cleistogene seed from ensheathed inflorescences matures later than panicle seed, in February (Slay 2002a). In the Melbourne region in 2006 under drought conditions, most panicle seed was shed in November-December, largely in late November-early December (pers. obs.). Puhar (1996) noted that seed began to drop at St Albans, Victoria, in early January 2006.

Slay (2002c) modified the Feekes Scale used to define the growth stages of cereals to classify the reproductive growth stages of *N. neesiana* (Table 2).

Table 2. Modified Feekes Scale for *Nassella neesiana* panicle seed (adapted from Slay 2002c). Point 10 on the scale was called the 'boot stage' by Pritchard (2002).

Feekes Scale	**Description of stage for N. neesiana**
10	Flag leaf completely grown out, sheath swollen [boot stage]
10.1	Tips of awns emerged from swollen sheath
10.2	25% of heads emerged
10.3	50% of heads emerged
10.4	75% of heads emerged
10.5	100% of heads emerged; panicle free of sheath
10.5.1	Beginning of anthesis
10.5.2	Anthesis complete to top of panicle
10.5.3	Anthesis finished at base of panicle
10.5.4	No unopened flowers, stamens dropped, some seed developing
11.1	Milky ripe (milky dough stage)
11.2	Mealy ripe, seed contents soft but dry
11.3	Seed firm, chalky
11.4	Seed shedding

Tillers usually die after flowering and fruiting (as for grasses in general - Wheeler *et al.* 1999) usually within about 2 months (personal observations). In southern Victoria the stems have usually browned off by mid January and begin to break down (D. McLaren, 26 October 2006). The dry culms can remain standing for up to 6 months (Gardener *et al.* 1999) and generally persist for several months before falling over and forming a dense mat that shades underlying vegetation (Gardener *et al.* 2005).

Cleistogene production

Separate hormonal influences appear to independently control panicle seed and cleistogene production (Connor *et al.* 1993). Stem cleistogenes occur at two different periods:1. during the vegetative growth stage of the tiller - initiated in spring as single spikelets under the leaf sheaths of young shoots, reaching maturity by the time of emergence of the aerial infloresence, and released when the leaf sheaths weaken or rupture; and 2. during the flowering period, resulting in cleistogenes tightly enclosed by the sheath and prophyllum (Connor *et al.* 1993). According to Slay (2001 2002c) basal cleistogenes are initiated after seedlings establish and on older plants in autumn, and are maturing or mature by the time that panicle production and flowering commences in mid spring. Stem cleistogenes are initiated as the stem elongates, and ripen by February. In southern Victoria, non-basal stem cleistogenes have formed by the time that panicle seed is dropped and are possibly stimulated to mature by panicle seedfall, and most stems have mature cleistogenes by the end of February (D. McLaren, 26 October 2006, based on observations of Shiv Gaur). Slay (2001) observed that the non-basal stem cleistogenes are immature when panicle seed is dropped, especially at the top node. Gaur *et al.* (2005) found that non-basal cleistogenes mature, and are shed, after the fall of panicle seed.

Dyksterhuis (1945) found a similar phenology with *N. leucotricha*: axillary cleistogenes with endosperm in the dough stage were present before anthesis of panicle flowers or before any panicle production. Seedlings were able to produce cleistogenes in the dough stage by the age of 6 months, and cleistogene seedlings 9-10 months old, that were clipped to a height of 38 mm every two weeks, produced very few tillers and on average less than half the cleistogenes (range of 0-3 cleistogenes per seedling) of unclipped seedlings (range of 2-5) (Dyksterhuis 1945).

Slay (2002c) noted that the ability of an autumn germinating seedling to produce cleistogenes within 6 months means that the species can survive as an annual.

Distribution

South America

Map: Gardener *et al.* (1996b) and Gardener (1998); records between 26º and 40º S from two herbaria and literature.

Argentina, Bolivia, Brazil, Chile, Ecuador, Peru, Uruguay (Torres 1997, Barkworth and Torres 2001, Martín Osorio *et al.* 2000, Barkworth 2006). It is also known from Paraguay (Ramirez 1951,USDA ARS 2006, Zanin 2008) although presence in that country was considered doubtful by Barkworth and Torres (2001) and Barkworth (2006). Longhi-Wagner and Zanin (1998) used the name *Stipa setigera* C. Presl. for *N. neesiana* ("syn. *S. neesiana* Trin. and Rupr.") and recorded it from Paraguay and Columbia in addition to the countries already cited.

Considerable uncertainty remains in the understanding of the South American distribution due to confusing use of specific names and differences of opinion about the actual identity of specimen material. Barkworth and Torres (2001), who did not refer to Longhi-Wagner and Zanin (1998), considered *S. setigera* to be a synonym of *N. mucronata* (Kunth.) R.W. Pohl, and the two *S. setigera* varieties *hispidula* and *glabrata* to be synonyms of *N. neesiana*, the latter synonymies established by Hitchock in 1925 (Torres 1993). They listed *N. mucronata* as present in Columbia, and did not list *N. neesiana* for that country. Zanin (2008) affirmed the opinion of Longhi-Wagner and Zanin (1998) that *N. neesiana* is present in Paraguay, but cited a single specimen that Barkworth and Torres (2001) considered to be *N. argentinensis* (Speg.) Peñail. Furthermore, Barkworth and Torres (2001) did not list Brazil, Paraguay or Uruguay as part of the range of *N. mucronata*, so it appears likely that the entity Longhi-Wagner and Zanin (1998) treated as *S. setigera* and considered to be the same as *N. neesiana* was not the same entity as the *S. setigera* assigned to *N. mucronata* by Barkworth and Torres, but was equivalent to the *N. neesiana* of Barkworth and Torres. *N. mucronata* is not recorded from Brazil (Torres 1997, Barkworth and Torres 2001), but it remains unclear how Longhi-Wagner and Zanin (1998) treated extra-Brazilian literature records of *S. setigera sens. lat.* and whether they considered which of them were *Nassella mucronata*. Further complicating interpretation, Barkworth and Torres (2001) listed Portugal, Spain, France and Italy as countries to which *N. mucronata* had been introduced, but Verloove (2005) found that the name *S. setigera* had been misapplied to these European records, i.e. the specimens were misidentified, and were in fact *N. neesiana*, not *N. mucronata*, and that this probably also applied to Mexican *S. setigera*, which was also *N. neesiana*. Given this confusing situation, the entities actually present in Columbia, and Mexico, and perhaps Brazil appear to require clarification.

Gardener *et al.* (1996b) stated that in South America as a whole *N. neesiana* had a latitudinal range of at least 22-51º S. Gardener (1998), corrected this to 26-40º, stating that the published record from Chile at 50º 53' S by Soto (1984) was most likely a misidentification of *Stipa brevipes* Desvaux. However even the wider latitudinal range fails to cover either Ecuador or Peru, and excludes Bolivia except for a small area in the extreme south.The narrower range excludes all of Bolivia, most of Paraguay and indicates the absence of herbarium and literature records from most of southern Argentina. In southern South America it has a continuous distribution from near the coast of Chile, across the Andean zone and the pampas of Argentina through Uruguay to the Paranaense (south east Brazil) region (Longhi-Wagner and Zanin 1998, as *Stipa setigera*). In tropical and subtropical South America it occurs in highland enviroments (Martín Osorio *et al.* 2000) north along the Andes to Ecuador, to c. 1.5°N. Columbia and Venezuela are probably the only South American countries in which *Stipa sens. lat.* has been recorded (Columbia has 3 spp. and Venezuela 5: Longhi-Wagner and Zanin 1998) but in which *S. neesiana* has not. However its presence in the province of Carchi of Ecuador suggests that it may well occur in south-western mountains of Columbia.

In Argentina it is found in the following provinces - in the east (Misiones, Corrientes, Entre Ríos), the centro del pais (Buenos Aires, Córdoba, San Luis, La Pampa, Santa Fé), the west (Mendoza, San Juan), the north (Chaco, Formosa), the northwest (Jujuy) and the northeast (Catamarca, La Rioja, Salta and Tucumán) (Caro 1966, Gardener *et al.* 1996b, Torres 1997, Gardener 1998). It is present in the Ventania land system in the south-west of Buenos Aires Province, north of Bahía Blanca (Amiotti *et al.* 2007). Large populations are common in the central west around the Sierra de Córdoba (Sierras Pampeanas) (Anderson *et al.* 2002), where the grasslands are at moderately high altitudes (Soriano *et al.* 1992). It is a common species in the pampas, a vast, humid, fertile plain stretching from the Rio de La Plata and the Atlantic coast west towards the Andes, occupying the provinces of Buenos Aires, parts of Entre Rios and southern Santa Fé, into western San Luis, northern La Pampa and southern Córdoba provinces (Soriano *et al.* 1992). In Santa Fe province it is a characteristic species of the Pampean phytogeographical province flechillar Stipeae community in Rosario County in the south of the province, and in San Cristóbal County in the central west of the province is the dominant species of another flechillar grassland community of the Espinal phytogeographical province (Feldman *et al.* 2008). In Entre Ríos it was recorded by Zucol (1996) from Santo Ana, Dpto. Federación; Puerto Yerúa, Dpto. Concordia; Dpto. Villaguay; San José, Dpto. Depto. Colón; Colonia Elia, Dpto. Uruguay; Dpto. Gualeguay; and Camino a Puerto Unzué, Dpto. Gualeguaychú. It is not a dominant grass in the semiarid southern Caldén District near Gaviotas, west of Bahía Blanca (Distel 2008), nor is it one of the major grasses in the whole Caldenal, a 10 million ha semi-arid region extending from the Atlantic coast south of Bahía Blanca north west to the Sierra de Córdoba, to the south and west of the Humid Pampa (Fernández et al. 2009). Martín Osorio *et al.* (2000) mention its presence in Patagonia (apparently citing Rivas Martínez) but other references to its presence there have not been found. In Uruguay it is common in pastures (Gardener *et al.* 1996b citing Rosengurtt *et al.* 1970) with records in the south, north-west and north-east (Gardener 1998) including Florida (Bowden and Senn 1962) and Montevideo (Barkworth *et al.* 2007). In Paraguay it was collected in 1989 at Chacoí in the far south of the province of Presidente Hayes, near the border with Central province, in the vicinity of Asuncion (Zanin 2008), east of Formosa province in Argentina. But it possibly occurs also in southern Paraguay, being known from close to the border in the states of Misiones and Corrientes in Argentina (Gardener *et al.* 1996b, Gardener 1998). Temperate grassland is present in Paraguay only in small area of the far south-east (Overbeck and Pfadenhauer 2007) in the vicinity of Encarnacion, immediately to the north-west of Misiones. In Brazil it is found in the south (McLaren, Stajsic and Iaconis. 2004), in the states of Rio Grande do Sul and Santa Catarina, where it is the most common species of *Stipa sens. lat.* (Longhi-Wagner and Zanin 1998). In Uruguay and Brazil it is mostly found in the campos, a temperate subhumid grassland formation similar to the Argentine pampas, covering most of Uruguay and the southern Rio Grande do Sul of Brazil (Soriano *et al.* 1992). In Brazil it is considered a characteristic species in the Pampa biome of the southern Rio Grande do Sul (Overbeck *et al.* 2007 – as "*Stipa setigera* C.Presl."). It was not recorded from a humid subtropical grassland site in the Atlantic Forest biome on Morro Santana (30°03'S) by Overbeck *et al.* (2006). The most southerly distribution on the continent is in Chile, where it is found over a wide latitudinal range, at least from c. 26º 30' to 40º S (Gardener *et al.* 1996b, Gardener 1998). In continental Chile it is found in the Metropolitan Region (Santiago 33-34°S) and Regions IV (29-32°S), V (32-33°S), VIII-IX (35-39°S) and X (39-44°S) (Baeza *et al.* 2007). It was collected at Concepcion (36°50'S) by Senn (Bowden and Senn 1962) and has been recorded on Robinson Crusoe Island (Más á Tierra) (33º 38' S 76º 52' W) (Nelis 2006, Baeza *et al.* 2007) and Alejandro Selkirk Island (Más Afuera), in the Juan Fernández group, c. 650 km west of mainland Chile, where it is considered to have been introduced (Baeza *et al.* 2007). It is known from Valparaíso (the types of *S. longiflora*) and near Santiago (the type of *S. trachysperma*) (Barkworth *et al.* 2007). In the northern part of its South American range its is found at high altitude. In Bolivia it is known from La Paz (Martín Osorio *et al.* 2000) and was collected at Cochabamba (17°26'S 66°10'W) by Senn (Bowden and Senn 1962). In Ecuador it is also native to the Andean region, at altitudes of 3000-3500 m in the Provinces of Carchi (c. 1.5° north of the equator near the Columbian border) and Canar (Clark *et al.* 1999-2008).

The type of var. *fernandeziana* is from the Juan Fernández Islands of Chile (Barkworth *et al.* 2007). Vars. *formicarioides*, *gracilior* and *virescens* are endemic to Argentina, vars. *hirsuta* and *longiaristata* are recorded from Argentina and Uruguay, and var. *neesiana* is recorded from Argentina, Bolivia, Brazil, Chile and Uruguay (Zuloaga *et al.* 1994). Populations in north-eastern

Argentina, in the provinces of Chaco, Corrientes and Misiones, are possibly not var. *neesiana* (Gardener 1998). The specimen from Paraguay was not assigned to a variety by Zanin (2008).

Introduced range outside Australia

Europe, first found in Europe in France by Touchy in 1847 at Port Juvenal, Montpellier; early records from imports on hides and wool (Hayward and Druce 1919). Mediterranean (unspecified, Jessop *et al.* 2006); occurs "from time to time, particularly in the Mediterranean region" (Martinovský 1980); believed to be an unintentional introduction to south-western Europe "apparently ... absent as naturalized ... from the rest of Europe" (Verloove 2005). Not recognised as present in Europe outside the British Isles and the Canary Islands and Madiera by Weber (2003).

British Isles: Weber (2003) considered it to be not invasive in natural areas nor solely a weed of agroecosystems. Scotland: a wool-alien first found on the banks of the River Gala below the town of Galashiels, County Selkirk by Ida Hayward in 1916 (Hayward and Druce 1919); now extinct in that area (Vines 2006); recorded near wool factories (Bourdôt and Hurrell 1987a).

England: found on a rubbish heap at Mortlake, Surrey, in 1916 (Hayward and Druce 1919); sometimes more or less naturalised in the south east, scattered in England (Stace 1997); "certainly" naturalised (Gardener 1998); first recorded at Mort Lake (sic) in 1916, Kirkheaton in 1960, Mossley and Mauldenin 1965, Flitton in 1969 and Ware in 1988 (Gardener 1998).

Portugal: including Azores (Madiera) (Martín Osorio *et al.* 2000, Verloove 2005), first recorded on Madiera in 1970 (Gardener 1998) and known from Coimbra on the Iberian Peninsula (Vàzquez and Devesa 1996 as *N. mucronata*).

Spain: including Alt Empordà, Rossellò near Lleida (Font *et al.* 2001) and Gerona in Catalonia (Verloove 2005), Madrid (Vàzquez and Devesa 1996 as *N. mucronata*) and the Canary Islands, specifically Gran Canaria, Gomera and Tenerife (Martín Osorio *et al.* 2000, Sans-Elorza *et al.* 2005, Verloove 2005); "becoming naturalised" (Scholz and Krigas 2004, p. 78); not considered an "established alien" in continental Spain (Gassó *et al.* 2009). First detected in the Canaries in May 1964 by J. Lid in the dominion of Monte Verde de Anaga on the island of Tenerife (Martín Osorio *et al.* 2000). Distribution maps for the Canary Islands and the Parque Rural de Anaga on Tenerife were provided by Martín Osorio *et al.* (2000).

France: including Corsica (Martín Osorio *et al.* 2000, Verloove 2005), where it rapidly proliferated (Font *et al.* 2001); "introduced into southern France" (Barkworth 2006); "becoming naturalised" (Scholz and Krigas 2004 p. 78); recorded near wool factories (Bourdôt and Hurrell 1987a); adventive in the Montpellier region, introduced with wool and "*plus et moins naturalisées ... dans des stations naturelles*" (Thellung 1912 p. 654), including Port Juvénal 1847-1877, Montplaisir 1877, Lodève 1877 and Bèdarieux 1894 (*op. cit.* p. 94), introduced to Lodève in wool (*op. cit.* p. 614); present in the neighbourhood of Port Juvénal "for a long period of years in the [wool] drying yards at Montplaisir near Lodève and Bèdarieux on the river Orb, both in the Hérault" in the 18th and 19th centuries, and in 1909 on beaches away from factories below St Hélène and Caras at Nice (Hayward and Druce 1919 p. 228). First recorded at Lodeve in 1847 (Gardener 1998) or 1877 (Thellung 1912), Montpellier in 1894 (Gardener 1998) and Nice in 1909 (Thellung 1912, Gardener 1998).

Germany: adventive in Berlin and Anhalt (Thellung 1912); recorded at Rodleben wool factory at Rosslau, Anhalt, in 1910 (Hayward and Druce 1919); recorded near wool factories (Bourdôt and Hurrell 1987a).

Italy: Map: Moraldo (1986 p. 237). 'Adventitious naturalised' in grassy areas (Moraldo 1986 p. 217); "becoming naturalised" (Scholz and Krigas 2004 p. 78). First reported on the banks of the Polcervera near Genoa, 1904, at a tan works that had hides from Argentina (Hayward and Druce 1919, Moraldo 1986), then in other localities in Liguria (Moraldo 1986); first recorded at Bordighera in 1910 (Gardener 1998). 'Most recently' in Rome at Villa Ada, first collected in 1970 (Moraldo 1986 p. 217). Rome and Liguria (Verloove 2005); recorded near wool factories (Bourdôt and Hurrell 1987a).

Greece: East Macedonia, Nomos and Eparchia of Thessaloniki, Thessaloniki city "mowed and watered lawn of a traffic island within the University campus, about 100 individuals in total, fragmented in patches of 10-20 individuals each", herbarium specimen 22 May 2002 (Scholz and Krigas 2004 p. 78).

South Africa (Gibbs Russell *et al.* 1985, Wells *et al.* 1986), "threatens to invade disturbed grassland areas from the Cape into the Transvaal" (Wells and Stirton 1982); first found in Barkley East in 1941, "emerging as serious weed" and common in the Eastern Cape province (Gardener 1998 p. 12), also in Free State province, at altitudes of 600-1700 m (Germishuizen and Meyer 2003). First recorded from Grahamstown and Bosberg in 1968, Adelaide in 1977, Ladybrand in 1988 and Sterkstroom at an unknown date (Gardener 1998).

New Zealand: Jacobs *et al.* (1989 Fig. 2) and Slay (2002a) provided country maps. First recorded in 1940 by H.H. Allan, with the earliest specimen undated, but probably collected in the late 1920s in Auckland (Jacobs *et al.* 1989, Edgar et al. 1991). A very restricted, discrete distribution. Limited to about 1500 ha of pasture in Marlborough and smaller areas in Hawkes Bay and Auckland (Bourdôt and Hurrell 1989a); 3000 ha in Marlborough by 2001, 600 ha infested in Hawkes Bay by 2002 (Slay2002). North Island: Auckland (first recorded during the late 1930s, "a few plants still occur today in a public domain at Western Springs" (Bourdôt and Ryde 1986) a "picnic area" and "a railway enthusiasts station" (Slay 2002a p. 11)), Waitakere Ranges, Waipawa (central Hawkes Bay) (Jacobs *et al.* 1989, Edgar *et al.* 1991, Edgar and Connor 2000); first collected probably in the late 1920s in the Waitakare Ranges, and c. 1962 at Hawkes Bay (Connor *et al.* 1993), although the Waipawa infestation possibly may have arisen from contaminated seed from Marlborough sown in the early 1950s (Slay 2002a); an estimated total of 600 ha infested in Hawkes Bay (Slay 2002a). South Island: Marlborough (roadsides and pastures near Blind River, Seddon and Lake Grassmere) (Jacobs *et al.* 1989, Edgar and Connor 2000), near Blenheim Airport and farms at Renwick (Connor *et al.* 1993), with first occurrence anecdotally dated to about 1930 (Bourdôt and Hurrell 1989a) but said to be first found there about 1945 (Bourdôt and Ryde 1986). 1n 1986 it was present on 7 farms and about 30 ha at Waipawa, with isolated plants over up to 1 km along the Waipawa River, and at Blind River it was present on at least 15 farms, with c. 100 ha densely infested (Bourdôt and Ryde 1986); recently located in the Awatere valley 33 km from Blind River (Slay 2002a). The Auckland and Marlborough-Hawkes Bay populations are distinct forms, differing in a few characters, and represent separate provenances (Connor *et al.* 1993). The Auckland material has long hairy laminae and lemma nerves, with hairs on the main lemma nerve almost reaching the corona (Jacobs *et al.* 1989). Weber (2003) considered it to be not invasive in natural areas or solely a weed of agroecosystems.

USA: once found on ballast dumps in Mobile, Alabama (Hitchcock and Chase 1971, McLaren *et al.* 1998, McLaren, Stajsic and Iaconis 2004), first recorded in 1935 (Gardener 1998), but "no recent collections" (Barkworth 1993) and "has not persisted" (Barkworth 2006), although it is currently mapped as naturalised in Mobile County (USDA NRCS 2006, Zipcode Zoo 2006).

Mexico: (Zipcode Zoo 2006); several records, earliest 1896 (Verloove 2005). Verloove noted the widespread misapplication of the name *Stipa setigera* (= *Nassella mucronta*) to *N. neesiana* in Europe and apparently considered Mexican material had also been misidentifed. *N. mucronata* was recorded as widespread in Mexico by Reyna and Barkworth (1994) and present in Mexico by Barkworth and Torres (2001), but these authors did not recognise the presence of *N. neesiana* in that country.

South America: Introduced prior to 1921 to the Juan Fernandez Islands of Chile, where well established (Baeza *et al.* 2007). Probably introduced elsewhere in South America, but the native range is difficult to determine.

Australia

Maps: Walsh (1994 - Victoria), Liebert (1996 - Victoria), McLaren *et al.* (1998 - Australia), Gardener (1998 all known Australian records, plus dates of important regional distribution points), Thorp and Lynch (2000 - Australia), ARMCANZ *et al.* (2001, Australia, with distribution points for each decade from the 1930s), Bruce (2001- mainly natural temperate grassland sites in the ACT), Mallett and Orchard (2002), Frederick (2002 - North Central Region, Vic.), Ens (2002a - Cumberland Plain, Sydney), McLaren *et al.* (2002b – south-eastern Australia, based on a survey of land owners and managers in areas thought likely to be infested and including absence data), Jim Backholer, DPI Victoria (2006 – Australia, reproduced in Snell *et al.* 2007and below as Fig. 3). The grid map of Thorp and Lynch (2000) allowed for display of areas of low, medium and high density but no high density areas were shown; the distribution displayed included only Victoria and a small area of south-eastern South Australia and was based only on records provided by Primary Industries and Resources South Australia and the Victorian Department of Natural Resources and Environment. Data consisted of 0.5° cells for South Australia and 0.25° cells for Victoria. The most recent and most comprehensive national map is that produced by Backholer in September 2006 for the National Chilean Needle Grass Taskforce (Fig. 3).

Anderson *et al.* (2002) noted that there were no published estimates of the area of Australia infested. McLaren, Weiss and Faithfull (2004) noted that there were also no published records of the area infested for the States in which it occurred. By surveying landholders in areas known to have *N. neesiana* populations in Victoria, New South Wales and the Australian Capital Territory, McLaren *et al.* (2002b) determined that infestations were dispersed over an area of over 4 million ha and that the plant was still actively dispersing in Victoria.

Distribution in the States and Territories of Australia is summarised below, and more detailed records are provided in the following section on the history of the plant's dispersal in Australia. *N. neesiana* was not recorded from the Australian Alps by McDougall and Walsh (2007).

Victoria: Northcote - first Australian record 1934 (McLaren, Stajsic and Iaconis. 2004); widespread in the Port Phillip, Corangamite, Glenelg-Hopkins, North Central, Goulburn and North East Catchment and Land Protection Regions with scattered records in West Gippsland and Wimmera Regions.

New South Wales: Glen Innes - first NSW record 1944 (McLaren, Stajsic and Iaconis. 2004); Central Coast, Northern Tablelands including Glen Innes, Guyra (Duncan 1993), Tenterfiled, Emmaville (Gardener 1998), Southern Tablelands (Wheeler *et al.* 1990) including Bungendore (Eddy *et al.* 1998), North West Slopes (Storrie and Lowien 2003), Cenral West Slopes (data points in map in McLaren *et al.* (2002b); widespread on roadsides in the Sydney region (bounded approximately by Rylstone, Singleton, Nowra and Taralga) (Carolin and Tindale 1994). 16 sites on the Cumberland Plain, Sydney region (Ens 2002a), first recorded in the Cumberland Plains at Mount Annan Botanic Garden in 1989 (Benson and von Richter 2009); within the Sydney region mainly in Western Sydney (Benson and McDougall 2005); Balranald (Sheehan 2008).

Australian Capital Territory: near Burbong "from where it may spread downstream along the Molonglo" River (Burbidge and Gray 1970). Found at 82% of sites investigated in the Canberra area in 2000-01(Bruce 2001); extensive additional sites detected in 2002 (Sharp 2002). Currently very widespread and a major component of suburban 'nature strips' and lawns (S. Sharp and J. Connelly pers. comms. 2006, personal observations).

South Australia: first recorded in 1988 (Jessop *et al.* 2006) at Lucindale (McLaren *et al.* 1998), considered naturalised (Storrie and Gardener 1998); South East (Thorp and Lynch 2000); Northern Lofty region (near Bundaleer), Southern Lofty region, South East (Lucindale) (Jessop *et al.* 2006).) Okagparinga Valley by late 2000 (Obst and How 2004). 53 infestations in the Mt. Lofty Ranges, Fleurieu Peninsula and greater Adelaide regions totalling 14.0 hectares recognised up to December 2003, including Modbury (moderate to heavy, 0.07 ha), Adelaide Parklands (5 plants removed by hand), Clarendon (one site, 0.02 ha, low density, grazed pasture) and Wirrina (several sites, 13.77 ha) (Obst and How 2004).

Queensland: southern (Mallet and Orchard 2002, Michael Hansford in Iaconis 2003), in the Shires of Clifton, Warwick and Cambooya (Phil Maher in Iaconis 2006b).

Tasmania: Hobart area (Mallett and Orchard 2002, Hocking 2005b).

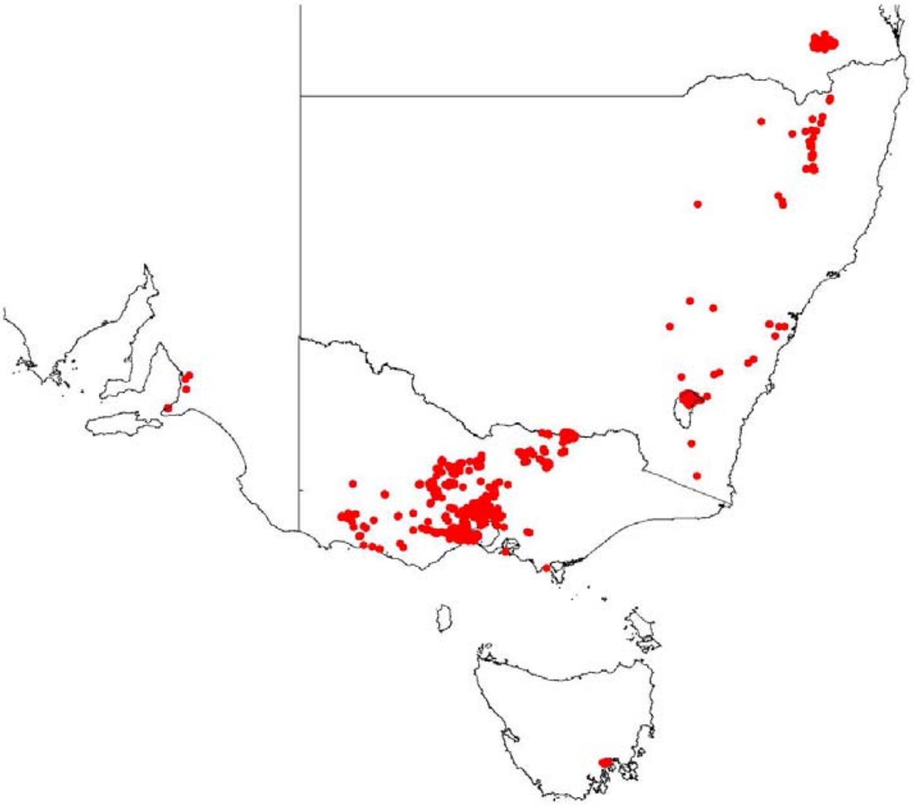

Figure 3. Recorded distribution of *N. neesiana* in Australia, September 2006. Source: J. Backholer, Department of Primary Industries Victoria; data from the Integrated Pest Management System (used in Snell *et al.* 2007). This map fails to include some significant outliers in South Australia including Lucindale in the South East, and the Bundaleer area in the Northern Lofty region.

N.neesiana has a very wide latitudinal range. In South America from approximately the equator (Columbia) to c. 40º S, in Europe from c. 28-51º N, and in Australia approximately 28-43º S.

There may have been more than one introduction of *N. neesiana* to Australia (Hocking 2002). Wide separation of initial populations in each State suggest that this is likely. The geographical origin of Australian populations is unknown (but see discussion of this question in the section, below).

N. neesiana has a synanthropic distribution (New 1994), strongly associated with towns and cities and within the web of major roads around Melbourne (Hocking 2007). It is currently most frequent in urban and urban fringe areas (in public open spaces, vacant land etc.), roadsides, agricultural pastures, and the cultural steppe, and its range expansion in Australia appears to be dependent to a large extent on human dispersal (Snell *et al.* 2007). Like many other weeds, its dispersal can be characteristed as stratified diffusion (Shigesada and Kawasaki 1997), with long distance propagule movement giving rise to isolated new populations and expansion at the edges of existing populations The extent to which it intrudes into natural habitats without facilitation by humans is one of the main focuses of this investigation.

History of dispersal in Australia

Identification failures and lack of recognition

The history of dispersal of *N. neesiana* in Australia is poorly documented because of a widespread lack of recognition of its presence and failure to accurately identify it. This appears to be a generalised problem with invasive grasses in native grasslands on a world basis, at least for members of the general public (Witt and McConnachie 2004). In southern Europe *N. neesiana* has been widely confused until recently with the closely related *N. mucronata* (Kunth) R.W. Pohl (Verloove 2005). In New Zealand, an infestation established at Hawkes Bay in the 1950s was not identified until 1982 (Slay 2001). In Australia, an infestation discovered at Tamworth, NSW, in 1996 had an estimated age of 30 years (Cook 1999). In discussing whether or not *N. neesiana* was spreading in the ACT, the ACT Weeds Working Group (2002 p. 2) suggested that "an increase in ability to identify the species" may have been the reason for its "presence/abundance ... now being noted": until awareness campaigns were implemented, few rural landholders were aware of its existence and even fewer could identify it.

According to Walsh (1998) *N. neesiana* has probably often been mistaken for native spear grasses *Austrostipa* spp. Such mistakes have been made "even by herbarium botanists" (McLaren *et al.* 1998). The first known Australian collection, made in October 1934 at Northcote (Melbourne) was originally mis-determined as the native *Stipa elatior* (Benth.) Hughes (a synonym of *S. scabra* var. *elatior* Benth., now *Austrostipa flavescens* (Labill.) S.W.L. Jacobs and J. Everett) (McLaren *et al.* 1998, McLaren, Weiss and Faithfull 2004), a common native species with a very wide distribution across southern Australia (Vickery *et al.* 1986).

Lack of recognition is widely acknowledged: *N. neesiana* “does not stand out in the landscape” (Frederick 2002) and is “difficult to identify” (Auckland Regional Council 2002). Gardener *et al.* (1996a) state that its spread “went unnoticed” until about 1981, while Virtue *et al.* (2004 p. 85) refer to the “relatively unnoticed spread” of *Nassella* species. Duncan (1993) noted that plants in the vegetative state “can be mistaken for many other winter green species, chiefly Danthonia and Fescue”. Even with intensive public education and awareness raising, public reporting rates have been very low, with most new reporting by people with botanical interests or previous familiarity with the plant (Frederick 2002). The date of arrival in a particular area or site is rarely known, so the rates at which invasion is occurring can generally only be approximately calculated.

Origin

The geographical origin of *N. neesiana* populations in Australia and the means by which propagules first entered the country remain mysterious. The means of introduction has been said to be “unknown” (Grice 2004b), and a common assumption has been that the species is an accidental introduction. No published records of quarantine interceptions appear to exist. Carr (1993 p. 291) listed both South and North America as possible origins of Victorian populations and was non-committal on the possibility of deliberate introduction. Kirkpatrick *et al.* (1995) suggested that New Zealand was “perhaps” the source. Slay (2002a) stated that *N. neesiana* was accidentally introduced into Australia in the late 1920s, but that is just speculation: the possibility of deliberate introduction has not been ruled out and the dates at which the species was first recorded are not necessarily a good guide to the actual dates of introduction. Caley *et al.* (2008) found in an analysis of herbaceous perennials naturalised in South Australia that the time between introduction and recorded naturalisation could extend up to 140 years, although the majority of species that naturalised did so within 40 years. A further complication in the Australian history of *N. neesiana* is the lack of certainty that the first herbarium specimens were from truly naturalised populations – current populations may have arisen from later introductions rather than being progeny of the earliest specimens.

Deliberate introductions of the plant to Australia for evaluation as a pasture grass have been made (see below), but some records of wild individuals existed before all of the known deliberate importations.

Agricultural contaminant

Gardener *et al.* (2003a), influenced by numerous European records of alien stipoids associated with commerce, including Hayward and Druce (1919), suggested the possibility of introduction in wool, on sheep or in fodder. Hayward (Hayward and Druce 1919) had found the species downstream of the woollen mills at Galashiels, Scotland, where the adventive flora, totalling 348 alien species, clearly reflected the naturalisation of species from seeds imported on wool from many parts of the world, including Argentina, Chile, Peru and Bolivia (Vines 2006).

Reflecting the diverse range of possible introduction methods, Muyt (2001) suggested that *N. neesiana* arrrived “probably as an agricultural impurity”, while Benson and McDougall (2005 p. 159) considered it an accidental introduction “probably as an agricultural contaminant”. In a newspaper article, quoting no source, Dalton (2000) stated that it was “believed to have hitchhiked to Australia on a haybale”. Slay (2001) stated that seeds were distributed to Australia on exported pelts and wool, a presumption apparently based on the 19th century European experience. Australia however has long been a major exporter of wool and sheep skins: wool exports were initiated in 1807, grew enormously from 1870 onwards and approximately quintupled in the following 70 years (Australian Wool Bureau 1963). Australia also appears to have been largely self sufficient in hide production for leather over the period when introduction may have occurred, except for a few specialised leather types, and had substantial exports of cattle, horse and sheep hides in 1938-39. However New Zealand was the chief source of hides and skins imported into Australia in the early 1960s (Anderson 1963).

Evidence of establishment of exotic (Australian) stipoids in New Zealand indicates that the late 19th century was “a prime time” for dispersal (Connor *et al.* 1993 pp. 303-304), however *N. neesiana* was probably first collected in that country in the late 1920s (Connor *et al.* 1993). Establishment of *Austrostipa* spp. and other Australian grasses in the Canterbury area of New Zealand has been correlated with the importation of Australian sheep in the 1840s and 1850s (Connor *et al.* 1993). Slay (2002a p. 4) thought it “possible” that New Zealand populations of *N. neesiana* may have resulted from importation of contaminated heavy machinery from Europe for the construction of bridges and railways, but stated (p. 11) that there was anecdotal evidence that the infestations in Marlborough had most likely arisen from pasture seed imported from South America.

Introduction to Australia in pelts or wool, or on sheep or cattle from South America or New Zealand seem unlikely given Australia’s long history as a significant exporter of these products, and its general low levels of trade with South America. Wild animal furs are a possible source of introduction: as recently as 1980 Argentina exported over 4 million Nutria (*Myocastor coypus* (Molina)) pelts to the USA and Europe (Soriano *et al.* 1992). Importation of fodder from these countries would seem to be similarly improbable, unless accompanying livestock. Introduction as an external contaminant of livestock is a possibility, the trade in racing horses perhaps being the most likely means. The possibility of importation as a seed contaminant deserves better evaluation, while further investigation of deliberate importation of potential pasture species may prove enlightening.

Coincidentally, another major pest species native to South America, the Argentine Ant *Linepithema humile* (Mayr), established in Melbourne for the first time in Australia at about the same time as *N. neesiana* was first detected. The ant first came to official attention in 1939, but was originally noticed in Balwyn about 1931 (Clark 1941). Surveys from late 1939 to March 1940 found a second major infestation at Yarraville and Footscray, and small infestations in Williamstown, Brunswick and Caulfield (Hogan 1940). The possibility that the same commercial vectors brought both species to Melbourne is perhaps worthy of further investigation.

Deliberate introduction

An alternative hypothesis is that of deliberate introduction, however the deliberate importations identified to date by weed researchers all post-date the first collection of *N. neesiana* in Australia. Cultivation of *N. neesiana*, leading to naturalisation would appear to be not unlikely, since “there are few modern examples of accidental first introductions of a weedy species to a new range” (Mack and Lonsdale 2001 p. 96) and a high proportion of invasive grasses are deliberately introduced (e.g. Lonsdale

1994). Only 3 of 186 exotic grasses imported for potential use as pasture species in northern Australia between 1947 and 1985 proved to be solely useful and not weedy, while 17% subsequently became weeds (Lonsdale 1994).

N. neesiana seed would not have been difficult to obtain. It was, for example, included in a widely circulated list of seed available from the 1948 harvest at Uppsala Botanical Garden, Sweden (Nannfeldt 1949). *N. neesiana* was imported to Australia under the Commonwealth Plant Introduction (CPI) program, established in 1930 to introduce exotic forage and pasture plants for the 'improvement' of grasslands (Cook and Dias 2006). Two CPI importations are currently known, in 1945 (CPI accession numbers 9731) and 1951 (CPI accession number 13476) (Cook and Dias 2006). The US Department of Agriculture ran a similar introduction program and imported 11 accessions of *N. neesiana* to the USA between 1945 and 1972 (Cook and Dias 2006). Two were still listed as available for distribution in 2006 (USDA ARS 2006): PI 237818 from Spain, donated in 1957 and PI 311713 from Chile, donated in 1966. Some of the USDA material may may have been exchanged with Australia (Cook and Dias 2006). From 1949 to 1952 *N. neesiana* was also imported to Canada from Argentina, Bolivia, Chile and Uruguay, and grown in experimental plots at the Plant Research Institute, Ottawa (Bowden and Senn 1962).

The full extent to which CPI *Nassella* accessions were trialled or released in Australia has not yet been adequately investigated. The fate of imported forage plant material was "often poorly recorded" (Cook and Dias 2006 p. 610), and the absence of trial information does not necessarily indicate a failure to grow the species in the field. Cook and Dias (2006) were unable to list any evidence of *N. neesiana* testing, but the species was trialled in Western Australia (Rogers *et al.* 1979), a State where it not known to be currently established. Testing of the plant was a component of "small sward" "nursery" trials for the Western Australian perennial grasses evaluation program during the period 1943-1968. The material grown was found to have 'little promise' (low to moderate productivity or survival or low leaf/stem ratios) at CSIRO Glen Lossie Field Station, Kojonup (some time between 1951 and 1968), and 'some promise' (fair to moderate production and fair to good survival) at Muresk Agricultural College (1943-47). Many other identified and two unidentified "*Stipa*" and *Nassella* spp. were also evaluated under this State Government program (Rogers *et al.* 1979). In nothern Australia, trial plots for testing potential pasture species were "often simply abandoned after use" leaving the plants free to naturalise and spread (Lonsdale 1994 p. 350). But although other tested grasses in the Western Australian trials have subsequently established in the Kojonup and Muresk areas, *Nassella* spp. have not been found (Sandy Lloyd, Agriculture Western Australia, *in litt.* 18 February 2008).

Cook and Dias (2006 p. 608) mistakenly claimed that Ratcliffe (1936) discussed the potential use of exotic "*Stipa*" for arid land rehabilitation. However Ratcliffe's study was influential in the establishment of State government soil conservation authorities in Australia (Cook and Dias 2006), which experimented with a wide range of exotic plants. In Victoria, the Soil Conservation Service was involved in trial uses of *Nassella* after 1963 (Cook and Dias 2006), but according to Zallar (1981) these involved only *N. hyalina* (CPI No. 25801 from the USA), although another stipoid, *Amelichloa brachychaeta*, was also trialled.

Detailed genetic comparison of world populations is probably capable of narrowing down the probable origin(s) of Australian material.

Victoria

McLaren, Stajsic and Iaconis (2004 pp. 64-65) suggested that an exotic stipoid grass 'introduction epicentre' in the northern suburbs of Melbourne was possibly linked to the trotting stables of Edgar Tatlow, east of Darebin Creek in Epping, and the possible importation of horses and hay from South America. This suggestion was sourced to a personal communication by P. Haberfield, who linked *Nassella leucotricha* to the Tatlow property, presumably marked today by suburban Tatlow Drive, east of Epping Secondary College. Numerous streets to the east including Trotting Place and Derby Drive suggest the probable extent of the property. *Nassella leucotricha*, a Mexican and southern USA species, was locally known as Tatlow grass and had, like *N. neesiana*, first been recorded in Victoria at Northcote in October 1934 (McLaren *et al.* 1998, McLaren, Stajsic and Iaconis 2004).

Tatlow, who died at the Epping property, 'Derby Lodge' stud, in March 1968 (Anon. 1968), cannot be blamed for the original introductions of *N. neesiana* or *N. leucotricha* to Victoria, because these precede the transfer of his business from Tasmania. However he may have been responsible for later *Nassella* introductions. Records indicate that in 1938 he purchased the horse 'Raider' in the USA and imported it to his Tasmanian stud, also called 'Derby Lodge', at Hagley (Pedigree Online 2007), near Launceston. Tatlow frequently imported horses, including 'Globe Derby', imported to Hagley in 1927, 'Belle Logan' from New Zealand, and 'Ayr', bought in Christchurch in 1932. He also regularly visited "America", where, in 1954, he purchased Stanton Hall and Volo Chief (Anon. 1968). Tatlow moved to Epping, some time after 1938. "Most of the broodmares at his studs in both Tasmania and Victoria were purchased in NZ, many from Southland, and he was a regular visitor to America, where he purchased ... successful sires" (Anon. 1968). *N. neesiana* might have been imported with horses from New Zealand, where it was probably present from the late 1920s, although it has never been recorded from Southland or Christchurch (Slay 2002a), and *N. leucotricha* might have accompanied animals purchased in the USA, where it is native in Texas and Oklahoma (McLaren, Stajsic and Iaconis 2004).

An equine connection otherwise appears to be sound speculation. Horses frequently create areas of bare ground in pastures, are commonly provided with supplementary fodder, and pass a high proportion of consumed seed in their dung. Horses readily carry weed seeds externally and create 'windows' on the ground surface for their germination and establishment, so horse pastures are commonly much weedier than those grazed by sheep and cattle (Gurr *et al.* 1996). Presence of grass seeds such as *Bromus diandrus* in horse dung and other data (Weaver and Adams 1996) suggest the possibility that horses could well have dispersed *N. neesiana* seed to Australia.

There is substantial evidence for the northern suburbs of Melbourne '*Nassella* epicentre' hypothesis. McLaren *et al.* (1998) referred also to a [another?] report by P. Haberfield of *N. charruana* being present near Cooper Street at Epping from before 1958. The east end of Cooper St is about 900 m south of Tatlow Drive. The first official record of this species in Australia was a specimen collected on 21 February 1995 at Thomastown by A. Muir (Hansford 2006). Thomastown is about 3.6 km south of Tatlow Drive, downstream along Darebin Creek. Later in 1995 *N. charruana* was found on a rural property at Epping in an infestation believed by the property owner to have been present since the 1950s (Hansford 2006). Mapping of 45 infestations that were known by April 1996 showed that they were all along the Darebin Creek and its tributaries, within or close to the Epping Road corridor (Hansford 2006). At its closest point, Epping Road is 400 m from Tatlow Drive.

Similarly the first recorded Victorian infestation of *N. trichotoma*, c. 4 ha, in 1958 at Broadmeadows (McLaren, Stajsic and Iaconis. 2004), "where it was believed to have existed for about 20 years" (Parsons 1973), was possibly about 8 km from Epping. Searches soon after the first discovery found five other patches "just north and north-east of Melbourne" in areas "apparently ... at one time butchers' holding paddocks ... presumably carrying sheep from infested areas in New South Wales" (Parsons 1973 p. 152). However both *N. neesiana* and *N. leucotricha* were first recorded in 1934 at Northcote, c. 14 km S of Epping (McLaren *et al.* 1998).

Ian Suitor, a farmer with property off Somerville Road, Greenvale (pers. comm. 22 November 2006) reported that the first place *N. neesiana* appeared in his area was on land managed by Tommy Thomas, a dealer in livestock, on a granitic hill, approximately 0.5 km north of Greenvale Reserve. Previously it had been believed (Charles Grech pers. comm. 22 November 2006) that Suitor's land had been invaded downstream along Moonee Ponds Creek.

N. neesiana was not recorded as a component of the basalt plains flora by Willis (1964), and was not found by Groves (1965) at St Albans, where it is now common. Its distribution in Victoria was described by Willis (1970 p. 182) as: "locally frequent on basaltic grassland north from Melbourne (Fairfield, N. Preston, Broadmeadows etc.) and along a railway embankment at N. Brighton." In 1972 its known distribution was still reportedly restricted to major grid N (the Melbourne region) (Churchill and de Corona 1972), however Gardener (1998) recorded a distribution point near Koroit in the Western District with the first collection there in 1967, shown in the ARMCANZ *et al.* (2001) map, which also showed a 1960s locality in the Horsham region. Stuwe and Parsons (1977) did not record it at any of 59 *T. triandra* grassland remnants they surveyed in 1976.

By 1986 it had been recorded from "Bung Bong", Yan Yean; Purnim; Woodstock, south east of Whittlesea; and Rosanna (Vickery *et al.* 1986 p. 81, herbarium material examined). Beauglehole (1987) recorded it in sector F of the Wimmera, bounded roughly by Horsham, Dimboola, Jeparit, Nyamville, Minyip and Lubeck. In the western region of Melbourne, McDougall (1987) recorded populations in remnant native vegetation at Napier Park, Essendon; O'Brien Park, Sunshine and the nearby Braybrook Rail Reserve Grassland, and Laverton North Grassland Reserve, Altona North, and recommended control or monitoring at each site. Gardener (1998) recorded a distribution point near Geelong with the first collection there in 1984, and another in the North East in the Wangaratta region, first recorded in 1989. Bartley *et al.* (1990) described the plant as a serious threat to remnant grasslands in the Melbourne area, including the Laverton North Grassland Reserve, Derrimut Grasslands and railway reserves. They summarised the then known Victorian distribution: major grid cells N (Melboure region), K (near Warrnambool) and C (in the Wimmera) (see Willis 1970 or Churchill and de Corona 1972 for a grid map), and sectors D, F and O within the Land Conservation Council's Melbourne study area (citing Beauglehole 1983). Staff of the Botany Department, LaTrobe University, had also found it at sites in sector B to as far to the south-west as Geelong (Grid P) (Bartley *et al.* 1990). Gardener (1998) recorded a distribution point to the west of Bendigo, with the first collection there in 1990. Carr *et al.* (1992) summarised the distribution as 'limited', in medium to large populations (rather than widespread, or rare and localised, or with small populations) in lowland grassland and grassy woodland and rock outcrop vegetation. Stuwe (1994 p. 94) warned that it threatened "to dominate several grassland remnants near Melbourne".

Walsh (1994) recorded the presence of *N. neesiana* in seventeen 6' x 6' grid cells (c. 9 x 10.8 km or c. 10,000 ha) based on records in the Flora Information System (managed currently by the Victorian Department of Sustainability and Environment), National Herbarium of Victoria records, and other "verifiable" reports. These were concentrated in the area west and north of Melbourne (8 grid cells) including Whittlesea, with 4 cells in the Ballarat-Maryborough-Tarnagulla area, 2 cells in the North East (Wangaratta-Beechworth area), 2 in the Geelong-Torquay area and 1 in the Warrnambool area. No Wimmera record was included. Walsh (1994 p. 378) mentioned also Cressy (65 km W of Geelong) but failed to map such a record. Kirkpatrick *et al.* (1995) noted that it was found at Cressy in 1994. Walsh (1994 p. 378) considered it "Locally common ... mostly on basalt soils and often near watercourses, but established and spreading on improved pasture and road verges".

By the 1990s *N. neesiana* distribution was ballooning. Kirkpatrick *et al.* (1995 p. 35) stated that its "rate of spread in the two grassland reserves in Melbourne [Derrimut and Laverton North] [had] shocked botanists". Intensive publicity and Victorian government investigations from c. 1993 greatly increased knowledge of its occurrence. The Victorian Government employed four regional facilitators, in the Port Phillip, North East, South West and North West regions, and they undertook mapping of infestations, with data being recorded on the Pest Management Information System (later the Integrated Pest Management System, IPMS), a Department of Primary Industries database (Iaconis 2006a). Mapping was also undertaken in the Rural City of Wangaratta, and of roadside infestations in the Shire of Indigo (Iaconis 2006a). In the North Central Region, Liebert (1996) reported 4 urban infestations in Bendigo, 1 infestation at Campbell's Creek, 1 at Clunes, 3 at Maryborough, 2 at Tarnagulla and 2 at Tooleen, mostly discovered by local field naturalists, and mostly on roadsides and railway sidings. Precise details were provided of the location and extent of each of these infestations along with a description of the habitat and the nature of the infestation. Almost all of them were on disturbed soils. An up-to-date Victorian distribution map (attributed to David McLaren) was also provided, showing that approximately 23 minor grids (6' x 6') contained infestations, including one in the North East near Wangaratta and one in the South West near Terang. *N. neesiana* found in the Sunbury-Bulla areas was believed to have originated by dispersal of seed or roadside slashers from the Greenvale district (Nair 1993). Stewart (1996) described extensive cover in Broadmeadows Valley Park.

According to Frederick (2002) the number of infested sites known in Victoria in 1998 was 43, and 338 in November 2001, approximately 60% on public land, nearly all on roadsides, along waterways or in flood zones, and mostly small patches or isolated plants. Infested areas totalling 350 ha had been discovered in that period with an estimated total ground cover of c. 24 ha, reduced to c. 15 ha after treatments. Frederick (2002) provided a detailed tabulation of the number of infested sites (land parcels or management units) and the year of their discovery at 19 localities in the North Central Region. New infestations were still being discovered in well investigated areas at the time of writing. In the Western District the plant had been detected in the Moyston area by 2000 (Dalton 2000).

According to Morfe *et al.* (2003) the reported area of infestations in Victoria by 2002 was 815 ha. Extensive further mapping occurred throughout the State in 2003 (Iaconis 2006a).

Matthews (2006) reported a sharp increase in the spread and occurrence in south-western Victoria. In addition to a large established infestation at Lake Hamilton and surrounding urban areas of Hamilton, there were various roadside populations in Southern Grampians Shire, and infestations in the general areas of Mt Napier Road, Digby Road, Kirkwood Road, roads between Portland and Digby Roads, Murndal Road and Lake Hamilton, with some spread from roadsides onto adjacent private land.

Infestations have recently been found on the Mornington Peninsula, south of Melbourne, by Gidja Walker (pers. comm. 7 December 2007). A "small colony of about 20 plants" was found on the roadside at Point Nepean Road next to the Shelley Beach turnoff, opposite Campbells Road, between Portsea and Sorrento (Anon. 2008a, Walker pers. comm.). It was also found at Rye c. late 2005 associated with the Mobil service station, growing in scoria (Walker pers. comm).

Major infestations were reported between Bairnsdale and Lindenow (100 and 60 ha) and at Dargo (several properties) in East Gippsland by Geoff Harman of the Department of Primary Industries in January 2009, much further east than the previously known range in Gippsland (Harman pers. comm. 12 January 2009).

New South Wales

The development of the invasion in New South Wales is poorly documented in published sources. A substantial contributing factor has been the absence of a State-wide weed mapping system (Linda Iaconis pers. comm. 2006).

The first known collection of *N. neesiana* in New South Wales was on the Northern Tablelands at Glen Innes in 1944 (McLaren *et al.* 1998) or 1948 (Gardener 1998). Duncan (1993) recorded that it had been widely present in the Guyra – Glen Innes area, in the northern half of the Tablelands from the 1960s. A major infestation, discovered in 1996 in the Reedy Creek catchment near Tamworth on the North West Slopes, had an estimated age of 30 years (Cook 1999). Tamworth is off the tablelands, on their inland, southwestern side. Slay (2001 p. 21) erroneously mentioned a "continuous sward" infestation at Deniliquin, citing Mulham and Moore (1970), but those authors refer only to *Austrostipa* spp. Duncan (1993) and Storrie and Lowien (2003) noted that *N. neesiana* was thought to have spread very slowly until the late 1970s. According to the map in Gardener (1998) it was first recorded in the Guyra district in 1968. A herbarium specimen from Bathurst on the Central Tablelands was collected in 1972 (Benson and McDougall 2005), shown in the ARMCANZ *et al.* (2001) map. It was first recorded in the Sydney area in 1974 (Gardener 1998) a herbarium specimen from Mt Druitt (Benson and McDougall 2005), and at Tenterfield close to the Queensland border in 1976 (Gardener 1998), both shown in the ARMCANZ *et al.* (2001) map.

In 1986 Vickery *et al.* (1986 p. 81) examined material collected at Mt Druitt, Tenterfield and Glen Innes and considered it to be "now spreading" on the Central Coast and Northern and Southern Tablelands. It was recorded in the Goulburn region in 1985 (Gardener 1998). Specimens from Pendle Hill, Ingleburn and Brush Farm Park in the Central Coast region were collected in 1986 (Benson and McDougall 2005). It was recorded in the Armidale region (Northern Tablelands) in 1990 (Gardener 1998). Wheeler *et al.* (1990) added no new information. Jacobs and Everett (1993) reiterated its presence in the four major botanical divisions of the State already noted (not including the then unknown Tamworth population) and stated that it "grows along roadsides". It was not recognised as an environmental weed in NSW by Swarbrick and Skarratt (1994). Carolin and Tindale (1994) recorded that it was widespread on roadsides in the Sydney region (bounded approximately by Rylstone, Singleton, Nowra and Taralga). In 1995 it was found in the Coonabarabran region (Gardener 1998).

Gardener *et al.* (1996a) observed that *N. neesiana* then dominated large areas of pasture on the Northern Tablelands and was becoming increasingly common on the Central and Southern Tablelands. Eddy *et al.* (1998) noted its presence at Bungendore (Southern Tablelands). By 1998 it had been declared noxious in the New England County (Northern Tablelands), Severn Shire and Glen Innes Shire (McLaren *et al.* 1998).

Ens (2002a) collated herbarium and other records and searched for populations on the Cumberland Plain (Sydney region), finding 16 infested sites, mostly with <50 plants, the largest (hundreds of m^2 and believed, on the basis of its size, to be the oldest) being a former private veterinary research station at Ingleburn. Infestations were recorded at Mount Annan Botanic Gardens, Campbelltown Station, Macquarie Fields, West Ryde (the most easterly), St Clair, Prospect Reservoir, etc. The most westerly were in the Hawkesbury district at Yarramundi Lagoon, Agnes Banks and at Navua Reserve, Grose Wold. Benson and McDougall (2005 p. 159) reported it was "spreading" in western Sydney, with the situation in Bathurst "unknown". Storrie and Lowien (2003) considered it well established on the Southern Tablelands and South West Slopes. Data points on the map in McLaren *et al.* (2002b) showed it was present on the Central West Slopes. The ACT Weeds Working Group (2002) recorded that it was found mainly in the mid to northern parts of the Southern Tablelands, to the east, north and west of Canberra, mostly at low abundance. It had recently been found at Bombala, not far north of the Victorian border, and Cooma, the first records for the Monaro region.

During 2003 distribution maps were produced by the NSW Department of Primary Industries and Southern and Northern Tablelands weeds officers detailing the areas throughout the State that were infested, but these were not made publicly available (Iaconis 2006a).

As of 2005 *N. neesiana* had been declared noxious in 11 local government areas (Benson and McDougall 2005) and by March 2007 was listed as a Regionally Controlled (not widely distributed) weed in 25 Local Control Authority areas and a Locally Controlled (widely distributed) weed in 103 areas (Australian Weeds Committee 2007).

Maps of the Southern Tablelands infestations were revised in 2006 (Iaconis 2006a). Verbeek (2006) described its distribution in southern NSW as "limited", as opposed to widely distributed.

In September 2008 an infestation of eight plants was found by a local Weeds Officer and co-workers "along side a bus transfer stop in Balranald township" (Sheehan 2008) close to the boundary between the South Western Plains and South Far Western Plains regions. The population was far beyond the previously known range. Balranald is on the lower Murrumbidgee River which has its origin in the Southern Tablelands. A distribution map was published in 2009 by NSW National Herbarium (Fig. 4).

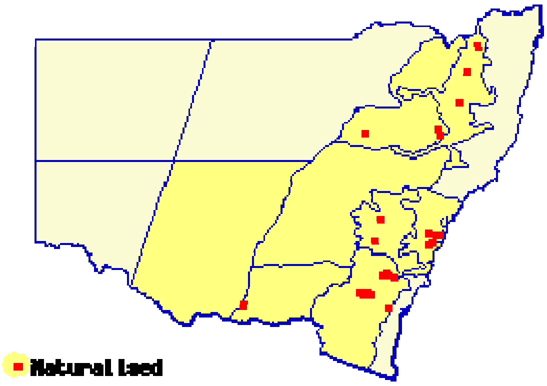

Figure 4. Distribution of *N. neesiana* in New South Wales (National Herbarium of New South Wales 2009).

Australian Capital Territory

Published information about early records of the grass in the ACT are scanty. Gardener (1998) dated the first record to 1960. The ACT Weeds Working Group (2002 p. 2) vaguely noted that it was “known to have occurred in the ACT for some time, but was not considered a species of concern until the late 1990s”. Vickery *et al.* (1986 p. 81) considered it was “now spreading” in the ACT, and examined material from Burbong, Black Mountain, Commonwealth Gardens in Canberra, and O’Connor. Berry and Mulvaney (1995) did not list the species as a significant weed in the ACT: it was not considered a “widespread or dominant” environmental weed, nor a “common weed” of any major habitat type except grasslands and road verges, and was not recorded from 40 or more 2.5’ x 2.5’ grid cells (c. 3.5 x 4.5 km), nor known to be dominant over an area of > 30 x 30 m. The weed database at that time recorded zero locations for it in the ACT. In fact the species was not properly recognised in the ACT in this period, and its presence was being overlooked (Sarah Sharp pers. comm. 11 October 2006). Berry and Mulvaney did note however (1995 Vol. 2 Appendices p. 261) that it was a weed of grasslands in Canberra, “observed as a dominant in a small patch of grassland in the Barton area ... also common along the bicycle path at Yarramundi” (at the western end of Lake Burley Griffin).

Eddy *et al.* (1998) considered it common in the ACT. Bruce (2001) surveyed 39 sites in the ACT including natural grasslands, parks and road verges in rural, urban and periurban areas and found *N. neesiana* to be widespread. It was most common in urban and peri-urban areas subject to mowing and was present at all urban and peri-urban sites investigated, but at only 67% of rural sites. Abundance data suggested that the invasion in the older urban areas was of longest standing and at a more advanced stage. Lowest levels of abundance were found on agricultural land and grazed areas (whether or not managed for agriculture).

Further surveys from 2000 to 2002 (ACT Weed Working Group 2002, ?Sharp 2002) revealed expansion of known infestations at numerous sites, plus numerous previously unrecorded patches and linear infestations along primary, secondary and semi-rural roadsides leading outwards from major infestations. The Tuggeranong Valley contained the most noteworthy severe new infestations. *N. neesiana* was found to be dominant in numerous areas in inner Canberra including most suburban nature strips and roadsides, and around Parliament House. ACT Government (2005) recorded that it had spread dramatically in abundance and distribution in the previous 10 years. The highest abundances in the ACT were in the central city and at Belconnen, with lower abundances in the Jerrabomberra and Majura districts, Gunghalin, but was absent from sites examined in the Tuggeranong, Tidbinbilla and Namadgi districts.

South Australia

The first known collection in South Australia was at Lucindale in the South East on 18 November 1988, where, according to J.P. Jessop of the Adelaide Herbarium, it ‘did not seem to be causing any trouble’ (McLaren *et al.* 1998). Gardener (1998) mapped a 1988 record in the vicinity of Mallala (north of Adelaide). Gardener *et al.* (1996a) mentioned its presence in the Adelaide Hills, and Gardener (1998) dated the first Adelaide area record as 1989. By 2000 it was recorded from the South East (Thorp and Lynch 2000) and was known from the Okagparinga Valley by late 2000 (Obst and How 2004). Infestations at Belair National Park were also identified. Field surveys in spring-summer 2003 enabled the mapping of all known infestations in Adelaide-Fleurieu Peninsula (Iaconis 2006a). 53 infestations in the Mt. Lofty Ranges, Fleurieu Peninsula and greater Adelaide regions totalling 14.0 hectares had been recognised up to December 2003, including Modbury (moderate to heavy, 0.07 ha), Adelaide Parklands (5 plants removed by hand), Clarendon (one site, 0.02 ha, low density, grazed pasture) and Wirrina (several sites, 13.77 ha) (Obst and How 2004). Further surveys in 2004 located a few additional sites. During 2003-2005 the original survey area was extended to include Randall Park and adjoining roads and railway infrastructure to Belair National Park, but no new infestations were discovered (Iaconis 2006a). Jessop *et al.* (2006) recorded its presence in the Northern Lofty region (near Bundaleer), Southern Lofty region and the South East.

Queensland

The presence of *N. neesiana* in Queensland may have been first recorded in published literature by Mallet and Orchard (2002). Michael Hansford (in Iaconis 2003) noted its presence in “southern” parts of the State, in the Darling Downs. Extensive surveying for *N. neesiana* was undertaken in 2005 and 2006 including roadside mapping in Clifton and Warwick Shires, with a delimiting survey planned for the whole of the eastern Darling Downs (Iaconis 2006a). As of October 2006 infestations were restricted to Clifton, Warwick and Cambooya Shires, and property management plans had been finalised for all known infestations (Phil Maher, Queensland Department of Natural Resources and Mines, in Iaconis (2006b)). Infestations were concentrated in the Darling Downs, with some along the Condamine River, and approximately 100 ha were known to be infested by 2007 (Snell *et al.* 2007). The largest infestation was at Clifton Showgrounds and polo field where anecdotal evidence suggests it may have been present since at least 1977 and have given rise to the other infestations (Snell *et al.* 2007). Additional populations have been found in the City of Toowoomba, probably spread by an energy utility company (Queensland representative on the National Chilean Needle Grass Taskforce 28 February 2007).

The Queensland infestations most likely are the result of seed movement via vehicles or livestock from the Northern Tablelands of New South Wales. A plan with the long term objective of eradication from the State is being implemented (Snell *et al.* 2007).

Tasmania

An infestation at Hobart is mentioned by Mallett and Orchard (2002) and Hocking (2005b). This infestation, at the University of Hobart, was mapped in 2005 and was the only one then known in Tasmania. The outbreak was sprayed with herbicide in autumn 2005, with a follow-up spray, mulching and planting of trees in winter. Other potential invasion sites were surveyed in 2006, including open space and grasslands at Montague Bay, Rose Bay, Rosny and Mornington (Iaconis 2006b). New infestations were discovered in 2005 that prompted further surveying (Iaconis 2006a). However according to the Tasmanian Department of Primary Industries and Water (DPIW)(2007 p. 2) *N. neesiana* had been recorded from only a single site, in Hobart, "from which it has ... been eradicated".

Hocking (pers. comm. 2006) noted that the recent reports were in central and southern Tasmania. As of July 2009 the core infestations were all located in urban settings on the eastern shore of the Derwent estuary in Hobart in the suburbs of Montague Bay, Rosny and Bellerive (National Chilean Needle Grass Task Force Agenda, July 2009). The main infestations were along walking tracks, road easements and the grounds of a primary school. It was also found west of the Derwent River, in small areas of The Domain and near the Technopark (Karen Stewart, DPIW Tasmania, pers. comm. July 2009). DPIW mapped and treated all known infestations during 2007-08. Hocking (pers. comm. 2006) noted that bioclimatic modelling indicated that establishment was highly likely in areas around Devonport and Launceston where ferries from mainland Australia regularly deposit large numbers of motor vehicles. Bioclimatic modelling indicated that much of eastern Tasmania was suitable for its establishment (ARMCANZ *et al.* 2001), although Hobart was outside the predicted area (Hocking 2005b). DPIW (2007) prescribed hygiene and quarantine procedures to prevent breaches of the Tasmanian importation prohibition.

This basic data for the whole of Australia suggests at least four very widely separated areas of introduction, excluding the deliberate importations to Western Australia: on the northern outskirts of Melbourne, the New England tablelands of NSW, southern NSW or the ACT, and South Australia, however dispersal from the earliest known area of infestation north of Melbourne to the other major foci cannot be ruled out.

It is apparent that the known extent of infestations during the course of the *N. neesiana* invasion has been closely related to the ability to identify the plant and the effort devoted to detecting it. As Grice and Ainsworth (2003) pointed out, the confounding 'awareness factor' means that very little can be concluded about the actual rates of population increase and dispersal. Ongoing control activity further confounds any attempts to determine whether *N. neesiana* might be reaching the limits of its potential range and population size. Nevertheless, understanding of the invasion would be improved through retrospective mapping of the extent of infestations at appropriate historical intervals and would assist in theoretical discussions of lag phases and the time courses of plant invasions, and potentially contribute to improving prediction abilities for weeds in general (Grice and Ainsworth 2003).

Potential distribution in Australia

Various predictions of the potential Australian distribution of *N. neesiana* based on climate parameters have been made. These all suffer from a poor understanding of the range of the grass, both in South America and in countries where *N. neesiana* has been introduced, resulting from misidentifications or uncertainty about the true classifications of material, and inadequate floral studies, and in the introduced ranges, of continued colonisation of new areas.

Gardener (1998) estimated a potential range in Australia of nearly 40 million ha, from Western Australia to south-east Queensland, using the climate modelling program CLIMATE, which analysed 16 parameters for each data point, based on temperature and rainfall. He made two separate analyses, using firstly the 224 then known locations of infestations in Australia, and secondly a sample of locations in the rest of the world, based on herbarium specimens and literature records.

McLaren *et al.* (1998 p. 63) used distribution and altitude data from a "representative sample" of known infestations in Australia, analysed the data with the BIOCLIM program and used CLIMATE to predict areas with a similar climatic profile. Their map showed a potential distribution range covering much of south-east Queensland, most of the eastern half of New South Wales, most of Victoria, southern parts of South Australia and Western Australia and parts of north-east Tasmania, covering a total of 41 million ha. A map provided by D. McLaren in Liebert (1996) derived using BIOCLIM based on the climatic parameters of all Victorian infestations then known, showed the potential distribution in Victoria was approximately 3.86 million ha. These climate-based predictions ignore other potentially important factors affecting distribution such as land use, tree cover and soil type (Liebert 1996). They also rely on geographical proximity of weather stations to assign climate parameters to a record, a problem likely to lead to major distortions when records are a long distance from weather stations, at a different altitude, etc.

Under the State of Victoria's weed risk assessment process (Weiss 2002, Morfe *et al.* 2003), the maximum potential distribution of *N. neesiana* was estimated based on world distribution data, climate modelling (rainfall and temperature data) and geographical information system layers of susceptible land uses, vegetation classes and soil properties. A map was produced showing the likely and unlikely distributions (Morfe *et al.* 2003p. 879). An additional estimate was made that *N. neesiana* would take about 75 years to occupy its entire potential range in Victoria, or 50 years if the rate of spread was "very high". Any future expansion of range and area occupied was acknowledged to be critically dependent on the extent and effectiveness of management activity directed against the weed. In the absence of government-coordinated mangement, the level of infestation in Victoria was predicted to expand from less than 1000 ha to c. 1.5 million ha in 30 years (Morfe *et al.* 2003).

Thorp and Lynch (2000) provided a grid map generated by Agriculture Western Australia based on the known world distribution of *N. neesiana*, using the CLIMATE system with 'core' and 'high' predicted densities (± 20% of the average climate required).

This indicated that a small part of south eastern NSW, parts of Tasmania, much of Victoria, south-eastern South Australia and parts of the southern coast of Western Australia had high climatic suitability, but ‘core’ areas were restricted to near-coastal Victoria and South Australia.

According to Gardener *et al.* (1999 p. 8) *N. neesiana* “appears to have the ability to colonise most grasslands and grassy woodlands in temperate areas of Australia with more than 500 mm of rainfall”. The expansion of range of an invasive plant at a regional level is generally faster from many, small infestations than from a single large one of similar area (Mack and Londale 2001). The presence of many small populations is certainly a feature of the Australian invasion, so continued rapid spread can be expected. Increases in the frequency and density in landscapes already invaded can be expected if inadequate management is undertaken. Lunt and Morgan (1998, 2000) documented an increase in frequency at Derrimut Grassland Reserve from 16% of quadrats in 1986 to 42% in 1996, largely driven by senescence of the dominant native grass *T. triandra*.

Habitat and climatic and biotic tolerances

N. *neesiana* is an “extremely hardy” (Benson and McDougall 2005) grass, adapted to a wide range of conditions (Muyt 2001). It reportedly “has the capacity to switch from being stress tolerant to being vigorous” (Bedggood and Moerkerk 2002). In South America it is the most widely distributed *Nassella* species with a distribution from the Pacific coast across the Andes, through the Pampean and Paranaense biogeographical provinces to the Atlantic, a range similar to the overall distribution of *Stipa sens. lat*. in that continent, and occupying a variety of habitats (Longhi-Wagner and Zanin 1998), “primarily” steppe (Barkworth 2006).

N. neesiana is a particularly prominent species in the 750,000 km^2 Rio de La Plata grasslands, consisting of the Argentine pampas and the Uruguayan and southern Brazilian campos (Soriano *et al.* 1992). Campos and pampas are similar formations and the Rio de la Plata is often considered the boundary between them (Overbeck and Pfadenhauer *et al.* 2007). The “typical” landscape of the Pampas south of Buenos Aires in 1960 was described by Durrell (1964) as “flat golden grassland in which the cattle grazed knee-deep ... a lush, prosperous and well-fed-looking landscape that only just escaped being monotonous”. Lorentz (1876 quoted by Schimper 1903 p. 503) described the pampas grasslands as consisting of “scattered dense tufts of stiff grasses, chiefly species of *Stipa* and *Meliea*, which rise like islets above the yellowish-brown loam ... between these isolated tufts of grass bare loam, which is frequently washed out and carried away by the rain, so that the separate tufts of grass rest on actual mounds; but also frequently, especially during the favourable season of the year, it is covered by all kinds of more delicate grasses and herbaceous perennials, few in species ... Viewed from a distance, these grasses seem to form a close grassy covering, and the pampa presents the appearance of extensive grassy tracts whose colouring varies with the seasons: coal-black in spring, when the old grass has been burned; bright bluish-green when the young leaves sprout; later on brownish green, the colour of the mature grass; finally – at the flowering time – when the silvery white spikes overtop the grass, over wide tracts its seems like a rolling, waving seas of liquid silver ... After the Gramineae ... the greatest number of individuals is that of Compositae; usually twiggy under-shrubs with inconspicuous flowers ...*Verbena*, species of *Portulaca*, of *Malva* and a few Papilionaceae are chiefly responsible for the meagre floral beauty ...”. A similar picture is presented by Soriano *et al.* (1992): Poaceae is the predominant family, with *Stipa sens lat*. the best represented genus (25 spp.), followed by *Piptochaetium* and *Poa* (each with 8 spp.) and *Aristida* and *Melica* (each with 6 spp.); Asteraceae are next most abundant, including species of *Baccharis*, *Eupatorium*, *Hypochoeris* and *Veronia*; native Fabaceae, sensitive to cultivation, poorly represented, with Cyperaceae, Solanaceae, Brassicaceae, etc, in order of abundance. In the Brazilian Campos region Asteraceaeare is the most diverse family (c. 600 spp.), followed by Poaceae (c. 400-500 spp.), Leguminosae (c. 250 spp.) and Cyperaceae (c. 200 spp.) (Overbeck *et al.* 2007).

N. neesiana was a dominant species in a climax grassland community that once covered the majority of the formation known as Rolling Pampa, extending south and west of the Río Paraná and the Rio de La Plata and encompassing the Río Salado basin. Rolling Pampa covered a gently undulating, well drained plain, commonly with very deep soils, and regular drought and flooding. In the very fertile soils common in Rolling Pampa, such as in La Plata district of Buenos Aires Province, *N. neesiana* was dominant along with the shortly rhizomed summer-autumn growing *Bothriochloa laguroides* (DC.) Herter and three smaller, tufted grasses *Piptochaetium montevidense* (Spreng.) Parodi, *Aristida murina* Cav. and *Jarava plumosa* (Spreng.) S.W.L. Jacobs and J. Everett (Cabrera 1949, Soriano *et al.* 1992). This type of grassland is called “flechillar”, in reference to the dominance of grasses with piercing seeds (Soriano *et al.* 1992). Shrubs are generally a minor component but include *Baccharis* spp. (Asteraceae), and the inter-tussock spaces are occupied by many species of small herbs and sedges (Soriano *et al.* 1992), with the “original” plant diversity in well-drained soils being c. 222 species (Aguiar 2005). The weed flora has many species in common with the more mesic grasslands of south-eastern Australia. In other areas of Rolling Pampa *Nassella charruana* and *Amelichloa brachychaeta* were the dominant grasses, the former in parts of the eastern zone and the latter in the north west (Sante Fe province) (Soriano *et al.* 1992). Distribution of *N. neesiana* in Rolling Pampa has probably been radically altered by development. Six million ha of the formation had been cultivated by c. 1900 but by 1984 this had increased to 26 m ha (Aguiar 2005).

N. neesiana was a dominant species in thhe natural vegetation of the Southern Pampa, covering much of southern Buenos Aires province, along with *N. clarazii* (Ball) Barkworth, *N. trichotoma*, *N. tenuis* (Phil.) Barkworth, *Piptochaetium napostaense* (Spegazzini) Hackel, *P. leiopodum* (Spegazzini) Henrard and *Poa ligularis* Nees ex Steud. with many other grasses also abundant and very similar non-grass components to Rolling Pampa (Soriano *et al.* 1992). Some of the stipoid species in Southern Pampa “often ... form pure stands in areas that have never been cultivated” (Soriano *et al.* 1992 p. 385). The stipoids are largely displaced by shrubby vegetation on hills, rocky sites and wet areas in this region.

N. neesiana is one of the most abundant species in mixed flechilla-*Paspalum quadrifarium* Lam. grassland in the Tandilia Range system of the southern Pampas of Argentina, where the stipoid dominants include *Piptochaetium* spp. and *Nassella trichotoma*

(Honaine *et al.* 2006). The flechillar (*Nassella-Piptochaetium*) community in this area has especially high biodiversity and is ecologically significant as a faunal refuge (Honaine *et al.* 2009).

To the north in Argentina, in the department of Gualeguay in the south of Entre Rios Province, *N. neesiana* occurred in undulating treeless plains covered in grasses (Marco 1950), an area classed as Mesopotamic Pampa and characterised by a more subtropical climate (annual rainfall c. 900-1200 mm), and a network of water courses lined with gallery forest (Soriano *et al.* 1992). Stipoids generally are of lesser importance in this formation than in the southern pampas, but *N. neesiana* was one of the dominants along with *N. tenuissima*, *Eragrostis cilianensis* (All.) Janchen. and species of *Axonopus*, *Paspalum*, *Digitaria*, *Schizachyrium* and *Bothriochloa* (Soriano *et al.* 1992).

The Flooding Pampa, an extremely flat coastal plain covering 9000 km^2 (Perelman *et al.* 2001) in eastern Buenos Aires province that includes the Laprida and Río Salada basins and extends in tongues into the interior (Soriano *et al.* 1992), has some dominant grasses in common with Rolling Pampa but *N. neesiana* is not a major species (Soriano *et al.* 1992). Nevertheless it occurs through most of the region across its latitudinal range (c. 35-38°S) and with a frequency of ≥20% (in 25 m^2 samples) in 8 of the 11 Flooding Pampa grassland community types identified by Perelman *et al.* (2001), reaching a frequency of 87% in one community. In the Flooding Pampa it has been classified in a three-species floristic group with *Jarava plumosa* (Spreng.) S.W.L. Jacobs and J. Everett (as *Stipa papposa*) and *Bothriochloa laguroides* (Perelman *et al.* 2001).

N. neesiana is of minor importance in most of the Inland Pampa, a drier, more open grassland, lacking a river and stream network, found to the west and south-west of Rolling Pampa. However it is one of a number of grasses of lesser importance in a community dominated by *Poa ligularis*, *Nassella tenuissima*, *N. trichotoma*, *N. filiculmis* (Delile) Barkworth and *Panicum urvilleanum* Kunth on the border between the provinces of Buenos Aires and La Pampa (Soriano *et al.* 1992). Its minor importance in the Caldenal, an ecotonal region between the Humid Pampa and the Monte desert, is reflective of the regional climate with an annual rainfall of 300-400 mm concentrated from spring to autumn, annual potential evaporation of 800 mm and cooler temperatures than the pampas (Fernández et al. 2009).

Little native grassland remains in Uruguay, and protected areas of natural grassland landscape are non existent (Cosse et al. 2009). In the Juan Jackson region of south-western Uruguay *N. neesiana* was considered to be the third most important grass in “virgin and regenerated” caespitose grasslands on granitic soils, after *Piptochaetium stipoides* (Trin. and Rupr.) Hackel ex Arech. and *P. montevidense* (Spreng.) Parodi (Gallinal Heber *et al.* 1946). Soriano *et al.* (1992) considered it to be the most frequent grass in the Southern Campos, a formation extending over most of southern part of the country, along with other *Nassella* spp., *Paspalum* spp., *Poa* spp. and other grasses. On deep fertile soils the natural vegetation was probably dominated by *Nassella charruana*. In the Atlantic coastal south-eastern plain Stipeae are less abundant, being displaced by an abundance of subtropical genera, and are dominant only in relatively restricted “upland prairies” located on hills and knolls with shallow soils, dry in the summer (Iriarte 2006).

In Brazil *N.neesiana* is most common in ‘cleared and treed fields’ (rough translation of Longhi-Wagner and Zanin 1998). It is not an important component of the natural vegetation of the Northern Campos of northern Uruguay and the campos of the southern Brazilian State of Rio Grande du Sol, which have fewer Stipeae and more numerous representatives of Paniceae and Andropogoneae (Soriano *et al.* 1992). *N. neesiana* was not found by Overbeck and Pfadenhauer (2007) in surveys on Morro Santana, near Porto Alegre in Rio Grande do Sul, near the eastern edge of Brazilian campos, an area with rainfall exceeding 1200 mm per annum and no dry season, but Overbeck *et al.* (2007 p. 106) list it (as *Stipa setigera* C. Presl) as a subtropical area “characteristic” species of grasslands in the southern Rio Grande do Sul of Brazil, along with *N. megapotamia, N. nutans* (Hack.) Barkworth and *N. philippii* (Steud.) Barkworth. The northern boundary of the Pampean province of southern Brazil is at about 30°S (Overbeck and Pfadenhauer 2007).

On the Juan Fernández Islands of Chile it is found on rocky slopes near the sea, in dry or humid gorges, rocky cliffs, on and between rocks and in open places (translation from Baeza *et al.* 2007).

In south-western Europe most exotic Stipeae occur on disturbed land or higly modified areas and have failed so far to occupy more natural areas, with the exception, to date, of *N. neesiana*, which “penetrates into natural, protected areas ... and behaves like an aggressive invader” in the Canary Islands (Verloove 2005) e.g. in the Garajonay National Park, Anaga Rural Park and Osorio Reserve (Sanz-Elorza *et al.* 2005). Since the mid 1960s it gradually spread along roads and through gaps and sparse vegetation on the island of Tenerife in nitrogen enriched environments (Martín Osorio *et al.* 2000). The larger Tenerife infestations occur on hard, basaltic substrates (Martín Osorio *et al.* 2000). South-western European *N. neesiana* “inhabits a wide range of usually anthropogenic biotopes varying from road-verges, abandoned vineyards, urban parks ... more or less ruderalized pastures, etc.” but also occupying rocky slopes in river valleys in France and Italy (Verloove 2005 p. 108). In Catalonia (Spain) small populations have been found on path margins and in abandoned vineyards (Font *et al.* 2001).

In New Zealand it occurs mainly in pastures and on roadsides (Edgar and Connor 2000) in dry, low-fertility, open habitats (Bourdôt and Ryde 1986) on various soil types, but not normally in fertile pastures where there is good competition from other plants (Bourdôt and Ryde 1986, Auckland Regional Council 2002). It occurs on “rolling hills and flats” at Waipawa (Bourdôt and Ryde 1987a), and often occurs on “steep inaccessible eroded land” (Bourdôt 1988). It invades unimproved pastures, infesting two of seven paddocks dominated by native tussock grasses in the Lake Grassmere area (Bourdôt and Hurrell 1989a). Its invasiveness in New Zealand sheep pastures was attributed by Bourdôt and Hurrell (1989a) to adaptations enabling survival in semi-arid, poorly fertile environments, rather that high competitive ability.

The little information available on the native vegetation formations invaded by *N. neesiana* in areas of its exotic range outside Australia is summarised in Table 3.

Table 3. Native vegetation formations invaded by *N. neesiana* outside Australia.

Vegetation class	Locations	Country	Major associated spp.	Reference
Bidenti pilosae-Ageratinetum adenophorae community	Teneriffe, Canary Islands	Spain	*Bidens pilosa* *Ageratina adenophora* *Myrica faya, Salix canariensis*	Martín Osorio *et al.* 2000
(*Erica platycodon*): *Ilici canariensis-Ericeto playcodonis*	Teneriffe, Canary Islands	Spain		Martín Osorio *et al.* 2000
Aeonietum cuneati	Teneriffe, Canary Islands	Spain		Martín Osorio *et al.* 2000
Periploco-Phoenico canariensis	Teneriffe, Canary Islands	Spain	*Phoenix canariensis*	Martín Osorio *et al.* 2000

Within Australia, occurrence in disturbed anthropogenic habitats is usual: e.g. North Central Region of Victoria: roadsides, waterways, small neglected semi-urban allotments (Frederick 2002), Sydney region "roadsides, pastures, grassy areas, along creeks and rivers" (Benson and McDougall 2005). In the ACT it occurs under a wide range of conditions "from heavily mown or grazed sites, from damp gullies and depressions out to drier slopes, to sites with low to medium levels of disturbance and in shaded and unshaded locations" (Bruce 2001). Areas in which it is most likely to occur include roadsides, tracks and paths (vehicle, walking, animal), mown areas, waterways and drainage lines (Bruce 2001). It is generally more abundant in grasslands that are small in size (<10 ha) but is recorded reaching subdominance levels in grasslands with areas exceeding 20 ha. Australian native vegetation formations that have been invaded are largely grasslands and grassy woodlands (Table 4).

Table 4. Native vegetation formations invaded by *N. neesiana* in Australia.

Vegetation class	Locations	State	Associated spp.	Reference
Lowland grassland and grassy woodland		Vic		Carr *et al.* 1992
Rock outcrop vegetation		Vic		Carr *et al.* 1992
Lava plain grassland	Western Melbourne	Vic	*Themeda triandra*	McDougall 1987
Temperate grassland	Derrimut and Laverton North Grassland Reserves	Vic	*Themeda triandra*	M. Bartley in McLaren *et al.* 1998
Red gum woodland	Western Melbourne	Vic	*Eucalyptus camaldulensis*	McDougall 1987
Grassy woodland	Tarngulla and Tooleen Flora Reserves	Vic	*Eucalyptus microcarpa*	Liebert 1996
	Melbourne Airport	Vic	*Eucalyptus microcarpa*	V. Stajsic in McLaren *et al.* 1998
	Long Forest Flora Reserve	Vic	*Eucalyptus microcarpa*	P. Wlodarcyzk in McLaren *et al.* 1998
Riparian vegetation	Lollypop Ck, Little River (You Yangs), Coimadai Ck. (Long Forest Flora Reserve), Tullaroop Ck.	Vic		V. Stajsic in McLaren *et al.* 1998
		Vic		Liebert 1996
	Tarnagulla	Vic		
Coastal river flat forest	St Clair	NSW	*Eucalyptus amplifolia*, *Angophora subvelutina*	Ens 2002a
Alluvial woodland	Mount Annan	NSW	*Casuarina cunninghamiana*, *Eucalyptus terticornis*	Ens 2002a
Natural grassland	Suburban Canberra	ACT	*Themeda triandra,* etc.	Bruce 2001

Trials on sandy loam soils in Western Australia showed that *N. neesiana* had low to moderate productivity or survival, or low leaf/stem ratios, in an area with 550 mm annual rainfall and a 6.4 month growing season, and fair to moderate production/fair to good survival in an area with 430 mm mean annual rainfall and 5.2 month growing season (Rogers *et al.* 1979).

Altitude

In its presumed native range *N. neesiana* occurs from low altitudes to increasingly high elevations in the tropics. In in the low hills of the Tandilia Range in the south-east of Buenos Aires Province of Argentina it occurs at least over an altitudinal band of c. 140-200 m (Honaine *et al.* 2009) and in the Ventana land system in south-west of that province it occurs at c. 500-650 m (Amiotti *et al.* 2007). In.northeast Argentina *N. neesiana* is found at a maximum altitude of 2700 m (Torres 1997). Specimens in the Herbarium of the Missouri Botanical Garden were collected at 2200 m at Tucumán, Argentina and 3500 m at La Paz, Bolivia (Martín Osorio *et al.* 2000). The record at Cochabamba, Bolivia by Senn (Bowden and Senn 1962) must also be at high altitude, at least exceeding 3000 m. In Ecuador it is present in an altitudinal range of 3000-3500 m (Clark *et al.* 1999-2008).

Specimens on record from the Juan Fernández Islands of Chile were collected in the altitudinal range 60-490 m (Baeza *et al.* 2007). In South Africa it is found in an altitudinal range of 600-1700 m (Germishuizen and Meyer 2003). In the Canary Islands it was collected as high as 850 m on Teneriffe and La Gomera (Martín Osorio *et al.* 2000).

In Australia the altitudinal range is from near sea level (e.g. in the Altona area near Melbourne) to c. 1200-1400 m at Guyra on the Northern Tablelands of NSW (Gardener *et al.* 2005). In the Sydney region it is found from 0-600 m (Benson and McDougall 2005).

Climate

Stipeae are generally classic xeromorphs or mesic, *Austrostipa aristiglumis* (F.Muell.) S.W.L. Jacobs and J. Everett and *Trikeraia* being exceptions (Arriaga and Jacobs 2006). In south-eastern South America members of the tribe increase with increasing latitude, being absent in the megathermic zones, a major vegetation component in mesothermic zones and dominant in Patagonia (Perelman *et al.* 2001). Indeed, increases of c. 15 to 23% in the average relative cover of Stipeae compared to other grass tribes has been measured across the narrow latitudinal range (c. 35-38°) of the Flooding Pampa, in Argentina (Perelman *et al.* 2001). The distribution of particular Stipeae, including several *Nassella* species, in this region shows strong latitudinal correlations, with a group including *N. hyalina* and *N. charruana* found only in the north, and others found only in the south (Perelman *et al.* 2001).

N. neesiana is unusual in that it has a very wide climatic tolerance. It has invaded areas outside the climatic range it occupies in South America (Gardener 1998). The stronghold of *N. neesiana*, the pampas region, has warm, often humid summers, mild, usually drier winters with temperatures uncommonly below freezing, annual rainfall of 600-1000 mm, and little drought (Mack 1989). In the pampas, "grass is driven out only where water is very abundant in the soil, as ... along the banks of rivers ... the climate is a perfect grassland-climate, with ... rainfall not more than moderate but well distributed ... humid, moderately warm vegetative season [and] strong winds ... with moderate atmospheric humidity ... hostile indeed to woodland" (Schimper 1903 p. 459). Summer rainfall is prevalent in eastern South America south of 30° including Rio Grande do Sul, eastern Uruguay and Argentina (Schimper 1903). Restricted occurences in southern Brazil, where the grasslands are considered to be relicts of drier, cooler conditions, may be determined by the more subtropical, humid climate (Overbeck and Pfadenhauer 2007). *N. neesiana* is one of the dominant grasses in La Plata district of Buenos Aires where the climate is warm temperate and humid, with a mean annual temperature of 16.5 ºC and mean annual rainfall of 992 mm (Cabrera 1949). It occurs across the Flooding Pampa of north-eastern Argentina which has annual rainfalls of 850-900 mm, average annual temperatures of 13.8-15.9°C and average minimum temperatures in July of 1.8-6°C (Perelman *et al.* 2001). It is a major grass in the Tandilia Range of south-east Buenos Aires province where the annual rainfall is about 800 mm and the mean monthly temperatures for the coldest and warmest months are 13 and 23°C (Honaine *et al.* 2009), and in parts of south-west Buenos Aires Province, where the climate is humid temperate with a mean annual temperature of 14.5ºC and annual average rainfall of 850 mm (Amiotti *et al.* 2007). It occurs in the littoral areas and lower parts of the La Plata basin where the climate lacks a marked dry season (Schimper 1903). Large tracts of northern Argentina, the base of the Andes and the Provinces of Entre Rios and Corrientes have annual rainfall of 1000-1200 mm (Schimper 2003) and in those areas *N. neesiana* loses its dominance in grassland to species better adapted to a wetter, more subtropical climate (Soriano *et al.* 1992). In Uruguay *N. neesiana* is supposedly "resistant to adverse climates" (Gardener *et al.* 1996b p. 3, citing Rosengurtt *et al.* 1970). In the Pampean province of southern Brazil the annual rainfall is in the range of c. 1200-1600 mm and mean annual temperatures are 13-17°C (Overbeck *et al.* 2007). On the Juan Fernández Islands of Chile it grows in dry or humid areas (Baeza *et al.* 2007).

In continental South America as a whole *N. neesiana* is found in the 500-1500 mm annual rainfall zones, with some extreme outliers, and its northern distribution is "limited by lack of low winter temperatures necessary for vernalization" (Gardener *et al.* 1996b), so is restricted to higher altitudes in the tropics. It occurs in southern Chile near Valdiva where the average annual rainfall exceeds 2600 mm and maximum/minimum temperatures are 22.8/11.1 in January and 11.1/5.0ºC in July (Gardener *et al.* 1996b). Similar seasonal temperatures occur in montane-alpine areas of south-eastern Australia, although few such areas have rainfall exceeding 1600 mm. It occurs in areas of far north-east Argentina near Posadas, where the rainfall was over 1900 mm per annum, with January and July maximum/minimum temperatures of 33.2/21.8ºC and 21.9/11.4ºC (Gardener *et al.* 1996b). The closest approximations to such a climate in Australia occur in the wet tropics. In western Argentina it occurs at Medoza, where the climate is very dry (223 mm) with January/July maximum/minimum temperatures of 32.0/19.4ºC and 14.7/2.4ºC (Gardener *et al.* 1996b), similar to some arid areas of inland southern Australia. In arid regions of South America it may only occur where the microclimate is more mesic, e.g. along rivers (Gardener *et al.* 1996b).

In South Africa *N. neesiana* has been recorded in temperate summer rainfall areas (Wells *et al.* 1986). The climate parameters of one of its stronghold areas in New Zealand are an annual average rainfall of 650-900 mm, warm summers with frequent droughts and moderate winters, conditions said to be very similar to the climate in its Argentinian range (Bourdôt and Hurrell 1989a). The 900 mm isohyet has been quoted as a limiting factor in north-facing hill slopes in the Hawkes Bay area of New Zealand (Slay 2002) where its potential range was considered to be "northerly facing hill country in low to medium rainfall (700-900 mm)" (Slay 2001 p. 5).

In south eastern Australia *N. neesiana* occurs primarily in areas with 500-800 mm average annual rainfall (Muyt 2001) in a range of climates including the warm wet summer/cold dry winter of the Northern Tablelands of NSW, and hot dry summer/cold wet winter of southern Victoria (Gardener *et al.* 1999). In the Sydney region it is found in areas with 700-1000 mm mean annual rainfall (Benson and McDougall 2005).

N. neesiana appears to be well adapted to seasonal dryness (Bourdôt and Hurrell 1987b) and is drought tolerant (Muyt 2001, McLaren *et al.* 2002b, Slay 2002c, Storrie and Lowien 2003). Tsvelev (1977 p. 2) thought that the small chromosomes and small pollen grains (general stipoid characters), lemma and palea structure protecting the flowers, a dense clumping habit and the presence of intravaginal shoots (as in *N. neesiana*) all indicated specialisation for xerophytic climates. Slay (2002a p. 10) thought that the bare ground resulting from drought was "the catalyst for seedling establishment".

Fire

Fire is a feature of the campos and pampas grasslands of South America, but as in other areas of the world, the ancient and pre-European fire regimes are poorly understood. Darwin (1845 p. 114) reported that the plains from Bahía Blanca to Buenos Aires were commonly deliberately burnt, "chiefly for improving the pasture": "it seems necessary to remove the superfluous vegetation by fire, so as to render the new year's growth serviceable". Great fires across the pampas were reported in 1853 (Soriano *et al.* 1992).

The fire history of Southern Brazil is "poorly known" but palynological studies indicate that fires were rare before c. 7400 years ago and then became frequent, possibly as a result of deliberate burning for hunting (Overbeck and Pfadenhauer 2007 p. 28). In southern Brazilian grasslands, where *N. neesiana* is native, fire became more frequent from the beginning of the Holocene, proabably as a result of the advent of human populations, and currently grazed native grasslands are burned approximely biannually, usually in August (Overbeck *et al.* 2007). Most of the grassland species of southern Brazil "seem to be adapted to frequent ... burning" (Overbeck *et al.* 2007 p. 107).

Honaine *et al.* (2009) stated that winter burning, along with grazing, in the flechillar community of the Tandilia Range of Buenos Aires province, in which *N. neesiana* is a major component, led to the dominance of *Achillea millefolium* L. and *Carduus acanthoides* L. (Asteraceae). Historical observations suggest that fire occurred at intervals of 5 years in the stipoid dominated savannah grasslands of the more arid Caldenal, to the south and west of the Pampean region, before the introduction of livestock (Fernández *et al.* 2009).

Bourdôt (1989) noted that in New Zealand "regular burning promotes the grass" and that after fire "tussocks quickly begin to re-establish from clandestine seeds present in old tiller bases". Liebert (1996 p. 15, quoting Craig Bay on the plant's behaviour at Organ Pipes National Park, Victoria) stated that it is "usually the first grass to resprout after fire". Stewart (1996) recorded that dense *N. neesiana* quickly regained high cover after a wildfire at Broadmeadows Valley Park, Victoria, in December 1994, reaching 50% cover after approximately 6 months and 70% cover after 7 months, and reaching a height of over 50 cms after 11 months. Kirkpatrick *et al.* (1995 p. 35) considered that it "generally ... recovers more quickly than other species" and is "as well adapted to fire as the native dominant" *T. triandra* (*op. cit.* p. 82). However the precise timing of fire in relation to rainfall likely has a large influence on which plant species recover first.

Young seedlings and small plants are possibly killed by fire, but larger plants lose most of their above-ground biomass and resprout from protected buds. In the classification used by Overbeck and Pfadenhauer (2007) the seedlings are "non-sprouters", while tussucks are fire "resistors", retaining some dead stem biomass after burning. The above-ground meristems are protected by the densely packed basal leaf sheaths (Overbeck and Pfadenhauer 2007), some of which burn, but many of which resist burning because of their high moisture content and tight packing and merely char on the outside. Thus, older tussocks are best adapted to frequent burns.

Britt (2001) found that burning, after application of 1 litre of methylated spirits to square metre areas surrounded by a metal frame, eradicated adult plants in an infested pasture. Hocking (2005b) reported on small scale experimental burning of thickets at the Iramoo native grassland, Victoria, in late spring and summer 2002. Both early and late spring burning resulted in less than 10% of mature tussocks resprouting after the autumn break, much lower than unburnt treatments, a reduction of more than 75% in mature tussocks, but an increase in the number of small tussocks and very immature tussocks, likely resulting from fragmentation of what had previously been large plants. Late spring burning removed all viable seed from the site, reduced seed production in the subsequent fruiting period by c. 50% and appeared not to lead to any major seedling recruitment, up to and including the following spring. Early spring fire had no effect on subsequent seed production.

As with other grasses, the specific effects of fires are likely to be dependent on the intensity, severity and precise timing of the fire. Seed that has found its way into the soil is likely to survive, presumably in a similar way to that of *Austrostipa*.

Other disturbances

Weed invasion of natural communities is often facilitated by disturbance, and the more frequent, intense or prolonged that disturbance the greater the invasion is likely to be (Fox and Fox 1986, Carr *et al.* 1992, D'Antonio *et al.* 1999). According to Weber (2003 p. 280) in a survey of environmental weeds of the world, based on a very limited literature review, *N. neesiana* "invades mainly degraded and disturbed plant communities". Bartley *et al.* (1990), commenting on the situation in Victoria, wrote that "prior disturbance does not appear to be necessary for invasion" for *N. neesiana* invasion of native grasslands. This was echoed by Kirkpatrick *et al.* (1995 p. 35), who nevertheless added that "its spread is certainly facilitated by soil disturbance". According to Slay (2002a p. 4) *N. neesiana* "evolved under conditions of low disturbance", however Gardener (Gardener 1998, Gardener *et al.* 1996, 1999, 2003b) found that *N. neesiana* seeds only germinate on bare ground, in gaps or areas bared by herbicides and other disturbances, and that seedlings only survive in bare areas. The plant survives well in the Rio de Plata grasslands where trampling by cattle "is the main anthropic disturbance" (Soriano *et al.* 1992). Bedggood and Moerkerk (2002) recorded regrowth of *N. neesiana* in wheel tracks after treatment of infestations with glyphosate using vehicle mounted wick wipers. Liebert (1996) recommended the avoidance of unnecessary soil disturbance to minimalise *N. neesiana* invasion.

Bruce (2001) attempted to determine the importance of different types of disturbance in determining the level of *N. neesiana* infestation in native grasslands in the ACT. She assessed the current extent of four 'disturbance types' on a four point scale from absent (0) to high (5): bare ground, other exotic weed populations, soil disturbance (earthworks, erosion, cultivation, animal diggings etc.) and the amount of refuse dumping (garden waste, soil, rubbish). The literature contains numerous mentions of the importance of 'bare ground' to enable seedling establishment. The usual meaning appears to be soil lacking other vascular plants above ground and devoid of litter. Bruce (2001) found that *N. neesiana* had wide levels of abundance, from absent to dominant, where bare ground was present at low and medium levels. It had the largest range of abundances (0-5) at high weed levels, and the lowest (0-3) at low weed levels (perhaps suggesting that *N. neesiana* facilitates invasional meltdown). The single site with no soil disturbance had occasional patches of the weed, sites with low soil disturbance had a range of infestation levels (0-5) and sites with medium soil disturbance were overall more highly invaded (1-5). No sites had high soil disturbance. Infestation levels varied widely for all levels of dumping, but *N. neesiana* was observed to have established and be spreading from scattered piles of lawn clippings at one site.

Proximity to urban development appeared to be the most important predisposing factor for *N. neesiana* invasion in the ACT, and use of the land as urban open space appeared to almost guarantee that it would become infested, probably as a result of seed dispersal by mowing (Bruce 2001).

No-one appears to have comprehensively evaluated past disturbance in relation to present *N. neesiana* infestations. Historical disturbance patterns are more difficult to determine and there are more difficulties in assessing their intensity, frequency and duration. Consensus opinion appears to be that disturbances of various types can facilitate invasions and it appears likely that in those cases where invasion has been recorded without disturbance, there has been inadequate appreciation of the effects of prior disturbances. The effects of various disturbances including fire, grazing and herbicides on *N. neesiana* establishment and survival are discussed in more detail below.

Shade

N. neesiana has been called a sun loving ("heliófilas") species (Martín Osorio *et al.* 2000 p.39) but is adapted to moderate shade (Muyt 2001). It has considerable shade tolerance, up to medium level tree densities, e.g. in wooded areas around Bendigo, Victoria (Hocking 1998). Bruce (2001) found it was commonly present in shaded areas in the ACT , e.g. in windbreaks, very open woodlands, under oak trees, pines, eucalypts including *Eucalyptus melliodora* A. Cunn. Ex Schauer, *Acacia* spp. and shrubs. It grew in both shaded and unshaded locations at 59% of sites investigated (Bruce 2001). In the Sydney region it occurs in woodlands with *Eucalyptus moluccana* Roxb. and *E. tereticornis* Sm. (Benson and McDougall 2005). In New Zealand, *N. neesiana* plants growing under 25 year old *Pinus radiata* are generally weaker than plants growing in the open and have reduced seeding potential (Slay 2002a). *N. neesiana* was present in 3 of 6 treed paddocks examined by Bourdôt and Hurrell (1989a) in New Zealand. In the Canary Islands it "thrives" under the evergreen *Laurus azorica* (Seub.) Franco and the deciduous *Castanea sativa* Mill. (Verloove 2005).

The literature appears to contain no precise informat.ion on the effects of solar radiation levels. *N. neesiana* plants growing under *Eucalyptus* in the ACT in early-mid summer were much greener and in an earlier reproductive stage than those in the open (Bruce 2001). Plantations with 2500 trees per ha have been established in New Zealand to examine the effects of shading as a possible control option (Slay 2002a 2002c).

Soils and nutrients

N. neesiana occupies areas on a wide range of geological substrates with a diversity of soil types. The soils may heavy or light textured (Cook 1999) and have low or high fertility (Muyt 2001, Slay 2002c).

In Argentina it is found on well-drained, drought-prone soils (Bourdôt and Hurrell 1989b citing Cabrera and Zardini 1978, Lewis *et al.* 1985). In the Argentine pampas it is found on deep, generally fertile loessic silts and clays (Gardener 1998). These soils were formed on very deep (>c. 300 m) deposits of silt or loess, rich in swelling clays, and are mainly mollisols (commonly very deep, high fertility argiudolls) or frequently vertisols, of very young age (Soriano *et al.* 1992). In the Flooding Pampa t is not a component of the floristic groups characteristic of deep, non-saline, well-drained soils, nor the group that characterises areas subject to long flooding, nor in areas with saline alkaline soils (Perelman *et al.* 2001). It is most frequent in areas with higher topographic position, being scarce in depressions and lower lying areas, and occurs over a pH range of c. 6-8.2, disappearing in the more alkaline soils that occur in wetter depressions and are correlated with salinity (Perelman *et al.* 2001). In the Ventania land system in south-west Buenos Aires Province the soils are formed on a more complex mosaic of Palaeozoic sedimentary rocks (Soriano *et al.* 1992) and are"Typic and Lithic Argiudolls and Hapludolls developed from pure loess sediments or mixed with rock detritus", slightly acid (pH 6.4-6.8), a high saturation with bases, organic carbon levels > 5.5. g kg^{-1} and total N > 0.4 g kg^{-1} (Amiotti *et al.* 2007 p. 535). In the Gualeguay area of Entre Rios province it is found on light loam, with much organic matter to a depth of 40-60 and pH in the range 5-6.8 (Marco 1950). In the Tandilia Range it occurs on soils derived from loess over quartzite, that are typic Haludolls 10-25 cm deep and Argiudolls 20-70+ cm deep with organic horizons less than 5 cm deep (Honaine *et al.* 2009). Although widely dominant in the Rolling Pampas, it is replaced by *Sporobolus* spp., *Jarava plumosa* and other plants where the soils are slightly alkaline (Soriano *et al.* 1992). Mollisols and vertisols predominate also in the southern campos (Soriano *et al.* 1992). Soils of the Southern Pampa and Flooding Pampa are noteably deficient in P (Soriano *et al.* 1992).

In Europe it is generally found on well-drained, "sometimes slightly eutrophic" soils and on rocky slopes (Verloove 2005 p. 108). On Tenerife, Canary Islands, it prefers the nitrogen-enriched ruderal areas of fringe roads (Martín Osorio *et al.* 2000).

In New Zealand the substrate rock types are loess, mudstones, and sandstones on slopes commonly 16-25° (Bourdôt and Hurrell 1989a), and it prefers acidic soils, low in phosphate, calcium and summer moisture (Esler *et al.* 1993, Champion 1995). It is recorded from Yellow Grey Earths, particularly when acidic or low in P, Ca or summer moisture (Bourdôt and Hurrell 1989b). Slay (2002a p. 4) considered it "apparently better adaptated to low fertility sites" in that country.

Gardener (1998 p. 10) considered it was then generally found in Australia on "more fertile ... predominantly volcanic" soils, but noted its presence on granitic soils at Tenterfiled and Emmaville, NSW, on rich clay at Lucindale, South Australia, and alluvial soils near Melbourne. Infestations are widespread on the primarily heavy clay soils derived from basalts on the Victorian Volcanic Plains. Liebert (1996) found infestations on granitic and sedimentary soils in North Central Victoria. In the ACT it does not tend to establish on slopes with westerly aspects and shallow soils (Bedggood and Moerkerk 2002). In the Sydney region it occurs on clays on shale substrates with medium nutrient levels (Benson and McDougall 2005).

According to Bedggood and Moerkerk (2002 p. 6) *N. neesiana* "does not establish well where nutrient levels are really low such as hillsides", but "does better on flats where nutrient levels are moderate". When P is added to pastures, desirable pasture grasses respond better than *N. neesiana* (Bedggood and Moerkerk 2002) and increase their basal cover at its expense, with the effect apparent with or without strategic grazing at 300 DSE ha^{-1} (McWhirter *et al*. 2006). Grech (2007a 2007b) found that *N. neesiana* responds to phosphorus fertilisation.

Landform

N. neesiana is widespread in the pampas, which generally consists of completely flat plains alternating with gently undulating landscapes (Soriano *et al.* 1992), although it appears to be restricted to slightly elevated areas, i.e. away from minor depressions in Flooding Pampa (Perelman *et al.* 2001). *N. neesiana* occurs in the vegetation of other landforms in Argentina including rocky terrain in the low hills of the Tandilia Range of south-east Buenos Aires provine (Honaine *et al.* 2009).

Bruce (2001) found that *N. neesiana* occurred mostly in the ACT on slopes (rather than valleys, watercourses, gullies or flats), where it had a wide range of abundances, and at sites with combinations of these landforms. Slay (2002c) considered that it colonised the dry northerly faces of hills in New Zealand.

Water, drainage and flooding

N. neesiana reportedly tolerates seasonal water-logging (McLaren, Stajsic and Iaconis. 2004) but the tolerable frequency and duration of such stress are not precisely known. In Argentina, Gardener *et al.* (1996b) found that it did not occur on wetter, often-inundated low ground, although such depressions were often saline, or on deep clays. Stipoids do not occur in the saline and alkaline soils of halophytic steppes of shallow, wet depressions of Flooding Pampa (Perelman *et al.* 2001) and appear to be entirely absent from saline soils in the pampas (Soriano *et al.* 1992). *N. neesiana* is not an important species in the Flooding Pampa of Argentina, an area subject to drought and very dry summers, and flooding “almost every year”, mainly lasting c. two weeks and 5-10 cm deep, with “extensive and lenthy flooding ... 3 to 6 times per century” (Soriano *et al.* 1992 pp. 394 and 374).

In Australia *N. neesiana* was found on alluvial flats subject to seasonal waterlogging at Wattle Park, Burwood, Victoria by Geoff Carr (McLaren *et al.* 1998), often establishes in damp depressions (Liebert 1996) and on land subject to periodic inundation (Muyt 2001), and is “more common in low-lying, wetter areas” (Hocking 1998 p. 90). Swarbrick and Skarratt (1994) erroneously isted a single habitat known to be invaded, saline wetlands (atttributed to Carr and Yugovic 1989). Bruce (2001) found that it occurs in wetter areas in the ACT, as well as on slopes, and that an association with drainage lines, streams and damp depressions was apparent at most sites surveyed, with an infestation in one case radiating up-slope from a creekline. She illustrated a plant overhanging a drain, downstream of which patches of further plants were found. Kirkpatrick *et al.* (1995 p. 35) stated that it “can grow in a large range of soil moisture regimes”. Slay (2002c) noted that it thrives under moderate to severe stress due to low soil moisture.

High rainfall in spring promotes panicle proliferation (Cook 1999) and plants flower in response to summer rain (Bedggood and Moerkerk 2002). *N. neesiana* prospers on roadsides where there is run-off and good soil moisture (Bedggood and Moerkerk 2002). F. Overmars (in Iaconis 2006b) reported that it was growing and setting seed in drains in the Melbourne area in October 2006 during severe drought.

Other plants

Other plants or plant associations in areas invaded by *N. neesiana* might provide biotic resistance to invasion, or may alone or in combination faciltate or prevent *N. neesiana* establishment or survival.

The pampas grasslands, which have probably persisted without major change since the late Miocene (c.14 mybp) (Webb 1978), are treeless and dominated by caespitose grasses with a wide variety of smaller herbs. In the Argentine pampas *N. neesiana* occurs as one element of a diverse grassland flora that normally includes summer growing grasses, including *Bothriochloa*, *Panicum* and *Paspalum* as common components (Gardener *et al.* 1996b). In the Flooding Pampa it is closely associated with *Jarava plumosa* and *Bothriochloa laguroides*, and is commonly found in communities with high frequencies of *Paspalum dilatatum* Poir., *Piptochaetium montevidense*, *P. bicolor* (Vahl) Desvaux, *Vulpia* sp., *Bromus catharticus* J. Vahl and other grasses and with a rich array of forbs (Perelman *et al.* 2001). It is “one of the dominant grassland species” in the pastoral zone around Buenos Aires (Gardener *et al.* 1996b). In the department of Gualeguay in south-west Entre Rios (Argentina) it is of secondary importance as a winter grass in pastures of the high campos (better drained areas with grasses maintaining a height of 20-40 cm), along with *N. hyalina*, the more important winter-spring forage plants being *Bromus catharticus*, *Lolium multiflorum* Lam. and *Medicago* spp. (Marco 1950). The co-occuring spring-summer grasses of most importance include *Paspalum* spp., *Axonopus compressus* (Sw.) P. Beauv., *Setaria* spp., *Andropogon saccharoides* Sw. and *Eleusine tristachya* (Lam.) Lam. (Marco 1950). In the Ventania land system in south-west Buenos Aires Province it naturally occurs in association with *Stipa ambigua* Spegazzini and *Amelichloa caudata* (Trin.) Arriaga and Barkworth in grassland with isolated trees of *Prunus mahaleb* L. (Amiotti *et al.* 2007). Genera that include dominant or subdominant species south of Buenos Aires include *Agropyron*, *Aristida*, *Briza* and *Piptochaetium*. Other *Nassella* species are widespread components with *N. hyalina* and *Jarava plumosa* common around Buenos Aires. In drier western areas *Jarava ichu* Ruiz and Pavon, *N. tenuissima* and *N. trichotoma* are more prominent, along with *Poa ligularis* (Mack 1989).

In southern Santa Fe province (Pampean phytogeographical province) it is a characteristic species of a flechillar community along with *N. hyalina* and *Jarava plumosa*, with *Bothriochloa laguroides*, *Sporobolus africanus* and *Carex bonariensis* Desf.ex Poir. (Feldman *et al.* 2008). The Espinal phytogeographical province occurs in dier areas to the north, west and south-west of the Pampean phytogeographical province. Espinal vegetation is woodland or savannah with *Prosopis*, *Acacia* and *Celtis* as the main (woody) dominants but in San Cristóbal county of Santa Fe province includes a flechillar grassland community over 1 m tall strongly dominated by *N. neesiana* (Feldman *et al.* 2008).

In the Tandilia Range of south-east Buenos Aires province it is a major species in a community of diverse grasses, the most abundant of which include *Piptochaetium biocolor* (Vahl) Desv., *P. medium* (Speg.) M.A. Torres, *P. hackelii* (Arech.) Parodi, *Stipa bonariensis* Henr. and Parodi, *Briza* spp. and *Bothriochloa laguroides* (DC.) Pilger, and some shrubs, but not in the monospecific pajonal community which is dominated by *Paspalum quadrifarium*, a grass that produces large accumulations of dead standing biomass in its tussocks (Honaine *et al.* 2009).

N. neesiana is not a grass of major importance in the semi-arid Caldenal of Argentina, where the vegetation was orginally grassy steppe, but which is now largely savannah grassland with scattered trees, mainly *Prosopis caldenia* Burkart, known as caldén, and shrubland with rich shrub diversity. The main grasses are other species of Stipeae and *Poa ligularis* (Fernández et al. 2009).

In the southern Brazilian campos of Rio Grande do Sul, *N. neesiana* occurs along with a wide range of both C_3 and C_4 grasses including *Aristida* spp., *Paspalum* spp., *Piptochaetium* spp. and other *Nassella* spp. (Overbeck *et al.* 2007).

On Tenerife, Canary Islands, *N. neesiana* occurs in environments characteristic of the *Bidenti pilosae-Ageratinetum adenophorae* community, especially in areas cleared of vegetation along margins of roads and gutters and is especially prevalent relatively humid areas in gorge bottom inhabited by such species as *Myrica faya* and *Salix canariensis* (Martín Osorio *et al.* 2000). The vegetation invaded was characterised in detail by Martín Osorio *et al.* (2000) (see Table 3).

In Villa Ada, Rome, Italy, it has 'colonised some hectares of hedges and lawns' and it is found in grassy areas in Italy generally (Moraldo 1986 p. 217).

These records in the native and invaded habitats indicate that *N. neesiana* coexists with a diverse array of other dominant and subsidiary grasses and a wide variety of forbs in natural grasslands but is rarely associated with trees and shrubs.

In southern New South Wales *N. neeisana* forms dense monocultures that can dominate pastures (Verbeek 2006). In New Zealand pastures, dense clumps of *N. neesiana* also exclude other pasture species (Bourdôt and Ryde 1986) and replace more desirable grasses, particularly *Lolium perenne* (Bourdôt and Hurrell 1989b). Bourdôt and Hurrell (1989b) sprayed out a dense infestation of *N. neesiana* on low-fertility soil, rotary hoed the area and sowed plots of *Lolium perenne*, *Dactylis glomerata* L.and *Phalaris aquatica*. Plots were fertilised with superphosphate and lime or unfertilsed, and *N. neesiana* germinated uniformly across the area. 13 months later, *N. neesiana* ground cover in unsown areas was greatest in fertilised plots (69%) than unfertilised (53%) and its dry mass production in fertilised plots was also greater (3.43 t/ha vs. 2.72 t/ha). In *Lolium* plots *N. neesiana* cover was only 1% in fertilised plots and 11% in unfertilised plots. In *Phalaris* plots *N. neesiana* cover was approximately equal in fertilised and unfertilised treatments. In *Dactylis* plots *N. neesiana* cover was much higher in unfertilised plots (39%) than fertilised plots (19%). Plots were fertilsed again in year two. Over three years the dry mass of *N. neesiana* in both fertilised and unfertilised unsown plots as a proportion of total dry mass in the plot fell significantly from c. 95% to c. 75%, the balance being "litter and other species", but mainly litter. In competition with the other grasses, dry mass production of *N. neesiana* as a proportion of total plot biomass was greatest with *Phalaris*. *N. neesiana* was less productive in competition with all three pasture grasses in fertilised plots, with the effect most pronounced for *Lolium* and least with *Phalaris*. Seeding of *N.neesiana* was considerably reduced in the sown plots compared to the unsown and most reduced in competition with *Dactylis*. In unfertilised plots with *Lolium*, *N. neesiana* became the dominant biomass component after three years, with *Dactylis* remained at a constant proportion over the period and with *Phalaris* declined as a proportion of total biomass. Fertiliser treatment induced temporal stability in terms of the proportion of contributions of the sown grasses and *N. neesiana* to total biomass production. In conditions of low fertility *S.neesiana* appeared to suppress *Lolium*, but under high fertility the dominance was reversed. *S. neesiana* was considered to be a stress-tolerant competitor, "evolved under conditions of low disturbance but moderate-severe stress from low soil moisture and probably low fertility" (Bourdôt and Hurrell 1989b p. 324).

During the early period of invasion at Derrimut Grassland, Victoria, *N. neesiana* occurred occasionally in a *Vulpia* association often with *Austrostipa bigeniculata*, along drainage lines and in areas ploughed during the 19th century or subsequently heavily grazed (Lunt 1990a). This formation was considered to be occupying areas probably previously dominated by *T. triandra*.

N. neesiana has poor competitive abilities with grasses and clovers that respond to high soil fertility (Connor *et al.* 1993, Liebert 1996). Vigorous pastures can resist invasion including *Phalaris*, although *Phalaris* pastures are sometimes invaded (Bedggood and Moerkerk 2002). Grech (2007a 2007b) found little difference between *Phalaris aquatica* and *N. neesiana* responses to increased phosphorus. Lunt and Morgan (2000) found a negative relationship between *T. trianda* and *N. neesiana* at Derrimut Grassland Reserve which indicates that this competitive summer-growing C_4 grass can resist invasion. There is evidence for similar resistance to *N. trichotoma* by *T. triandra* (Hocking 1998) and *Bothriochloa macra* (Steud.) S.T. Blake when maintained in a healthy condition (Michalk *et al.* 1999), but distribution surveys suggest no such resistance is provided by C_3 winter-growing native grasses (Badgery *et al.* 2002). *N. neesiana* is reported to have "choked out" *N. trichotoma* in trial plots (Hunt 1996, McLaren *et al.* 1998) and to have invaded infestations of this grass (Liebert 1996 citing David Boyle). Bruce (2001) compared the level of *N. neesiana* invasion to the "botanical significance" rating of 39 grassland sites in the ACT and found no clear trends,both rich and poor sites having both zero and high level infestations.

Such data indicate that *N. neesiana* can be excluded from vegetation that is dominated by healthy growth of other perennial grasses. Management practices that reduce competition by other plants, such as slashing of *N. neesiana* on roadsides, might therefore be counterproductive (Bedggood and Moerkerk 2002).

Herbivory

Grasses have coevolved with large grazing mammals and have a wide array of adaptations to grazing. One of the most important is the presence of intercalary meristems at the base of the leaves, rather than on the plant apices, a defence that probably played an important role in the evolution of the family (Stebbins 1986) and enable a plant to more readily regenerate after it is grazed. As in some other grasses (de Triquell 1986), the presence of multiple inflorescences on the panicle of *N. neesiana* allows the first developed, upper panicle to be sacrificed to herbivores, while the inflorescences closer to the ground and concealed beneath leaf sheaths, remain protected. The basal cleistogenes of *N. neesiana* are well protected from grazing mammals and develop even under conditions of heavy grazing (Dyksterhuis 1945, Gardener and Sindel 1998). *N. neesiana* thus has major advantages compared to Australian native grasses which lack cleistogenes.

Little information appears to be available about the native mammalian herbivores that utilise or once utilised *N. neesiana* in South America. Before human occupation the pampean region was occupied by"outlandish humpless camels and giant flightless birds" (Crosby 1986 p. 159). Large grazing animals went extinct at about the same time as indigenous human occupation of the southern Brazilian grasslands in the early-mid Holocene (Overbeck *et al.* 2007). According to Overbeck and Pfadenhauer (2007) large native herbivores became extinct in the pampas c. 8000 years ago, at the end of the last glacial period. The Pleistocene megafauna and other large grazing mammals through Argentina, Uruguay and southern Brazil included such species as *Toxodon platensis* (Notoungulata), *Glyptodon* spp., *Megatherium*, *Pampatherium* sp., *Stegomastodon platensis* (Xenarthra), *Equus sp.and*

Hispidon sp. (Perissodactyla: Equidae), *Hemiauchenia* sp., *Lama gracilis, Lama guanacoe* (Artiodacytla: Camelidae) and various Cervidae (Carlini *et al.* 2004, Norriega *et al.* 2004). The herbivorous megafauna of South America was comparatively large compared to other continents, and went extinct from the late Pleistocene into the Holocene (Johnson 2009). It appears probable that these animals strongly influened the distribution of grasslands and had strong selective effects on the grassland flora, although knowledge of these palaeoecological relationships is currently very deficient (Johnson 2009)..

Its ancestors may have subject to predation by dinosaurs and probably Gondwanatheria, about which little is known, but which had teeth which indicate that grasses may have been major components of their diets (Prasad *et al.* 2005).

Before Spanish occupation in the 14th century, the pampas lacked bovids (cattle and sheep) (Mack 1989) and large herbivores were scarce from the end of the Pleistocene until European colonisation (Fernández *et al.* 2009). An array of medium sized mammals was present, of which the the largest grazers were deer (Darwin 1845), and the camelids, the most important of which was the guanaco *Lama guanicoe* (Müller). Large herds of grazing animals were absent at least from the Tertiary until the arrival of Europeans (Coupland 1992).

The camelids have broad, spreading, soft-padded feet that do not compact the soil (Castillo-Ruiz and Lundrigan 2007) and a digestive system with foregut fermentation, similar to ruminants (Siebert and Newman 1989). The Guanaco is a moderate sized herbivore about 1 m tall at the shoulders, which commonly forms herds of 4-18 with males troops of up to 200, and is a grazer and browser, consuming grasses, lichens, forbs, seeds, fruits, rushes and sedges. It has narrow foot pads and a more hoof-like nails than camels. The Alpaca *Lama pacos* (L.) and the Llama *L. glama* (L.) are domesticated forms, probably of the Vicuna *L. vicugna* (Molina) and the guanaco respectively, and all four of these taxa will interbreed. Recent evidence indicates that domestication of the wild species occurred 6000-7000 years ago. There were probably 10 million alpacas and several million llamas on the continent when the Spanish arrived in the 14th century, along with similar numbers of the undomesticed species, but within 100 years the populations collapsed, probably largely as a result of competition with domestic livestock (Long 2003), but no doubt greatly propelled by the destruction of the indigenous human cultures.

The Vicuna is now restricted to the central and southern Andes in arid and montane grasslands at altitudes of 3500-4800 m, but it formerly had a more extensive range now occupied by exotic sheep and goats (Long 2003, Castillo-Ruiz and Lundrigan 2007). It too feeds on grasses and forbs (Long 2003). The reported diet of the alpaca in highland Chile is dominated by grasses including *Festuca* spp., *Deschampia caespitosa* and *Agrostis tolucensis* (Castillo-Ruiz and Lundrigan 2007).

Darwin (1845) reported that the only large indigenous mammal still common in the extensive grasslands of the Maldonada region of Uruguay (near Montevideo) by 1852 was the Pampas Deer *Ozotoceros bezoarticus* L., but rheas *Rhea americana* (L.) were also common. The Pampas Deer is now extinct throughout the Rio de la Plata grasslands except in a few small reserves and ranches (Soriano *et al.* 1992, Cosse *et al.* 2009) while rhea populations have sharply decreased due to uncontrolled hunting and wire fences (Soriano *et al.* 1992). Cosse *et al.* (2009) investigated the diet of Pampas Deer on a ranch in south-eastern Uruguay and found that cultivated rice and *Lolium* sp. were the most important food plants in this agricultural environment, that the dietary overlap with sheep was complete, but that there was limited competition for food with cattle. Various grasses were recorded in the diet, not including *Nassella* or other Stipeae, although unidentified monocots generally comprised about one third of material found in faeces.

Wild cattle *Bos taurus* L. and horses *Equus caballus* L. became established in Argentina after the abandonment of Buenos Aires by the Spanish in 1537 (Long 2003). 80,000 horses were present around Buenos Aires by 1585, large numbers of cattle were present by 1609 (Soriano *et al.* 1992) and millions of cattle and horses were present on the pampas by 1699 (Long 2003). According to Darwin (1845 p. 120): “The countless herds of horses, cattle and sheep, not only have altered the whole aspect of the vegetation, but ... have almost banished the guanaco, deer, and ostrich” (Rhea). Horses and cattle were introduced east of the Uruguay River by Jesuit missionaries in the 17th century and rapidly proliferated in the feral state (Overbeck *at al.* 2007). The whole of the campos and pampas have been grazed by sheep, cattle or horses “generally for centuries” (Soriano *et al.* 1992 p. 380). Cattle grazing and other agricultural pursuits have greatly altered the landscape, with agricultural ecosystems replacing native grasslands in most of the region, and large areas of native grassland surviving only in Buenos Aires province due to wetter, more saline soils (Pedrano *et al.* 2008). As with other major grasslands lacking a recent history of grazing by hard-hooved livestock (Mack 1989) the pampas grasslands were invaded by a large suite of exotic species after European colonisation. Livestock grazing in the Flooding Pampas has actively promoted these invaders, 75% of which are annuals and 74% forbs (Perelman *et al.* 2001).

Livestock grazing of natural grasslands and improved pastures is a major economic activity in the Rio de la Plata grasslands (Soriano *et al.* 1992) as is cattle ranching in the natural grasslands of southern Brazil, where 13.2 million head were present in Rio Grande do Sul state in 1996 (Overbeck *at al.* 2007). In Brazilian campos, grazing is “often considered the prinicpal factor maintaining the ecological properties and physiognomic characteristics of the grasslands” (Overbeck *at al.* 2007 p. 104).

N. neesiana may have existed through much of the Quaternary period and into early historical times under grazing pressure from large mammals that was relatively light, and was then subjected in much of its core range to unprecedented grazing by feral livestock. Limited evidence indicates that *N. neesiana* declines under livestock grazing in its native range in Argentina. After exclusion of large ungulates from Flooding Pampa grasslands the relative basal cover of the major grass species (*Briza subaristata* Lam., *Danthonia montevidensis* (DC.) et Lam., *Sporobolus indicus* (L.) R.Br. and *N. neesiana*) more than doubled to 97% after 4 years, while annual and broad-leaved herbs disappeared (Soriano *et al.* 1992). Under a management regime of grazing and winter burning in the Tandilia Range of Buenos Aires province, the major grass components of the flechillar grassland (including *N. neesiana*) decreased and the broadleaved *Achillea millefolium*. and *Carduus acanthoides* began to dominate, while under grazing alone *C. acanthoides*, *Cirsium vulgare*, *Dactylis glomerata* L., *Vulpia dertonensis* (All.) Gola. and *Bothriochloa laguroides* became more dominant (Honaine *et al.* 2009)

The situation appears to be different in Australia where *N. neesiana* is generally considered to be tolerant of heavy grazing by sheep and cattle (Storrie and Lowien 2003, McLaren, Stajsic and Iaconis. 2004, Grech 2007a), in part because of its relatively low palatability to these animals compared with desirable pastures grasses (Bourdôt and Hurrell 1989a, Grech 2007a). It has relatively low herbage production compared to some such desirable pasture grasses used in Australia, notably *Festuca* *arundinacea* (Gardener *et al.* 2005). *N. neesiana* tillers profusely when grazed (McLaren, Stajsic and Iaconis. 2004) and produces large amounts of unpalatable flower stalks and very little leaf material during flowering and fruiting (Gardener *et al.* 1996b, Gardener 1998, Grech *et al.* 2004, Grech 2007a). Stock avoid eating it in the reproductive stage even at stocking rates of 300 DSE ha^{-1} (Grech 2007a). However plants are palatable to livestock during much of the year (Grech *et al.* 2004, Grech 2007a). Slay (2002a) reported observations that ewes grazed *N. neesiana* in preference to *Dactylis glomerata* and *Lolium perenne* in winter near Napier, New Zealand. It can be reduced by appropriately timed grazing at high intensity, but the stocking rates and practices required are generally unrealistic for Australian conditions (Grech 2007a).

The impact of goats on *N. neesiana* is unknown, but goats are able to substantially reduce infestations of *N. trichotoma* (McGregor 2003). Goats and alpacas have been considered as potential control agents in Australia (Bedggood and Moerkerk 2002) but no trials appear to have been undertaken and no observations of *N. neesiana* herbivory by these species in Australia appear to be on record. Studies of biotic resistance (e.g. Parker *et al.* 2006a) suggest that alpacas would preferentially utilise Australian native plants or European grasses rather than *N. neesiana* or other South American grasses with which they may have coevolved.

No studies of marsupial grazing of *N. neesiana* appear to have been undertaken. It is not recorded whether it is eaten by kangaroos and whether they prefer it to native grasses, as predicted by the biotic resistance hypothesis. Studies of the feeding preferences of Eastern Grey Kangaroos by Robertson (1985) indicate that species of *Austrostipa* and other grasses with sharp and long-awned seeds are avoided when their inflorescences are present, and that narrow-leaved species that develop substantial standing biomass of dead foliage that restists selective foraging for green shoots suffer less damage. Thus macropod grazing of *N. neesiana* is probably similar to that by domestic livestock, in that it is avoided when in flower and fruit and has partial protection of green shoots resulting from retention of dead biomass, but will be selectively consumed when it is comparatively more palatable and accessible.

Mammal grazing selects for prostrate or low-growing ecotypes of *Stipa* (Peterson 1962) and many other perennial grasses, but the low-growing forms of many grasses are the result of phenotypic plasticity (Cox 2004). The so called ‘sward form’ of *N. neesiana* in Australia (Randall Robinson pers. comm.) characterised by a large number of semi-prostrate stems and more limited development of an uptright tussock form, appears to occur where mowing is frequent as well as in heavily grazed situations, but whether the plants resume a more normal form if these pressures are relaxed is unclear.

Grazing of various European pasture grasses has been found to lead to the development of ecotypes characteristed by small size and increased silica concentrations (Tscharntke and Greiler 1995). The relationships between the silica defences of grasses and grazing are as yet poorly understood, but it may be presumed that the altered grazing pressures in the introduced environment will select for different leaf hairiness and phytolith profiles characters. The possibility that such selection has altered the morphology or other characteristics of *N. neesiana* in Australia has not been investigated.

Physiology and biochemistry

The dominant native grasses in Australian temperate lowland grasslands are all C_3 species except for the major dominant *Themeda triandra*. Various other C_4 species commonly occur (e.g. *Aristida* spp., *Dichanthium sericeum*, *Panicum* spp.) and some form dense subdominant populations (e.g. *Bothriochloa macra*) but none are dominant over wide areas. *N. neesiana* is a C_3 grass. C_3 and C_4 plants possess different biochemical pathways of photosynthetic carbon acquistion and consequently have markedly different leaf anatomy, different ratios of carbon isotopes in their tissues ($^{13}C/^{12}C$ ratios or $\delta^{13}C$) and different responses to climatic factors (Hattersley 1986). The biochemistry of these differences is complicated and will not be explained here. In the simplest terms, the species that produce acids with four C atoms as the main initial stable product of CO_2 fixation are C_4 species, while those that produce the three-C acid 3-phosphoglyceric acid as the primary product are C_3 species (Salisbury and Ross 1992). There are three biochemical variants of C_4 photosynthesis in grasses, that differ in the main enzymes that catalyse the decaroboxylation of the four-C acids, the output products of that process and, with some additional compications, the leaf anatomy that supports the biochemistry (Hattersley 1986). Those that form malate utilise PEP carboxykinase and are called PCK species, while the two types that form aspartate utilise either NADP malic enzyme or NAD malic enzyme and are NADP-ME and NAD-ME species respectively (Hattersley 1986). Eleven differing biochemical/structural combinations have been identified. Andropogonanae have the classic structural NADP-ME type (Hattersley 1986), possessed also by *T. triandra*.

C_3 grasses generally have a lower optimum temperature for photosynthesis, and grow better in cooler environments with less light than C_4 grasses, which often have temperature optima in the 30-40ºC range and are mostly native to unshaded environments (Monson 1989, Salisbury and Ross 1992, Sinclair 2002, Jessop *et al.* 2006), although some have a large ecological range (Christin *et al.* 2009). C_3 species are most numerous in areas with a cool, wet spring and become dormant in summer (Sinclair 2002). In contrast C_4 grasses grow mostly in summer and are more efficient users of water and N, in terms of CO_2 assimilation, in high-light environments (Monson 1989). C_4 species have a competitive advantage when photorespiration costs become important, and are more efficeint in high temperatures and arid and saline environments (Christin *et al.* 2009) and much more efficient at producing biomass in warm environments with high light intensity (Salisbury and Ross 1992). The variations in the evolved biochemical-structural types of C_4 grasses likely have other ecophysiological and ecological implications, for instance differential leaf digestibility (Hattersely 1986).

C_3 grasses tend to have shallower root systems than C_4 grasses, which require water for growth in summer when it is generally less available, so widespread replacement of C_4 with C_3 species may increase deep drainage to water tables, and contribute to dryland salinity (Sinclair 2002).

Reactions of C_3 and C_4 species to increasing atmospheric CO_2 are complex, with neither group necessarily advantaged (Sinclair 2002). The C_4 species grow more rapidly under elevated CO_2 levels and it is likely that they will expand southwards, but this is dependant on the N usage of C_3 spccies under the changed conditions (Keith 2004).

Little is known of the specific biochemistry of *N. neesiana*, however a photosystem IIA protein, A9YFV6, has been described from *N. neesiana* chloroplasts (Boeckmann *et al.* 2003). Yeoh and Watson (1986) included *N. neesiana* in a study of the taxonomic patterns of protein amino acids in leaves and caryopses of grasses, but provided only aggregrate data at the tribal level. Seeds of Stipeae are high in Asx (aspartic acid or asparagine), glycine, methionine and arginine and low in glutamic acid, proline, alanine and leucine. They are nutritionally richer than seeds of Danthonieae, *Aristida*, Chloridoideae and Panicoideae, have protein contents equivalent to cultivated cereals and superior nutritional value to wheat, sorghum and maize varieties. The "*Stipa*" spp. analysed (including *Nassella* spp.) in aggregate are very similar to *Oryza* in leaf protein pattern except that Stipeae are lower in alanine and higher in valine. Stipeae, *Oryza* and Ehrharteae have the lowest free Glx (glutamic acid or glutamine) and the highest free Asx levels in the Poaceae. The variation in leaf amino acids are "unlikely" to be of any nutritional importance for mammals but may influence insect herbivory.

Investigations have recently been undertaken by the Victorian Department of Primary Industries in an attempt to identify molecular fingerprinting techniques for identification of *Nassella* spp. (David McLaren, DPI, pers. comm.) but results have not been published.

Breeding system

N. neesiana is self fertile (Connor *et al.* 1993) but can cross pollinate. It produces both chasmogamous and cleistogamous panicle seeds, along with concealed cleistogamous seeds on the stem nodes (Slay 2002c) (see discussions above on floral morphology). Such a breeding system is well suited to colonising grassland habitats (Evans and Young 1972).

Cleistogamy is more common in grasses than any other plant family and occurs in c. 19% of genera and 5% of species (Groves and Whalley 2002). Culley and Klooster (2007) found that it had been reported in 326 grass species, including 41 spp. of *Stipa* and 5 of *Nassella*. Two types of cleistogamy occur in *Nassella*, complete and dimorphic. Plants that are completely cleistogamous produce only cleistogamous flowers. Plants with dimorphic cleistogamy have both chasmogamous and cleistogamous flowers, the latter characterised by prominent differences in floral morphology including reduction in size or number of floral parts. In the cleistogamous flowers of grasses, the anthers, pollen sacs, stamens, stigmas, and lodicules are much reduced in size and the flowers develop no further than the bud stage (Brown 1952). The different flower types can be separated spatially on the plant, or temporally (often seasonally), or both, and in some plant species the ratio of flower types can vary between individuals and populations (Culley and Klooster 2007). The proportion of cleistogamous and chasmogamous florets in grass species is often under environmental control, e.g. *Amphicarpum purshii* produces few cleistogenous seeds after fire, but larger numbers as the likelihood of fire becomes high (Groves and Whalley 2002, citing Quinn 1998). Brown (1952) found that such facultative or ecological cleistogamy occurred in *Nassella leucotricha* in response to low availability of soil water. The distribution of cleistogamous and chasmogmaous fruits in the panicle depended on the soil water potential at the time of floral initiation.

Chasmogamy allows for gene exchange between individuals via pollen, and has population and evolutionary advantages where there is greater environmental variability, or the prevailing genotypes produce phenotypes that are poorly adapted. Cleistogamy, on the other hand, ensures self fertilisation with consquent high uniformity of genotype frequencies, so maintains the existing frequencies of locally adapted phenotypes and genotypes (Groves and Whalley 2002, Culley and Klooster 2007). Meiosis occurs in both gametes of the cleistogamous flower, so gene resorting does occur (Groves and Whalley 2002), enabling continued "repatterning of the gene pool, differing only in degree from [that in] outbreeding populations" (Evans and Young 1972 p. 235).

Cleistogamous seeds may be energetically less expensive to produce because of their greater rate of fertilisation and savings in pollen (Connor 1986), so the seeds can be larger (Culley and Klooster 2007). However in *N. neesiana* they are generally smaller,with much reduction in the size of the appenedages. Cleistogamy has disadvantages, including increased inbreeding depression and the aforementioneddecreased genetic variation (Culley and Klooster 2007). Dimorphic cleistogamy requires that each flower/seed type offers specific selective advantages. In grasses, the most important of these may be the differential dispersability of the seed types. Variation in the incidence of cleistogamy in the panicle of *N. neesiana* does not appear to have been studied, nor have potential environmental influences of facultative cleistogamy.

Reproduction in *N. neesiana* is probably entirely sexual; apomixis, often evident by the production of twin seedlings from a single seed (Groves and Whalley 2002), does not seem to have been reported (e.g. Puhar 1996).

Seed production

In comparison to most other grasses the panicle seed of *N. neesiana* is large, and relatively few are produced per plant. In pastures at Waipawa, New Zealand, 793 ±128 culms m^{-2} were present in a pure ungrazed sward in pasture, and potential seed yield per panicle was 38, indicating a potential annual panicle seed yield of c. 30,000 m^{-2} (Slay 2001). In dense, ungrazed infestations on the Northern Tablelands of NSW Gardener *et al.* (1999 2003a) recorded maximum production of 1,584 panicle seed m^{-2} in 1995 (the preceding year and spring being as dry) and 22,203 panicle seed m^{-2} in 1996 (above average rainfall), determined from the number of infloresences m^{-2} and the number of glume pairs per inflorescence. The variation between the drought year and the wet year resulted from changes in the number of panicles m^{-2}.

Gardener's (1998) figure of 22,000 has subsequently been widely quoted (e.g. "20,000" in Snell *et al.* 2007). However the spring of 1995 was actually exceptionally wet (see Gardener 1998 Fig. 3.2 on p. 22) and may have resulted in a mast seeding event, accounting for the c. 14 fold increase in the estimated seed production over the previous year, and a c. 3.7 fold higher production than 1997. Masting has been defined as "synchronous highly variable seed production among years by a population" (Kelly *et al.* 2008) and may have evolved as a a seed-predator satiation strategy (Kelly *et al.* 1992). The prime characteristic of masting events is that a very high proportion of the population reproduce massively in mast years and poorly in non-mast years, cued by weather events (Kelly *et al.* 2008). Masting has been described in a number of long-lived tussock grasses including *Stipa tenacissima*, and appears to result from the build up of stored reserves and rapid responses to high water availability during the growing season (Haase *et al.* 1995). Conversely, poor seed set is a feature of dry years and drought periods. Bountiful weather is required for mass-seeding, but predator satiation, in which a much larger proportion of the seed crop survives in mast years than non-mast years, accounts for the evolutionary benefits of the phenomenon, at least in New Zealand *Chionchloa* grasses (Kelly *et* *al.* 2008). Cues for masting may be temperature based, since temperatures can be more effective in synchronising dispersed populations than rainfall, and masting may involve plant anticipatory responses that associate weather events with future conditions that would improve recruitment (Kelly *et al.* 2008).

In a dense pastures sward in New Zealand potential *N. neesiana* cleistogene production was 10,300 m^{-2} if all culms produced the maximum of 13 seeds (Slay 2001). Potential cleistogene numbers represented about 25% of total potential seed production. Under drought conditions, Slay (2002a) found more basal cleistogenes per vegetative tiller on autumn-germinated juvenile plants in December than on culm-bearing tillers of mature plants. In Northern NSW, an average of 7.2 cleistogenes per flowering tiller was produced, and a dense ungrazed infestation in 1996 produced an estimated 6,100 m^{-2} (Gardener *et al.* 1999 2003a); but note again that this was probably a mast year. Cleistogenes represented an estimated 21.5% and 26.1% of total seed production in 1996 and 1997. Clipping of flowering tillers above the basal node, and above and below the top node, had no effect on the number of cleistogenes produced on the nodes below the clipping point (Gardener *et al.* (1999 2003a).

The numbers of panicle seeds produced per tiller on the Northern Tablelands of NSW (38) and Argentina (27 – small sample size) are similar and the number of cleistogenes per tiller identical (Gardener *et al.* 1996b). But there is wide variation in plant density in the pampas, tussocks are much smaller, and the maximum % basal ground cover is less than half the maximum on the Northern Tablelands. The number of inflorescences m^{-2} in the Argentinian sites examined varied from 0 to 200, giving a maximum seed production of c. 8000 seeds m^{-2} (Gardener *et al.* 1996b).

Awns of several seeds often twist together while still attached to the plant, forming a tangled mass that usually includes infloresence branches, etc. (McLaren, Stajsic and Iaconis. 2004; illustrated by Frederick 2002). Seeds that become entangled are retained on the plant for a longer period than seeds that do not. According to Groves and Whalley (2002 p. 158) the "ecological implications of [such] retention are obscure"; however potential advantages of retaining seed in the canopy include protection from predation and decay processes on the ground surface.

The morphology of the seed and its presentation on the plant are evidently defenses against mammalian herbivores. Sheep and cattle stop eating the plant as soon as the flowering stalks are produced (Grech 2007a).

Dispersal mechanisms

Poaceae in general have very effective dispersal mechanisms: they comprise approximately 4% of world Angiosperm genera but account for 13% of cosmopolitan genera (Wheeler *et al.* 1990). The proportion of introduced grasses in a regional flora is usually much higher than for the flora as a whole, for instance in the Juan Fernández Islands of Chile 81% of the 53 grass species are adventive compared to 70% of the whole flora (Baeza *et al.* 2007). Alien grasses account for a large proportion of the grass flora in many regions, particularly in "livestock-based economies" (Milton 2004 p. 69). Grazing has long been a backbone of the economy in Victoria, for example, and 62% of the vascular plant genera in that State and 44% of the species are exotic, with another 10% of the genera having both native and exotic species (data from Ross and Walsh 2003). In comparison, in southern Africa 15% of the genera and 12% of the species are exotic (Milton 2004). In mainland Spain Poaceae account for a larger proportion (16 of 106 spp.) of the established alien plant flora than all other families except Asteraceae (20 spp.) (Gassó *et al.* 2009). More species of Poaceae are considered to be environmental weeds in New Zealand than any other plant families, but in Australia more Asteraceae are environmental weeds (Williams and West 2000).

Stipeae are commonly adventive species (Watson and Dallwitz 2005) and numerous species have dispersed to remote islands and intercontinentally. According to Tsvelev (1977 p. 7) "it can hardly be doubted" that *Stipa capensis*, described from and very common in South Africa, was carried there by the first colonists. *Amelichloa brachychaeta* was described in 1853 from French material by Godron "who at that time was unaware of its native home" (Hayward and Druce 1919 p. 226). Hayward and Druce (1919) recorded seven South American species (*N. neesiana*, *N. poeppigiana* (Trin. and Rupr.) Barkworth, *N. pubiflora* (Trin. and Rupr.) E. Desv., *N. caespitosa* Griseb., *N. leptothera* (Speg.) Torres, *Amelichloa caudata* and *A. brachychaeta*) in the adventive flora of Tweedside, Scotland, on wool refuse heaps or otherwise associated with wool factories. Nine (Connor *et al.* 1993) or 12 (Edgar *et al.* 1991) stipoids have been recorded as naturalised in New Zealand including *Nassella* spp. and *Austrostipa* spp. The Argentinian and Uruguayan *Nassella manicata* (E. Desv.) Barkworth, established in California,was probably introduced in the 19th or early 20th centuries (Barkworth 1993 2006) and "apparently hitched a ride ... with South American vaqueros and their livestock looking for greener pastures" (Amme 2003). California also has introduced populations of *N. tenuissima* derived from horticultural plantings (Amme 2003). Five of the 25 "Stipa" species recorded in Italy are exotic species, all from South America: *N. neesiana*, *N. hyalina*, *N. trichotoma*, *N. formicarum* (Delile) Barkworth and *A. caudata* (Moraldo 1986).The two *Nassella* species (*N. neesiana* and *N. laevissima* (Phil.) Barkworth) found on the Juan Fernández Islands of Chile are both introduced (Baeza *et al.* 2007). On a world basis, at least 12 *Nassella* species have been reported growing outside their native range (Randall 2002, Barkworth 2006, Baeza *et al.* 2007), c. 10% of the species.

There is general consensus that human activities are the major cause of *N. neesiana* seed dispersal in Australia (Bedggood and Moerkerk 2002, Snell *et al.* 2007). The panicle seed, like that of stipoids in general, has many adaptations that enable it to attach to a wide range of objects: according to Slay (2002c p. 23), it "attaches to almost everything".

However records of actual seed dispersal are very limited and the conclusion that anthropic factors account for current distributions is surmise based on patterns of infestations, seed biology, and general observations of the carriage of seed on machinery, vehicles and livestock.

Based on evidence of exotic stipoid dispersal to New Zealand and within that country, Connor *et al.* (1993) suggested that stipoids with falcate awns may be more highly dipersible than those (such as *N. neesiana*) with geniculate awns.

Creeping diaspores

The panicle seeds of *N. neesiana* are classed as creeping diaspores (Davidse 1986, Connor *et al.* 1993) that are able to move along the ground and position themselves in microsites favourable for germination (Gardener and Sindel 1998, Sinclair 2002). Creeping diaspores of grasses generally result in little actual dispersal via 'creeping', the adaptations being more important in enabling microsite lodgement (Peart 1979, Davidse 1986). The awn provides the hygroscopic torsion mechanism by which the seed is supposed to drill itself into the soil (Murbach 1900, Davidse 1986). Peart (1979) however argued that horizontal rather than vertical propulsion by awn torsion is usually of greater importance, even in those species such as *N. neesiana* with a sharp callus and long, stout active awns that appear best adapted to actually drill into the soil. Alternate wetting and drying of the awn twists the column, driving the seed forward, the artista provides a brace for leverage, and the retrorse spines on the corona, and the hairs on the awn, callus and lemma-body restrict backward movement (Bourdôt and Ryde 1986). The awn of *Piptochaetium avenaceum* increases in length by 20% when wet, assisting propulsion of the seed (Murbach 1900) and this effect likely occurs also with *N. neesiana*. As with similar species (Murbach 1900), the sharp *N. neesiana* callus leads the seed into the ground and the callus hairs hold it in place once ground penetration has started and anchor the seed after germination, countering the opposing force provided by the radicle. The depth to which a stipoid seed is buried is related to the length of the awn: "species growing in areas where seeds need to be buried to ensure adequate amounts of soil moisture for germination tend to have a long callus, a long, narrowly cylindrical floret, and long, persistent awns" (Barkworth and Everett 1986 p. 254).

Awns of awned grasses are able to drill seeds into cracks and crevices in the soil but there is little evidence that penetration of an unbroken soil crust occurs (Peart 1979, Bourdôt and Ryde 1986, Sinclair 2002) although stipoid seeds are often credited with the ability to 'bury themselves' in the soil by this mechanism (e.g. Whittet 1969 p. 129).

Non-hyroscopic straight awns have another function immediately after seed shedding: to rotate the seed while falling in such a way that the seed lands vertically on the callus (Peart 1984, Sinclair 2002). This is also appears to happen with *N. neesiana* seeds, even though their awns are strongly twice-bent and hygroscopic (personal observations).

The dispersal ability of lone panicle seeds of *N. neesiana* is lost by a significant proportion of seeds, which aggregate in the panicle when the awns twist together, forming a tangled mass that usually includes infloresence branches (Connor *et al.* 1993, McLaren, Stajsic and Iaconis. 2004; illustrated by Frederick 2002). The aggregation often ultimately falls to the ground as a unit (Gardener *et al.* 2003a) or may become attached to a vector enabling seed transport *en masse* (Slay 2002c). These seed clusters frequently hold seed in the canopy for a longer period than would otherwise be the case. The adaptive significance and ecological implications of such seed retention is obscure (Groves and Whalley 2002). However seed held in the panicle over a longer period will be accessible to a greater variety and intensity of dispersal factors, so may have adaptive advantages in areas where the potential range of the plant has not been reached. Similar seed aggregrates formed by twisting together of awns occur in a range of other grass tribes, e.g. the East African *Acritochaete* (Paniceae), in which the whole mass, or parts of it, may be dispersed by attachment of the exposed calluses to passing animals (Davidse 1986).

Zoochory

Seed dispersal by animals (zoochory) occurs in more than half of all plant species, most commonly by ingestion (endozoochory) and external attachment (exozoochory) (Stanton 2006), and also by deliberate animal carriage. *N. neesiana* seeds can be dispersed via all of these processes.

Slay (2002a p. 15) recorded a report by C. Lee in New Zealand that unspecified birds "use awn/seed clusters for the building of nests". Such deliberate dispersal is probably of little significance, but may enable the plant to cross otherwise impenetrable barriers. Dispersal of *N. neesiana* seeds by accidental attachment to birds does not seem to have been reported. Conole (1994) observed Red-rumped Parrots, *Psephotus haematonotus*, "wading up to their bellies" in drifts of seed-bearing panicles of *Nassella trichotoma* in southern Victoria, and suggested that they were highly likely to be exozoochorous dispersal agent of this much smaller seeded *Nassella* species.

Endozoochory is certainly much rarer in birds than in mammals but in general has been very little studied (Whelan *et al.* 2008). It may occur via faeces, regurgitated pellets, or secondarily via predator consumption of the bird (Twigg *et al.* 2009). Conole (1994) also observed *N. trichotoma* seed consumption by Red-rumped Parrots and argued that a proportion of the seed ingested could survive and be dispersed. Twigg *et al.* (2009) found that seed fed to finches, pigeons and ducks was generally passed in the faeces within 0.3-5.0 hours, with longer passage times in the larger species, and that very few whole seeds survived the digestion process. Most of the seeds tested were not grasses, but gut passage reduced the viability of wheat seeds by 33%, and significantly reduced the viability of millet seeds. Finches and parrots are probably less likely to disperse seeds than pigeons because of their efficient digestive systems, while generalist omnivorous/herbivorous birds are probably the most likely to dispese viable seed endozoochorously (Twigg *et al.* 2009).

Some grasses in the Paniceae, Andropogoneae and Olyreae have evolved presumed elaiosomes (lipid-cotaining diaspore appendages) that may attract ant seed dispersers (Davidse 1986). The structures, containing stable oils, occur in the rachilla, pedicel, glume base or lemma. They are difficult to identify on herbarium specimens and no field observations that confirm their function have been identified (Davidse 1986). In other plant families the eliasome is removed by the ants after carriage of the diaspore to the nest, and the seed itself may often not be damaged. There appears to be no evidence of such eliasomes in Stipeae.

The panicle seed of *N. neesiana* is able to attach to a wide range of materials. Seeds attach to the coats of livestock and clothing, and lodge on machinery (Gardener *et al.* 1999, Slay 2002a). The hairs and corona of the seed, and the twisting together of awns of adjacent seeds that come into contact, can enhance the adhesion of seeds to objects which the callus cannot penetrate.

Transport of *N. neesiana* seeds on livestock has been recorded in New Zealand (Bourdôt and Ryde 1986) and Australia (Gardener 1998). Grazing of sheep is the probable cause of spread in the Hawkes Bay area of New Zealand (Slay 2002c). Panicle seeds are carried in the fleece of sheep (Connor *et al.* 1993) and can remain there for at least 166 days (Gardener and Sindel 1998). Larger grass seeds with long appendages are generally retained for longer periods in long pellage than in short, and retention time is probably little affected by environmental factors (Stanton 2006). Gardener *et al.* (2003a) found that 25% of *N. neesiana* seed naturally lodged in the wool of sheep remained after 5 months, and that shearing prior to seed production reduced the lodgement rate. However lodged seed often lost their awns, so would have reduced dispersal, and probably survival ability when shed from the fleece. A high proportion of lodged seed was subsequently shed (Gardener 1998), but details of natural seed shedding from fleece are scanty, so sheep may not be particularly effective dispersal agents (Connor *et al.* 1993).

Approximately 200 alien grass species introduced with imported wool have been recorded in the British Isles (Hubbard 1968) and 25 species of *Austrostipa*, *Stipa* and *Nassella* have been recorded there as casuals regarded as mainly "wool-aliens" that have entered the country as seed contaminants of raw wool (Stace 1997). Some exotic stipoid populations in France may also have this origin (Verloove 2005). Noting European records near wool factories and tanneries, Bourdôt and Hurrell (1987a 1989a) suggested that that *N. neesiana* was likely to have reached New Zealand from South America in the wool and hides of grazing animals. In 19th century Europe the treatments applied in wool processing, including scouring in alkali and acid baths, dry heating and crushing through rollers (Vines 2006), were intended to remove all such contaminants, which were nevertheless dispersed in waste streams from the treatment plants, including water discharges and in wool waste or "shoddy" which was used as garden fertiliser in Scotland (Hayward and Druce 1919, Vines 2006). Installation of a sewage treatment plant at Galashiels, Scotland, soon eliminated viable seed discharge to waterways (Vines 2006). Dispersal in wool has been a major method of introduction of weeds to Australia, and has possibly been the most important overall dispersal method within the country, after their arrival (Carr 1993). Movement of wool in bales after shearing in Australia is possibly responsible for some *N. neesiana* spread. Seed was probably able to penetrate and move through hessian or jute bale bags (which probably went out of use in Australia in the early 1990s), but appear to be unable to penetrate the densely woven high density polyethylene or nylon fabrics used in modern bales bags (personal observations).

Movement of livestock between farms is the most likely cause of intermediate range expansion in New Zealand (Connor *et al.* 1993). Slay (2002c) stated that stems bearing seed can be walked across tracks by livestock. Seeds are unlikely to attach to the pelts of cattle but could be moved in mud on hooves (Gardener *et al.* 2003a). They may also adhere to other animals including kangaroos and rabbits (Gardener and Sindel 1998). Ens (2002a) suggested dog and rabbit dispersal as possibilities at a number of Sydney sites. Bruce (2001) found patches of the plant in *Macropus giganteus* Shaw daytime rest areas under trees, and suggested that kangaroos may disperse seed. Liebert (1996 p. 8) implied that dispersal by native animals was unknown, however Bedggood and Moerkerk (2002 p. 6) stated that "dogs, humans and wild animals such as kangaroos and rabbits spread the seed", presumably on the basis of general experience of presence in areas where wild animal movements are concentrated, and other informed speculation. Peart (1979 p. 860) however noted the absence of any awned grasses seeds in the fur of "some 100 carcasses of wild marsupials in Australia". Slay (2002c p. 16) mentioned "birds" and "vermin" as probable dispersal agents in New Zealand and stated that stems bearing seed can be walked across tracks by livestock. No documented records of carriage on animals other than sheep in Australia appears to be available.

Both panicle and stem seeds of *N. neesiana* can be distributed and remain viable after ingestion by livestock, but usually a high proportion of ingested plant seeds are digested, and the viability of the seeds that survive gut passage is significantly reduced (Stanton 2006). Gardener *et al.* (2003a) found that an average of 1.7% of *N. neesiana* panicle seeds and 5.3% of cleistogenes fed to Angus cattle (*Bos taurus*) were voided in dung within 4 days, mostly within 1-2 days. Less than half the voided seeds remained viable and no viable seed was passed after 4 days. Endozoochorous dispersal was considered to be less likely by sheep, which digest a higher proportion of seed (Gardener *et al.* 2003a), probably because they chew their food more thoroughly (Stanton 2006). Sheep, but not cattle, fed with a range of pasture seed digest a greater proportion of long seeds than short (Stanton 2006). Rabbits also void a wide range of seed in their dung (Bloomfield and McPhee 2006) but would be unlikely to eat *N. neesiana* seed.

Even at high stocking rate livestock avoid eating *N. neesiana* once the reproductive stage is reached (Grech 2007), and the extremely sharp callus and rough texture of the panicle seed assist in making the panicle unpalatable. These seeds evidently are adapted to avoid being eaten.

Cleistogene dispersal

Gardener *et al.* (2003a p. 614) thought that cleistogenes "have no obvious dispersal mechanism" but that ingestion by grazing animals was one possibility. Barkworth and Everett (1986) suggested that stipoid seeds adapted to zoochory by animal ingestion may have short, deciduous awns, globose florets and obtuse calluses, a set of characteristics possessed increasingly by *N. neesiana* stem cleistogenes from upper to basal.

Cleistogenes can develop even if the flowering tiller is damaged, and are important in maintaining the species during climatic extremes (Gardener and Sindel 1998) and under conditions of heavy grazing or fire (Dyksterhuis 1945). They are better protected from some predators than panicle seeds (Gardener and Sindel 1998) being tightly covered by leaf sheaths during their formation and after maturity, and remain available for dispersal from the parent for as long as 6 months on standing dry culms (Gardener *et al.* 1999) e.g. in hay, and for much longer if attached on basal nodes. According to Connor *et al.* (1993), stem cleistogenes are released when the leaf sheaths weaken or rupture, so any dispersal of released cleistogenes requires tiller breakdown. According to Slay (2001 p. 38) the tiller dies after panicle seed is produced and its roots decay over a period of up to two years, "eventually releasing the cleistogenes and or producing the ideal germination conditions for their establishment, as evidenced by the seedlings that grow out of decayed clumps". He found old, rotted root/stem areas "up to three tiers deep, suggesting plants die and re-establish ... on top of each other" (p. 42), and that at least the basal cleistogenes are adapted to not disperse.

In terms of large grazing mammals, the tightly attached covering leaf sheath and stem node segment can be conceived of as an attractive 'fruit' containing the cleistogene 'seed', and when ingested this 'fruit' may enable better survival of the seed and faster passage through the gut (Davidse 1986). Lllamas and alpacas reportedly eat the straw and possibly disperse cleistogenes in their guts (Colin Hocking, 26 October 2006).

Cleistogenes are dispersed by cultivation machinery (Connor *et al.* 1993) and in decayed tussocks or sods (Slay 2002a). Old and broken culms bearing cleistogenes can be carried by livestock (Slay 2001). Bourdôt (1989) noted that basal cleistogenes in particular are likely to survive fire in situ, and have probably evolved not to disperse, but rather to replace the parent plant should it die.

Grasses that are 'herbivore exploiters' are palatable, recover well after grazing, and have seeds adapted for dispersal by grazing mammals (Milton 2004). *N. neesiana* appears to have a mixed dispersal strategy, probably being an exploiter of large grazers via endozoochory in terms of non-basal stem cleistogenes, a repeller of grazers at the time of panicle seed production, and a ‘sit and wait’ strategist in terms of basal cleistogenes.

Wind

Carr (1993) listed wind as a dispersal agent, but the panicle seeds have no particular adaptations for wind dispersal. In windless conditions the seed falls vertically (Slay 2002a). Of the 39% of panicle seed recovered in a wind dispersal experiment, Gardener *et al.* (2003a) found none more than 2.8 m from the centre of the source plant, and the majority of seed within 1 m. However these findings may create a misleading impression about the frequency of wind dispersal and the distance that wind may carry the seed. Small scale, short duration, high intensity atmospheric turbulence events have a very strong impact on aerial transport, and strong vertical winds associated with thunderstorms can lift seeds that lack special wind dispersal adaptations (Nathan *et al.* 2005). Seeds could certainly be blown along flat surfaces such as roads, possibly assisted by vehicle eddy or suction currents (Barwick 1999). Willy willies (small whirlwinds) that carry large amounts of loose plant debris occur frequently in summer in Australia, particularly in inland areas. Surprisingly large grass seeds can be lifted to high altitudes by natural processes, e.g. the spikelets of *Paspalum* spp. have been obtained by aircraft sampling at altitudes of up to c. 1500 m in Louisiana, USA (Hitchcock and Chase 1971).

Slay (2001 2002c) noted that panicles and stems can be blown short distances by strong winds, resulting in dispersal of cleistogenes. Wind dispersal of late maturing seed on ‘secondary panicles’ could presumably occur more readily since the remainder of the panicle, with only glumes attached, could be more readily lifted and carried.

Water

Extensive distribution along floodways and watercourses has led to the inference that movement of *N. neesiana* seeds in flowing water is important (Frederick 2002). According to Bourdôt and Ryde (1986) seeds are “carried along water courses, giving rise to isolated patches of the plant”. Slay (2002b) stated that running water disperses seed. Hayward (Hayward and Druce 1919) found plants along the river bank downstream of wool processing factories in Scotland. Cook (1999 p. 91) stated that *N. neesiana* is a weed of “flood zones” and Iaconis (2003) stated that flood waters are responsible for dispersal. In urban and peri-urban Canberra, seeds have possibly been dispersed widely in the drainage system (Jenny Connolly and Sarah Sharp pers. comms. 2006). Bedggood and Moerkerk (2002 p. 6) state that “run-off water can carry seed from one property to another”. There is very little detail to support these claims, which mostly appear to be based on the pattern of distribution of infestations in small catchment areas. No published information appears to be available on the buoyancy of the seeds, their presence in flood debris, etc. Preliminary observations indicate that they remain afloat in still water for at least 4 days. The awns quickly become entirely straight while acquiring extreme flexibility, and the seed becomes ‘sperm-like’, a characteristic that would enhance more rapid and effective carriage in moving water.

Human activities

The consensus view among most commentators is that human activities, little mediated by domestic animals or physical environmental factors are the major cause of dispersal in Australia (Snell *et al.* 2007), but the vector strength and tempo are unknown. Roadside management activities including slashing, mowing and grading, particularly when the plants are seeding (Frederick 2002), are generally the inferred causes. Roadsides carry some of the densest Australian infestations (Snell *et al.* 2007) and infestations in a new area frequently occur first along roads. Transport of seeds in hay has been recorded in New Zealand (Bourdôt and Ryde 1986) and dispersal in contaminated fodder has been called “a primary mechanism” of dispersal (Frederick 2002 citing Liebert 1996), although there appear to be no specific incidents of such dispersal on the public record in Australia.

Seeds are said to “adhere” to machinery “via [the] ... callus” (Gardener and Sindel 1998 p. 77) but there are few points on vehicles and machines which the sharp end of the callus could penetrate, so such adhesion presumably involves the callus hairs and a range of leverage options with the callus tip, lemma body and awn. The actual mode of lodgement needs to be far better described. For instance, penetration of rubber vehicle tyres has not been reported – piercing by the callus does not seem to be a factor. Various characteristics of the whole seed alone and in aggregates are responsible for attachment.

Linear distribution of infestations along roadsides and vehicle paths is widespread and commonplace (Bruce 2001, Frederick 2002, ?Sharp 2002) but this could have a variety of causes unrelated to direct movement attached to machinery or vehicles. In particular roadsides are subject to a variety of disturbances such as mowing, soil compaction and pollution that can reduce the competitive abilities of native vegetation (von der Lippe and Kowarik 2007a). Studies of the seed rain from motor vehicles in long road tunnels along a German motorway have demonstrated that roadsides are “preferential migration corridors” for invasive plants and that long distance dispersal (> c. 200 m) is routine (Von der Lippe and Kowarik 2007a). Grass species accounted for four of the 20 most frequent species in the seed rain (including the two cereal crop species *Triticum aestivum*, L. and *Secale cereale* L., plus *Poa annua* L., and *Lolium perenne* L.), but at least one long-awned grass *Bromus tectorum* L., highly invasive in the USA, was represented. Half of the 204 species detected were not local natives. Seeds of 42% of the regional roadside flora were found in samples, 69% of the species sampled in the tunnels were found growing within 100 m of the tunnel entrances and and 98.5% of all seeds sampled were from species in the regional roadside flora. Approximately one third of the species found were not present in areas near the tunnel entrances. Non-native species were more often subject to long distance dispersal than natives. Seeds represented <1% of the material trapped, the remainder being mud and other substrates that enable seed attachment to vehicles (Von der Lippe and Kowarik 2007a). The species richness and quantity of seeds deposited along lanes outbound from the city was higher than for inbound lanes suggesting the export of species from urban areas, and when crop species are excluded from the analysis there was higher deposition of exotic species on outbound lanes (Von der Lippe and Kowarik 2007b). *Festuca trachyphylla* (Hack.) Kroj. (?awned) and the awnless grasses *Poa compressa* L., and *Agrostis capillaris* L, were significantly correlated with outbound movement. The shortly-awned *Deschampsia cespitosa* (L.) Beauv. was another species dispersed (Von der Lippe and Kowarik 2007b). Ruderals and species of grassland habitats accounted for most of the species deposited in the road tunnels. Repeated short distance transport by more than one vehicle, enhanced airflow dispersal (Von der Lippe and Kowarik 2007a).

Dispersal of seed in contaminated soil has been recognised as a dispersal mechanism (Muyt 2001, Snell *et al.* 2007). Spread of seed along roadsides by graders and other earthmoving equipment was mentioned by Bourdôt and Ryde (1986), but no further information was provided.

Liebert (1996) observed that slashing of the plant while seeding was a "primary mechanism" for dispersal. Trengrove (1997) also observed that dispersal along roadsides is caused by slashers operating at the time of seed set. Bruce (2001) found that *N. neesiana* was generally more abundant at sites in the ACT that were mown to some extent, that it was never absent from areas that were entirely mown, and at infested sites where mowing occurred it was generally spreading from mown into unmown areas, in some cases very obviously along mown walking tracks into native grasslands. In fact, the overall distribution of *N. neesiana* in the ACT correlated extremely well with mown areas (Bedggood and Moerkerk 2002). Ens (2002a) suggested seed carriage on mowing equipment was the most likely explanation for a number of the infestations she examined in the Sydney area. Sharp (2002) noted continued expansion of infestations along roadsides in the ACT "despite efforts to control spread with more appropriate management practices".

Moerkerk (2005a 2005b 2006a 2006b) analysed the plant propagules found in material manually cleaned from vehicles and machinery used in natural resource mangement activities, particularly weed management, in Victoria. The flora of each vehicle reflected the flora of the region in which was used. Nearly three times as many species of Poaceae were found in 'clean-downs' than the next most abundant family, and grass species accounted for 6 of the 10 most frequently detected contaminants. *N. neesiana* was detected on 5 of 106 State government, local government and private contractor vehicles and machines sampled: 4 passenger vehicles and 1 slasher. A four wheel drive utility vehicle used by the Shire of Hume (an area where *N. neesiana* is common) cleaned in June 2005, yielded 24 weed species including *N. neesiana*, from 23% of the 810 g of material removed. A Hume Shire tractor and slasher cleaned in June 2005 yielded 26 spp., including *N. neesiana*, from 27% of 178 g of material. *N. neesiana* was found in the cabin, engine bay and tray of vehicles and in the wheel guards and chassis of two vehicles. Noxious weeds were mostly frequently found in the cabins and engine bays of passenger vehicles. 39% of passenger vehicles and 29% of machinery items were found to be carrying noxious species. Of the vehicle types examined, 4WD utility vehicles had the highest rates of contamination, while tractors with attached slashers, and graders had the highest rates of contamination (40%) of the machinery types examined.

Grech (2005b) 'cleaned-down' a four-wheel-drive utility vehicle used on a property infested with *N. neesiana* using brushes, manual plucking and high pressure water. The latter method was found to be ineffective and failed to dislodge entangled masses of *N. neesiana* seeds. Weighing of the removed material indicated in excess of 10,000 *N. neesiana* seeds, "equivalent in volume to a medium sized couch cushion".

These studies identified important potential vectors but failed to determine under what conditions seed become attached and are deposited in potentially suitable sites, and the actual spatial effectiveness of vehicles as seed vectors. Transport vehicles have much higher potential for long distance dispersal and are perhaps mainly to blame for inter-regional dispersal,while machinery is likely of greater importance at a local scale.

Slashing machinery actively disperses seed around the slasher. Detailed investigations have been undertaken of one particular model of slasher in relation to *N. neesiana* seed dispersal (Erakovic *et al.* 2003, Erakovic 2005). Rotating slasher blades caused upward air movement within the slasher frame, and high outlet velocities occured at the front of the slasher deck where the cutting process actually occured. At the commonly used slash height of 7 cm with this machine, most of the slashed material was deposited within the slashed strip. Over 98% of the expelled material (not deposited in the slashed strip) fell within 1 m and the remainder within 2 m, with more deposited on the left of the slashed strip than on the right (Erakovic 2005). Sigificant amounts of slashed chaff and seeds were deposited on the top of the slasher unit, and significant amounts lodged in the debris ejection protector chains (Erakovic *et al.* 2003). Pronounced accumulation of seeds on the top front of the deck resulted from direct dislodgement of seed from the plant that never came into contact with the slasher blades (Erakovic 2005).

More importantly, slashing was also found to disperse seed over longer distances if the slasher was not kept clean. Seed adhered inside the deck of the slasher in crevices and boltholes, and slashed material accumulated around front and rear internal walls, the blade shaft and in corners (Erakovic 2005). Decontamination and cleaning was time-consuming and tedious, and it was very difficult and unsafe to clean the underside of slasher decks in the field (Erakovic 2005). The use of counter-rotating twin blades and other improvements in a new slasher design, plus the development of slasher accessories (covers and shields, flaps to replace chains) showed great promise of reducing these problems (Erakovic 2005).

A range of other dispersal processes mainly related to trade and commerce have been implicated in *N. neesiana* spread. Seed has been spread in hay bales in New Zealand (Slay 2002c) and movement of contaminated fodder has been identified as likely (Muyt 2001). Some infestations in New Zealand have originated from contaminated pasture seed (Connor *et al.* 1993, Slay 2002a), sown as recently as 1980 (Slay 2002c). Spanish infestations may have originated in cereals imported from Argentina (Verloove 2005). Introduction in railway traffic may be the origin of a large population at Bédarieux-Nissergues in France (Verloove 2005). Cultivation can carry whole plants and seed within paddocks (Slay 2002c). Slay (2002a p. 11) noted that a small infestation at Waipawa, New Zealand, was thought to have been "spread by lawn mower/lawn clippings".

Like *N. neesiana*, other Stipeae spp. have been carried internationally in solid ship ballast, e.g. *Amelichloa brachychaeta* from Argentina and *N. chilensis* (Trin. and Rupr.) E. Desv. from Chile to Portland, Oregon, USA (Hitchcock and Chase 1971), the latter species "once collected" and not established (Barkworth 2006). Solid ballast such as beach sand and rocks began to be replaced by water ballast in the late 1870s and all large ships now use it (Jones 1991), so this invasion pathway is now probably largely obsolete.

Pollen

Pollen (the male gametophyte) is also dispersed. Grasses in general are wind pollinated and produce large amounts of pollen, and the pollen concentration downwind decreases at a rate inversely proportional to the square of the distance from the source (Connor 1986). Pollen may have an important role in gene flow and in promoting plant invasions (Petit 2004). For plants as a whole, gene flow via pollen is estimated to be on average an order of magnitude greater than gene flow via seeds, and most long distance gene flow is via pollen (Petit 2004).

Anthesis in grass species occurs at particular times of day, often in the morning or the afternoon (Connor 1986). Release of pollen occurs at times of high temperatures and low humidity.There appear to be few records of stipoid anthesis times. *Piptatherum holciforme* flowers at night and *P. virescens* early in the morning (Connor 1986). Ramasamy (2008) observed most *Nassella trichotoma* anthesis in the morning (7-11 am) with some later in the day. The structure of grass inflorescences and flowers influence their pollen dispersal and trapping characteristics (Connor 1986). Wind is the main dispersal agent for grass pollen, but insects may play some small role (Connor 1986).

Rates of spread

Few published records exist of the rate of change in the dimensions of *N. neesiana* infestations and the rates at which the plant spreads (Table 5). In New Zealand the maximum rate of dispersal on a linear front from known sources was 8 km over 59 years at Marlborough and 3.5 km over 30 years at Waipawa (Connor *et al.* 1993). Comparable Australian data does not appear to be available.

N. neesiana was rated by Platt *et al*. (2005) as having a rapid, rather than moderate or slow rate of dispersal. The ACT Weeds Working Group (2002 p. 4) stated that the “rate of spread and establishment is unknown, but believed to be rapid”. However perceptions of rapid spread in Australia may be partly false, due to recognition failures (Walsh 1998).

Table 5. Measured and inferred rates of spread of *N. neesiana*.

Locality	Distance (m)	Period (y)	Rate (m y^{-1})	Notes	Reference
Marlborouegh, NZ	8000	59	136	District infestation expansion	Connor *et al.* 1993
Waipawa, NZ	3500	30	117	District infestation expansion	Connor *et al.* 1993
New Zealand			120-140	With no active management	Slay 2002c
Hawke’s Bay NZ	3-10	5	0.6-2	Patch expansion	Slay 2002c
	Areas (ha)	**Period (y)**	**Rate (ha y^{-1})**		
Marlborough, NZ	1555-3000 (3071)	14-15	101-103	District expansion	Slay 2002a, 2002c
hypothetical	1	5	100	Expansion at 100 m per year	Slay 2002a
hypothetical	1	10	350	Expansion at 100 m per year	Slay 2002a

Rare long-distance dispersal events (e.g. by water or human transport) are thought to contribute to accelerating rates of spread that have been recorded as plant invasions proceed (Mack and Lonsdale 2001). This is because the likelihood of successful dispersal increases in proportion to the size of the propagule pool. This factor may also be contributing to the Australian perception.

Invasion patterns

Trengrove (1997) observed that *N. neesiana* dispersed along roadsides by slashers then invades into adjoining paddocks “in a front”. The pattern in the ACT is of movement outwards from a central Canberra source population along urban and periurban roadsides mainly via mowing and slashing, with spread outward from the linear corridors, often by the same means (ACT Weeds Working Group 2002). Slay (2002c) listed a range of situations where infestations occur in New Zealand that are indicative of seed dispersal patterns: “paddocks sown with uncertified seed between 1950 and 1980 ... holding paddocks close to the road ... the edges of farm tracks ... 1-3 m away from power poles, along fence lines or other places where stock ‘rub’ ... river banks ... around hay barns ... sheep yards”.

Soil seed bank

The soil seed bank may be thought of as the consequence of four different processes: dropping of individual panicle seeds, the shedding of inter-twined seed masses, the release of stem cleistogenes when the culm decays and the release of basal cleistogenes when stem bases decay.

Cleistogenes enter the seed bank as the culms decompose or after fire (Groves and Whalley 2002). Culms deteriorate slowly through summer and autumn and the leaf sheaths rupture in autumn or winter, releasing stem cleistogenes (Slay 2002c). Basal cleistogenes are released after the tiller or parent plant dies and decomposes, possibly 12-18 months after mortality (Slay 2002c).

Testing of panicle seeds of *N. neesiana* with triphenyl tetrazolium chloride (tetrazolium) reported by Puhar and Hocking (1996) indicated 80-95% viability. The seeds in general are reportedly viable for more than 12 years (Benson and McDougall 2005), “many years” (Quattrocchi 2006) or “in excess of three years” in the soil (Snell et al. 2007p. 4). Bourdôt and Ryde (1986) stated that both panicle and stem seeds have >90% viability and survive for “several years” in the soil. The soil seed bank was large and persistent in heavily infested sites investigated by Gardener on the Northern Tablelands of NSW in the 1990s (Gardener *et al.* 2003b).

Assessments of the seed bank in seven populations in the Argentinian pampas showed it be close to zero (Gardener *et al.* 1996b, Gardener *et al.* 1997). Possible reasons for this include high levels of seed predation by ants, attack by a seed pathogen after seed shed, or rapid microbial decomposition in the soil, however the closely related *Nassella clarazii* (Ball) Barkworth was found to have aseed bank of c. 1200 m^{-2} (Gardener *et al.* 1996b).

In New Zealand, Hurrell *et al.* (1994) measured a soil seed bank (to about 10 cm depth) under old established stands of 2,600-35,000 seeds m^{-2}, with an average density of 10,500 seeds m^{-2}, of which approximately 70% were cleistogenes, with few or no aerial seeds in some samples. Tetrazolium testing showed 58% viability of cleistogenes and 86% of aerial seeds, with a total average viability of 67%. In pastures at Waipawa, New Zealand, the seed bank was composed almost entirely of cleistogenes (Slay 2002c), with a mean of 6437 ±3437 viable cleistogenes and 660 ±1289 viable panicle seeds m^{-2} (Slay 2001). Bourdôt and Hurrell (1992) found 4000-18,000 viable seeds m^{-2} under pasture, 99% in the top 25 mm and 0% below 100 mm, on a silt loam at Marlborough. Viability (as determined by tetrazolium treatment) of seed buried in polyproylene mesh bags for 6 years in this soil increased with increasing depth of burial, 24% of seed remaining viable at 25 cm depth, 17% at 5 cm, 5% at 2.5 cm and 0.1% for soil at the surface (Bourdôt and Hurrell 1992). Analysis of decay data suggested that an increaing proportion of buried seed survived at increasing depth indefinitely in a state of dormancy, whereas no surface seed was viable after 1 year (Bourdôt and Hurrell 1992). However there are doubts about the reliability of tetrazolium tests for determination of seed viability (Puhar and Hocking 1996). Seeds that are hard when pressed between the thumb nail and forefinger are “almost certainly viable” (Bourdôt 1988).

In pastures in New Zealand in the absence of seed input, annual depletion rates of the soil seed bank were 38% when “regularly” mown to prevent panicle seeding, 61% with repeated glyphosate applications, and between 66% and 77% for single to repeated annual cultivations (Bourdôt and Hurrell 1992).

Smaller seed banks have been described in New England Tablelands pastures by Gardener (1998) who made direct counts of loose seeds in the soil to 4 cm depth, with all seeds considered to be of panicle origin (Gardener *et al.* 2003b p. 622). Under dense infestations 681-11,307 viable seeds m^{-2} were found. If basal cleistogenes, contained in tiller bases and not loose in the soil, are included, the estimated total seed numbers were increased by 35.5% (Gardener and Sindel 1998) or 20% (Gardener *et al.* 2003b). Within *N. neesiana* tussocks 44.1% of seeds were panicle seeds and 55.9% basal cleistogenes (Gardener *et al.* 2003b).

In native grasslands and grassy woodlands in the Melbourne area the viable seed bank appears to be substantially smaller. Seed banks at Iramoo Wildlife Reserve determined by Bram Mason (unpublished) were up to 7000 m^{-2} (Robinson 2003 2005). Beames *et al.* (2005) assessed panicle seed banks in areas of high quality native grassland at Laverton and Grey Box woodland at Melbourne Airport that had been subject to a range of different management regimes to control *N. neesiana*. They separated the seeds into four categories: filled, unfilled (caryopsis absent), successful germinants (germinating at the time of sampling) and unsuccessful germinants. At Laverton a maximum seed bank (seed of all categories) of ca. 2200 m^{-2} was found, however unfilled and unsucessfully germinating seed accounted for ca. 90% of seed. In areas subject to *N. neesiana* management, seed bank numbers did not exceed 1000 m^{-2} , with similar proportions in each seed category, except for filled seed, which comprised a much smaller proportion in two of the managed areas. At Melbourne Airport the maximum seed bank exceeded 7000 m$^{-2.}$ The unburnt, unsprayed treatement had a significantly smaller seed bank than most of the managed areas. Significantly more filled seed was found outside managed areas, which in most cases had zero filled seed. One major conclusion was that most of these differences were the result of reduced seed input due to ongoing herbicide treatment, which possibly reduces the proportion of viable seed produced and seed persistence. The study indicates that the seed bank in non-agricultural areas is much less persistent and easier to deplete than had previously been assumed.

Hocking (2005b) reported even lower levels in infestations subject to herbicidal control in southern Victora: <10 filled seed m^{-2} and seed banks comprised of >80% unviable seed. He suggested that the size of the seed bank may be widely variable on a regional basis and between sites managed for agriculture and conservation, and that agents in the soil at some sites may be destroying a high proportion of seed. Hocking (in Iaconis 2006b) reported no differences in the soil seed banks of agricultural and natural areas, but high variability between sites, and >50% of the seeds unfilled.

In New England pastures, dramatically better fruiting in wetter years (Gardener *et al.* 1996a) led to major addition to the seed bank (e.g. 41.6% of seeds incorporated in 1996), but in drier years input was only sufficient to maintain existing seed bank numbers or inadquate to maintain pre-existing levels (Gardener *et al.* 2003b).

Rates of decline of the seed bank determined for New England pastures without input after 3 y, were 4676 to 1323 seeds m^{-2} in bare plots and 4585 to 1507 seeds m^{-2} in vegetated plots, with no significant effect of ground cover on decline, and a predicted decline without input (based on a fitted exponential decay curve) to 10 seeds m^{-2} after 12.4 y (Gardener *et al.* 1999, Gardener *et al.* 2003b). The seed bank longevity was found to be >6 y (Gardener and Sindel 1998) and half-life 1.3 y (Gardener *et al.* 2003b). There is anecdotal evidence of gemination from continuously bared ground after 6 y (Gardener and Sindel 1998).

Where soil cracking occurs in summer, as in the clays of the Victorian basalt plains, seed dropped in late spring and early summer will certainly move into the soil to greater depths than was sampled in the two Australian studies, which both assumed a similar depth profile of the seed bank to that found on a silt loam in New Zealand by Bourdôt and Hurrell (1992). This may be especially significant since viability of seed increases with depth of burial (Bourdôt and Hurrell 1992). Grasses that produce relatively few large seeds “often emerge from seed located deeper in the soil …where … water is available for a longer time … and many have high seedling growth rates” (Groves and Whalley 2002).

Germination and seedling recruitment

Seed dormancy

The panicle seed have dormancy - the tight lemma may provide a barrier to water and gas exchange and mechanically constrain the embryo (Gardener and Sindel 1998) - and appear to have an after-ripening requirement after falling from the plant of between 3 and 12 months for maximum germination (Gardener *et al.* 1999, Gardener *et al.* 2003b). The overlapping margins of the lemma and its toughness make it difficult to break open to expose the caryopsis, a feature also of *Austrostipa* spp. (Barkworth 2006). Puhar (1996) found by staining with tetrazolium chloride that 93.5% of *N. neesiana* seeds collected in the previous summer were viable, but in laboratory tests less than 2% germinated under a day/night cycle of 30/20ºC and 14/10 hr light. Removal of the lemma enabled 100% germination within three days under the same conditions.

Dormancy mechanisms allow the seeds to persist in the soil for "many years" (Gardener *et al.* 1999 p. 10). Dormancy can be broken by scarification and de-hulling (removal of the lemma) (Puhar and Hocking 1996) but is not broken by stratification (chilling) at 3ºC for periods of 24, 72 and 168 hours (Puhar 1996). Heating of seeds to 60 ºC in an oven for 30, 60 or 240 minutes signficantly increased germination (Puhar 1996). Gardener *et al.* (2003b) found that de-hulling of seeds stored for 8 months increased germination from 48.5% to 82% at 15-25ºC with a 12 h light/dark cycle. Andersen (1963) found that germination of naked caryopses of the closely related *N. leucotricha* was usually complete after 21 days in light at 15-25 ºC and in darkness at 15 ºC, and that seed with intact glumes germinated best when sown upright in soil and sand for 28-35 days at 15-25 ºC. Chilling had little effect on germination.

An intact lemma may prevent germination by restricting the embryo or by acting as a barrier to water and oxygen. The lemma protects the embryo from dessication and other harsh environmental conditions. Germination occurs only when the lemma is broken or degraded by weathering (Puhar 1996, Slay 2002c) or the actions of decomposers. This may require 3-4 months in the soil, so germination of panicle seed is delayed until mid-winter (Slay 2002c). Germination rate increases with duration of ground burial: 90% of de-awned seeds buried in the ground for 2 y in terylene cloth bags germinated in the laboratory compared with 48% of laboratory-stored seeds, but seed viability did not vary significantly with burial depth (0-10 mm vs. 10-20 mm) (Gardener *et al.* 2003b). In New England Tablelands pastures, only a small proportion of the seed bank germinates over 2 y (Gardener *et al.* 2003b).

Dyksterhuis (1945) found that cleistogenes of *N. leucotricha* commonly failed to germinate within a year of their production and were usually not wetted by rains because of the tight wrapping of the leaf sheath. Disintegration of the sheath was required for germination. Few cleistogenes appeared to germinate on living plants. Basal cleistogenes reporrtedly gave rise to seedlings especially in old, closely grazed, dead tussocks. Here they were protected from frost heave, which caused major mortality of seedlings of panicle seed origin that germinated in areas cleared of litter and outside of tussocks. Seedling numbers were much higher in bare areas than areas with accumulated litter.

Germination

The panicle seeds of *N. neesiana*, like most of the awned grass species tested by Peart (1984), are probably adapted to germinate after lodgement in suitable sites at the surface with their lemmas only partially buried, and, contrary to the opinions above, to have no dormancy but to react whenever moisture conditions and temperatures are suitable. In vitro, fresh seed germinates after about 10 days at constant temperatures between 18 and 25ºC under a 16 h photoperiod, but not at constant temperatures of 18, 20 or 25ºC in continuous darkness, although germination is stimulated in darkness by a temperature fluctuation of 10-20ºC, "suggesting a mechanism for pasture gap detection" via both light and heat (Bourdôt and Hurrell 1992 p. 101).

The timing of seed germination is regulated by rainfall (Bourdôt and Hurrell 1992). Germination occurs mainly in spring and autumn but can happen at other times of the year if adequate soil moisture is available and temperatures are suitable (Bourdôt and Ryde 1986, Duncan 1993, Gardener *et al.* 1999, Britt 2001, Slay 2001). In New Zealand pastures, there are two distinct peaks in autumn or early winter, and in spring or late spring, and high winter rainfall may delay spring germination. Germination is probably limited by low winter temperatures, and almost certainly by summer drought (Bourdôt and Hurrell 1992). Similar patterns are apparent in Australia. Germination occurs predominantly in autumn and spring on the New England tablelands (Gardener *et al.* 2003b).

According to Muyt (2005 p. 4), germination is "likely ... in response to the death of adult plants". Seeds reportedly germinate only in bare areas (Gardener *et al.* 1996a) or when gaps are created in pastures (Gardener *et al.* 1999).

Establishment of seedlings and juvenile plants

Many characters of seedling grasses may be useful taxonomically (Sendulsky *et al.* 1986), but those of *N. neesiana* do not appear to have been systematically described, nor has the development of seedlings and juvenile plants been adequately documnted. Internodes of grass seedlings are initially meristematic but new roots form mainly at the nodes, and the production of more, larger, adventitious roots from the increased stem surface is enabled as the stem increases in diameter (Clark and Fisher 1986). Later the thickening process of the stem changes to an elongation stage, with nodes forming on the stem at the leaf insertion points where there is no elongation. Unlike most other plants, the most proximal nodes and the upper sections of the internodes mature first, leaving an intercalary meristem, capable of cell division and growth, at the base of the internode, surrounded by the base of the leaf sheath (Clark and Fisher 1986). The seedling gradually transforms into a juvenile plant that produces new leafy shoots (tillers) from basal buds, each with their own roots. In tillering grasses the initiation of the inflorescene in the culm generally corresponds with cessation of new vegetative tiller production, which may resume after flowering (Clark and Fisher 1986).

Peart (1979 1984) established that grasses with hygroscopic awns and a barbed callus like *N. neesiana*, have a distinct seedling recruitment strategy, involving lodgement in an upright position on the soil surface with c. half the lemma exposed and no dormancy. Seeds that fail to lodge by the callus produce seedlings in which the radicle is less likely to successfully penetrate the soil. These seeds lie on the surface and were found to be destroyed by fire.

Recruitment of *N. neesiana* seedlings is often high. Slay (2001) recorded 1108 seedlings m^{-2} in winter in densely infested pasture in New Zealand. Earlier germinating cohorts have better survival rates than later cohorts (Gardener *et al.* 2003b). On bare ground, 78% of seedlings survived over 20 months (Gardener *et al.* 2003b). Seedling emergence from a natural seed bank on bared ground varied from 5-136 m^{-2} in any 6 month period (Gardener *et al.* 2003b). Seedlings emerging from de-awned panicle seeds deliberately placed, callus-downwards, 2 cm apart, at shallow depth (0-10 mm) had lower survival rates than seedlings from seeds buried at 10-20 mm depth (Gardener *et al.* 2003b).

Where there is a seed bank, areas bared with herbicide "generally produce a large germination ... within 12 months" (Duncan 1993) and are 'quickly reinvaded' (Bourdôt and Ryde 1986). Cover and abundance data from surveys at Derrimut Grassland Reserve, Victoria, suggested that seedling establishment is uncommon in areas of dense *T. triandra* (Lunt and Morgan 2000). In experimentally bared ground (glyphosate application) emergence ceased after the regrowth of surrounding vegetation (Gardener *et al.* 2003b), suggesting that disturbance that creates bare ground and sunlight are germination triggers (Gardener *et al.* 1996a).

No emergence was observed in undisturbed vegetated areas (Gardener *et al.* 1999), however on vegetated ground it is difficult to determine if recruitment is from new tillers of existing plants or from seed (Gardener *et al.* 2003b). According to Bourdôt and Hurrell (1987a), after herbicide treatment seedlings "may establish within the tiller bases of the dead tussock". Pritchard (2002) recorded widespread seedling presence after herbicide treatment at Laverton North, Victoria, in April 2001, "often growing from within dead tussocks".

Approximately 50% of seedlings were derived from cleistogenes in a Marlborough, New Zealand pasture (Bourdôt and Hurrell 1992). When plants were treated with herbicide giving total kill and preventing seed head production, seedling establishment in the following autumn and winter was from cleistogenes (Slay 2001). Slay (2002c) reported that cleistogenes in the soil seed bank germinated on bare soils (resulting from herbicidal control during spring) in autumn, before panicle seed. Earlier germination of these seeds was considered likely to be due to the much reduced toughness of the cleistogene seed coat.

The soil surface conditions needed for germination do not appear to be adequately known. The necessity of bare ground is generally recognised as a requirement (Gardener *et al.* 1996a, Gardener 1998, Slay 2001) and this has been attributed to a light requirement (Slay 2002a). Awns are shed when the seed has penetrated 10-30 mm into the soil and remain on the soil surface (Slay 2002a).

In summary, Bedggood and Moerkerk (2002) wrote that seedlings establish best in the open but can also establish in shaded situations under the canopy of other plants. However the evidence for establishment in shade is weak and uncertain.

The seedling "does not appear ... very vigorous" (Duncan 1993) and "grows quite slowly" (Storrie and Lowien 2003).

Demography, growth, persistence and dominance

N. neesiana tussocks are long-lived and "very hardy" (Storrie and Lowien 2003). 73% of plants survived over 3 years (Gardener *et al.* 1999) and individual plants have a longevity of over 20 years (Benson and McDougall 2005).

The physical structural characteristics of infestations, their spatial arrangement, patchiness and dynamics have been poorly described. Bourdôt and Hurrell (1987a) reported that "pure stands" occupying areas from several hectares to several square metres were common in pastures near Lake Grassmere in New Zealand. When fruiting, such infestations can look like cereal crops (Slay 2002c). Slay (2001 p. 11) reported that herbicide treatment that reduces competition from other pasture species can eventually result in "a dense mat, and total cover". Kirkpatrick *et al.* (1995 p. 35) stated that *N. neesiana* in native grasslands "generally grows to the exclusion of all other species".

Bourdôt (1988 p. 1) described its areal pattern in New Zealand as "scattered ... clumps and small patches". Slay (2002c p. 11) recorded that plants "are generally found in circular patches" in pasture in New Zealand and that infestations may be 3-10 m in diameter 5 years after establishment, with individual tussocks 5-12 cm in diameter. Slay (2002c fig. 28) illustrated a pasture with an array of scattered, irregularly rounded patches in New Zealand. Pritchard (2002) recorded a mean tussock density of 20.5 m^{-2} ("relatively dense") at Laverton North Grassland, Victoria, in October 2000, in a stand selected because it was "almost pure"; the tussocks mainly being "large, mature" and "up to 30 cm high".

Hurrell and Bourdôt (1988 p. 237) stated that *N. neesiana* "often does not have a dense and well-defined tussock form when in association with other grasses", while the ACT Weeds Working Group (2002) noted that it forms "dense thickets". Gardener (1998 p. 4) found that it "can completely overrun pastures resulting in canopy ocover of up to 60%". Slay (2002c) noted that it can from "continuous pasture" (in contrast to discrete tussocks). Stewart (1996) recorded cover in two 5 x 5 m quadrats in Broadmeadows Valley Park, Victoria, which ranged from 50-70% in one quadrat and 5-50% in the other over a 6 month period. Grech *et al.* (2005) reported that its canopy cover can exceed 60% in invaded pastures. Gardener *et al.* (2005) stated that it can can have high basal cover of 20%. Muyt (2005) estimated foliar cover across 102 quadrats each 25 x 25 m (= 25.5 ha) at ungrazed and not recently burnt ACT natural grassland (Yarramundi Reach) and found cover in excess of 75% in 2 quadrats, 50-75% in 1 quadrat, 25-50% in 21 quadrats, 5-25% cover in 30 quadrats, many individuals and up to 5% cover in 24 quadrats, and 3-20 individuals in 9 quadrats. Bourdôt and Hurrell (1989a) assessed cover in 161 paddocks in New Zealand and found that most had ≤5% cover with plants present mainly as clumps or dense groups. Where cover was >25% the plants were present mainly in pure stands. Plants had persisted at the probable first introduction point in the area for c. 60 years and in 1988 that infestation consisted of a pure stand of several hundred m^2 (Bourdôt and Hurrell 1989a). Gardener *et al.* (2005) described an infested paddock near Guyra, NSW, as consisting of two communities. *N. neesiana* was dominant in the slightly better drained areas while the second community on lower, poorly drained areas was dominated by *Festuca arundinacea* with little *N. neesiana*.

Bruce (2001) found it was dominant at 8% of sites investigated in the ACT, subdominant at 13% and common at 22%. Liebert (1996 p. 8) stated that it can "almost completely displace perennial native grasses" including *T. triandra* and had "destroyed" two wetlands at Laverton, Victoria, by excluding all other plants, in less than 10 years. In the Geelong area isolated plants on roadsides had become monocultures within 3 years (Liebert 1996 citing David Boyle). Slay (2002c) noted that it persisted when other pasture grasses fail.

McDougall and Morgan (2005) measured the cover and frequency of *N. neesiana* on native grassland re-establishment areas on former agricultural land at Organ Pipes National Park from 1989 to 2003. The site was burnt in autumn 1993, 1995 and 1997 and there was a severe drought from March 1997. From initial values close to zero, both % cover and % frequency varied markedly. Percentage cover never exceeded c. 5% and was much <1% during the period when biennial burning occurred. % frequency remained relatively stable over this period at c. 14-20%, declined to around 7% in 2001 and increased to about 22% in 2003. The variations in cover and frequency were possibly attributable to spot spraying , however the spike in frequency in 2003 suggested a significant recruitment event (McDougall and Morgan 2005). The 2003 peak in *N. neesiana* frequency corresponded with peaks in cover and frequency of the exotic legumes, *Trifolium* spp., a major weed at that time, and *Vicia sativa*, and the frequency of *Trifolium* spp. and *N. neesiana* followed very similar trends, suggesting that increased N fixation may have had a role in increasing *N. neesiana* abundance. There was extensive mortality of *T. triandra* in 1997 due to fire, followed by severe drought. At Derrimut, *N. neesiana* was unable to form dense swards where *T. triandra* was dense (Lunt and Morgan 2000).

Campbell (1977, quoted by Gardener 1998) observed that *Nassella trichotoma* first appears in an area as widely sccattered tussocks, seven to twelve years later as patches, with scattered plants between them, and four to six years later as complete infestations. It appears that the development of *N. neesiana* infestations may show a similar pattern.

Weed status

Nassella species appear to become a problem wherever they naturalise. Verloove (2005, p. 112) that the complex of exotic stipoids including *Jarava* and *Nassella* spp. naturalised in Europe were“a serious threat for native vegetation” and “worldwide among the most troublesome weeds” the control and eradication of which was “very time consuming and expensive”.

In New Zealand *N. neesiana* has been rated as extremely undesirabable (Bourdôt and Ryde 1986). It was declared a Class B noxious plant under the *Noxious Plants Act 1978* by the Marlborough District Noxious Plants Authority in 1979 (Bourdôt and Hurrell 1987a) and later Class B in the whole country(Bourdôt 1988). However some have questioned its potential for major impact. Jacobs *et al.* (1989 p. 569) considered it “a localised troublesome weed of pastures”, Connor *et al.* (1993 p. 301) thought it has achieved only ‘modest success’, and that there were “no serious grounds” for predicting it would become a widespread problem, while Edgar and Connor (2000) considered to be only. “locally troublesome”. As of 2002 it was classed under the *Biosecurity Act 1993* as requiring “Progressive Control” in the Marlborough region , and “Total Control” with the aim of eventual eradication in Hawkes Bay region (Slay 2002a).

Although native to Chile, it was classified as a weed there because of the effects of the seeds on livestock and livestock produce (Gardener *et al.* 1996b - see their citation).

N. neesiana was listed as one of 20 Weeds of National Significance (WONS) in Australia in 1999 (Iaconis 2003). The process of determining WONS was “the first attempt to prioritise weeds over a range of land uses at the national level” and was “not a purely scientific process” (Thorp and Lynch 2000 p. v). Of 71 weeds nominated by States and Territories *N. neesiana* was ranked 12th, based on evaluation by technical experts on six invasiveness questions, seven impact questions, potential for spread, and documentation of socioeconomic and environmental impacts (Thorp and Lynch 2000, McLaren *et al.* 2002a). The environmental impact assessment was rudimentary and “could be achieved only by taking a few pertinent environmental indicators and combining them into a ranking” (Thorp and Lynch 2000 p. 6). These were: 1. presence in a biogeographical region (each region being assigned equal value); 2. monoculture potential (ability to form pure stands giving a high score); 3. biodiversity indicator - based on the number of threatened species and special conservation areas (Thorp and Lynch 2000). *N. neesiana* was rated medium impact in respect of impact on threatened species, low impact in terms of threatened communities, “minimal national relevance” based on presence in less than 25% of biogeographic regions and low monoculture potential (Thorp and Lynch 2000 pp.15-16). Despite this, the species given a national listing. Recognition as a WONS resulted in a National Strategic Plan (ARMCANZ *et al.* 2001), increased mapping and recording, codes of practice to prevent spread and the development of better management methods (McLaren *et al*. 2002a).

Groves *et al.* (2003b) developed a weed rating system for invasive plants in Australia and came up with the following ratings for *N. neesiana*:

Australia	5S
New South Wales	5nceS
Victoria	5S,
Tasmania	OXS
South Australia	OXS
Queensland, Western Australia, Northern Territory	no rating

where:

5 = naturalised and known to be a major problem at 4 or more locations within a State or Territory
0 = naturalised but only known naturalised population now removed or thought to be removed
S = potential to spread further
n = naturalised in part of a State
c = under active control in part of a State
e = eradication being attempted in part of a State
X = potentially a greater agricultural problem than the rating shown

The weed risk assessment process in Victoria, known as the the Victorian Pest Plant Prioritisation Process (Weiss *et al*. 1999, Weiss and McLaren 2002) enables the relative importance and potential impact of a species to be determined by scoring weeds on their invasiveness characteristics, current and potential distribution, and impact criteria. On a scale of 0-1, an invasiveness score of 0.72 was determined for *N. neesiana*, slightly less than that for *N. trichotoma* and much higher than *Eragrostis curvula* (0.50) (McLaren, Weiss and Faithfull 2004).

There is little dissent from the view that *N. neesiana* is a serious pasture and environmental weed in south-eastern Australia (McLaren *et al.* 1998), however Grice (2004b) did not rate it as a threat in terms of non-pastoral agriculture, forestry, fire or amenity. Carr *et al.* (1992 pp. 41, 51) considered it to be a “very serious threat to one or more vegetation formations in Victoria”. McLaren *et al.* (1998) considered it to be potentially the worst environmental weed of indigenous grassland in Victoria, while McLaren, Stajsic and Iaconis (2004) considered it to be rapidly degrading critically endangered native grassland remnants in Victoria. It was listed as a perennial grass ‘weed of concern’ for South Australia (Virtue *et al.* 2004). Groves *et al.* (2003b) determined that it was having a direct impact on rare or threatened native plant species. In Victoria it has been portrayed as a strong resource competitor, “even choking out *Nassella trichotoma* ... in indigenous grasslands” (Iaconis 2003 p. 6).

McLaren *et al.* (2002b) undertook a survey of land owners and managers in Victoria, the ACT and NSW and found that 5% of respondents, all from NSW, considered it a beneficial plant, while 86% did not. Even in the Angahook-Otway region of Victoria, an area largely occupied by forest, heathy woodland or heathland it has been rated by expert opinion as a weed of importance and high impact (“ability to cause actute disruption to ecological processes, dominae vegetation strata, cause severe loss of biodiversity”), with a “moderate” area that could be occupied in a “low” range of habitat types (Platt *et al*. 2005).

Noxious weed status
The noxious weed status of *N. neesiana* in Australia States and Territories has developed as follows:

ACT: Declared Pest Plant under the *Land (Planning and Environment) Act 1991* (Bruce 2001, ACT Weeds Working Group 2002), then from 12 November 2005 the *Pest Plants and Animals Act 2005* (Australian Weeds Committe 2007). It is classified as a C3/C4 pest plant: control is required (Glanznig and Kessal 2004), infestations must be contained and propagation and supply is prohibited.

Victoria: First declared noxious on 27 October 2005, as a Restricted Weed under the *Catchment and Land Protection Act 1994* (Anon. 2005). It is an offence to trade and transport the plant and to deposit it on land, but there is no legal requirement for landowners to control infestations on their land. Listed as a high priority ‘New and Emerging Weed’ in the North Central Region Weed Action Plan 2001-2005 (Frederick 2002) and as a ‘Priority weed’ in the Regional Weed Action Plans for Port Phillip, North East, Goulburn-Broken, North Central, Wimmera,Corangamite andGlenelg-Hopkins regions (McLaren *et al.* 2002b).

New South Wales: Declared noxious in 11 local government areas (Benson and McDougall 2005). In 2004 regional control and declaration was applied under the *Noxious Weeds Act 1993*,with prohibition of trade and eradication or control required (Glanznig and Kessal 2004). Declared a weed statewide in 2006 (Iaconis 2006a) and listed as a Class 3 (Regionally Controlled) weed for 25 Local Control Authority (LCA) areas and a Class 4 (Locally Controlled) weed for 103 LCA areas as of March 2007 (Australian Weeds Committee 2007). According to Snell *et al.* (2007) it is Class 3 species in 30 LCA areas and a Class 4 species in all other areas. Both Classes cover weeds considered to be a serious threat to agriculture of the environment in the area. Class 3 weeds are not, and Class 4 weeds are widely distributed in the area in which they are declared. Declarations of a Class 3 weed must include a minimum of three adjoining LCAs. LCAs may be either a local municipal government or a special purpose county council. *N. neesiana* is not prohibited from trade since Class 3 and 4 weeds are not “notifiable” (Australian Weeds Committee 2007).

Tasmania: Under the *Weed Management Act 1999*, as of June 2004, prohibited in trade, prohibited import and control required (Glanznig and Kessal 2004). It is a declared plant under the *Act* and the details on actual restrictions imposed are contained in the weed management plan (Australian Weeds Committee 2007). These include prohibitions of the importation of seed, the importation of contaminated livestock, sale and distribution of the plant and measures to manage infestations and quarantine items contaminated with seed (DPIW 2007). Importation is also restricted under the *Plant Quarantine Act 1997* (DPIW 2007).

South Australia: Proclaimed under the former *Animal and Plant Control (Agricultural Protection and Other Purposes) Act 1986* for control in the whole State in 2001, and after repeal of that Act declared under matching sections of the *Natural Resource Management Act 2004* (Iaconis 2006a). A Class 2 weed, requiring to notification by land owners to the relevant authority and control throughout the State (Australian Weeds Committee 2007). Prohibited in trade, prohibited import (Glanznig and Kessal 2004).

Queensland: Under the *Land Protection (Pest and Stock Route Management) Act 2002*, as of 2004, prohibited in trade and for importation, eradication required (Glanznig and Kessal 2004). Declared a Class 1 weed throughout the State in 2005 (Iaconis 2006b). Class 1 weeds are not commonly present in the State are prohibited in trade, and where established are subject to eradication (Australian Weeds Committee 2007).

Western Australia: Classed as ‘unassesed’: not risk-assessed under Western Australian protocols, so not included in the ‘Permitted and Prohibited List’ under the *Plant Diseases Act 1989*, but recognised as a declared pest plant in other States and therefore prohibited from importation (Glanznig and Kessal 2004, Australian Weeds Committee 2007). According to Snell *et al.* (2007) prohibited under *Plant Diseases Act* and listed as a P1 plant under the *Agricultural and Related Resources Protection Act 1976* which prohibits movement and trade in the species.

Northern Territory: Under the *Weeds Management Act 2001* not declared as of June 2004 (Glanznig and Kessal 2004), but declared by March 2007 as a Class A and Class C noxious weed under the *Weed Management Act 2001*: “to be eradicated”, prohibited from sale, and prohibited from introduction to the Territory (Australian Weeds Committee 2007, Snell *et al.* 2007).

Undesirable characteristics

In its introduced range including south-western Europe (Verloove 2005), New Zealand and Australia, *N. neesiana* forms dense stands in invaded vegetation, including bushland and parkland (Liebert1996), and in pastures, where it can form canopy cover of up to 60% (Gardener *et al.* 2003a). *N. neesiana* possesses many environmental traits that allow it to outcompete native vegetation (Gardener and Sindel 1998), being competitive for space, light, water and nutrients (Wells *et al.* 1986), and very competitive when mature (Cook 1999).

N. neesiana is resilient after cutting and grazing. Like other grasses, the intercalary meristems (at the base of each leaf) are stimulated to grow by removal of the upper stems or leaves (Wheeler *et al.* 1999), an adaptation to vertebrate grazing, so plants usually produce new flowering stems after mowing (Muyt 2001). Grass leaves also continue to elongate after being cut, and their stems often return to an upright position after being flattened by wind or water (Wheeler *et al.* 1999).

N. neesiana has the capability of dispersing rapidly e.g. south western Europe (Verloove 2005) over long distances.

Its recorded impacts on biodiversity includes the ability to replace preferred indigenous vegetation (Wells *et al.* 1986), to cause loss of species, loss of food sources for wildlife and seed damage to wildlife (Liebert 1996). Kirkpatrick *et al.* (1995) considered it a threat to the Kangaroo grass – Blue Devil – Common Bog Rush Basalt Plains Grassland community, the main grassland type of the Victorian basalt plains.

The seeds of various species of Stipeae have long been recognised as harmful to animal husbandry. *Stipa capillata* L. seeds penetrate the coats and flesh of cattle, “often leading to mortality or seriously injuring the oral cavity” (Tsvelev 1984 p. 859). *N.*

neesiana seeds are similar to those of some of the more robust seeded *Austrostipa* spp. which McBarron (1976 p. 135) considered to be "undoubtedly ... the major cause of seed troubles for livestock, especially sheep in New South Wales". These *Austrostipa* spp. are commonly cited as one of the main undesirable attributes of native pastures, requiring timely destocking to avoid problems (Garden *et al.* 2000). Seeds of *Austrostipa* spp. penetrate the eyes, mouthparts (Whittet 1969), skin and flesh (Mulham and Moore 1970) of sheep. "Wrinkled, long-woolled and young sheep are particularly susceptible ... the wrinkles and long wool collecting more of the seed, and the softer skin of young sheep allowing easier and deeper penetration. Severe damage to the eyes, jaws and feet can be caused by the seeds, which have also been known to penetrate the abdomen and internal organs ... in extreme cases blindness, lameness, fever and death can result" (Mulham and Moore 1970 p. 105). *Austrostipa* and *Aristida* spp. are the most common contributors to 'vegetable fault' (plant contamination) of wool in Australia (Grice 1993).

N. neesiana seeds are an irritant of skin (Wells *et al.* 1986) and "readily bore into the skins of animals, causing painful wounds" (Hayward and Druce 1919). Irritation of livestock by attached seeds causes discomfort and loss of condition (Wheeler *et al.* 1990). Lambs appear to be particularly susceptible to eye injury (Bourdôt and Ryde 1986).. Infestation of livestock with seeds may be exacerbated by rain, as happens with *Austrostipa* (McBarron 1976). The hides of cattle are too thick for the seed to penetrate (Gardener *et al.* 1996b) but cattle may suffer injuries to the mouth and intestinal tract. The seeds "cause discomfort" for dogs and humans (Liebert 1996), and can injure pet animals (Snell *et al.* 2007) and could be expected to cause a range of serious medical problems based on their similarity to other stipoid seeds (see McBarron 1976). Awned seeds in general can readily penetrate the soft tissue of the buccal and gastrointestinal tracts, producing inflammation, abcesseses and tooth and gum disease (McBarron 1976). They may pass through the skin into muscle and can occasionally penetrate internal organs, potentially causing fatal injuries (McBarron 1976). However penetration of skin, carcases and eyes by *N. neesiana* seeds is rare on the northern tablelands of NSW (Cook 1999).

The seeds are a contaminant of wool (Hayward and Druce 1919, Wells *et al.* 1986, Auckland Regional Council 2002). The half-life of seeds in the coats of sheep exposed to seeding plants for 17 days and then removed from exposure was measured at 7.5 days, with nearly half the seed remaining embedded after 100 days and only very slow subsequent seed loss (Gardener *et al.* 2003a). Upon removal of exposure, half the seeds on sheep had the callus embedded in the skin, but this reduced to 5% after 35 days, and few seed penetrated through the skin into flesh (Gardener *et al.* 2003a). The seeds damage pelts, and reduce the quality of carcases and hides (Bourdôt and Ryde 1986, Bourdôt and Hurrell 1992, Slay 2002, Auckland Regional Council 2002).

In the context of livestock grazing *N. neesiana* is a 'conflict of interest' species (Grice 2004b) because it is a valuable fodder for much of the year (Gardener 1998, Grech *et al.* 2004, Grech 2007a). Although it has harsh, often hairy leaves and tall course culms (Connor *et al.* 1993), it is considered to produce moderate quality, palatable forage during winter and early spring (Slay 2002c) and to be of "modest" grazing value (Connor *et al.* 1993). In Argentina "it produces fairly good fodder" (Hayward and Druce 1919 p. 228) and is considered one of the most important winter grazing species, valued because of its perenniality, persistence, long life and good quality feed with relatively high crude protein levels in the young foliage (Gardener 1996, Gardener *et al.* 1999). Its undesirability as a pasture species results not only from the problems caused by the seeds but from the rapid reduction in foliage that accompanies the production of large numbers of unpalatable flowering stems in late spring and summer, which results in a large seasonal reduction in carrying capacity at a critical time of year. Livestock avoid the plant in its reproductive phase, so it gradually displaces more valuable pasture grasses (McWhirter *et al.* 2006). Its feed value (crude protein and digestibility) is less than that of deliberately grown pasture grasses at the same stage of growth (Gardener *et al.* 1996b, Gardener 1998, Cook 1999). It generally has a lower feed value than the widely cultivated, moderate feed value *Dactylis glomerata* and is less reponsive to applications of N fertiliser (Grech *et al.* 2004, Gaur *et al.* 2005). But it responds well to clipping (as a simulation of grazing), the regrowth sward after clipping having significantly higher crude protein, metabolisable energy and digestible dry matter contents than growth in unclipped swards (Grech *et al.* 2004). Fertilisation and clipping can be used to improve its usefulness as fodder (Grech *et al.* 2004) but grazing can promote its dominance when pasturage consists of more palatable species (Liebert 1996, Gardener 1998).

N. neesiana is undesirable also because it can contaminate other agricultural produce, including hay (Frederick 2002).

Increased fire risk has rarely been seen as a problem. Bartley *et al.* (1990) argued that "the greater height and density" of *N. neesiana* swards at Laverton North Grassland Reserve presented "a much greater fire hazard than native grasses". According to Liebert (1996 p. 9): "Regional fire authorities recognise the fire risk ... and consequently slash swards from November to December". However, comparative biomass production and breakdown assessments appear to be lacking and there appears to have been no proper evaluation of fire risk, which should involve comparisons with alternative vegetation states.

All plants deplete soil moisture and the amounts of water used at particular times may have implications for co-occuring species or have a wider ecological impact. Slay (2001) observed that soil moisture in early January under a dense ungrazed sward was 20.8%, while where the sward had been sprayed with glyphosate at flowering time it was 26.6% due to reduced transpiration and the reduction of evaporation due to dead thatch. Infestations in *T. triandra* grasslands presumably deplete soil moisture in spring and early summer, at the same time as the inter-tussock species are growing and before the main growing period of *T. triandra*. The overall effect could be a premature drying-out of the grassland landscape.

Like other weeds *N. neesiana* can have beneficial impacts, although apart from its fodder value, these have hardly ever been recorded in its invasive range. Slay (2002a) noted that well stablished populations can provide erosion control on steep land.

Control and management

N. neesiana is difficult to control and according to Gardener and Sindel (1998 p. 78) there is "overwhelming evidence" that it is "almost impossible to eradicate" because of the difficulty of killing mature plants, the size and longevity of the soil seed bank and the production of basal cleistogenes. Gardener *et al.* (1996a p. 243) considered there then existed "no widely successful management techniques which result in the eradication or long term reduction", while Gardener *et al.* (2003a p. 613) judged that "chemical and mechanical control have had little success to date, at best temporarily slowing its spread". Slay (2002c p. 24) considered that the "overall tenacity" of Chilean needle grass made it "an extremely stubborn weed to manage and control". He also noted that despite a wide range of control measures applied over a long period, land managers in New Zealand had reported "no success in terms of eradication" (Slay 2002a p. 7). Kirkpatrick *et al.* (1995 p. 35) claimed that it "seems impossible to control in its early invasive stage without causing great damage to native vegetation". Liebert (1996) also considered it difficult to manage. Recent overviews of control techniques include Slay (2002a), Michelmore (2003) and Snell *et al.* (2007) the latter providing the most comprehensive details.

An initial requirement in all management plans, but one often neglected, is to obtain a good representation of the plant's distribution and the status of populations. Thus the ACT Weeds Working Group (2002) listed survey and monitoring as the first priority in their management plan, and Muyt (2005), for example, undertook one such survey. Site assessment should include mapping and density assessment (Snell *et al.* 2007). Targeted surveys, a public reporting mechanism and mapping of infestations have been identified as important elements in a regional management approach (ACT Weeds Working Group 2002).

The critical foci of management activity is on techniques for depleting the soil seed bank by controlling seed input through mowing, herbicide application or cultivation/cropping (Bourdôt 1988, Bourdôt and Hurrell 1992, Slay 1992, Duncan 1993), slashing, burning or grazing (Slay 2002c, Beames *et al*. 2005, Grech 2007a, Snell *et al.* 2007), on reducing recruitment and density of established plants (Beames *et al*. 2005), along with prevention of spread (Bourdôt 1988, Frederick 2002, DPIW 2007, Snell *et al.* 2007). In pasture situations where eradication is unlikely, the emphasis has been on the development of methods for better utilisation, including strategic stocking (Duncan 1993, Gardener *et al.* 1999, McWhirter *et al.* 2006, Grech 2007a, Snell *et al.* 2007), and on agronomic techniques to maximise production of palatable foliage and minimise production of flowering culms and seed, including spray-topping or wick wiping, fertiliser application and intensive grazing (Slay 2002c, Grech *et al.* 2004, Grech 2007a). Long term management requires replacement by competitive species in pastures (Slay 2002c, Grech 2007a) and non-agricultural areas including native grasslands (Mason and Hocking 2002, Hocking 2005b) or conversion to another land use such as cropping or forestry (Slay 2002c).

Morfe *et al.* (2003) presented a cost-benefit analysis of alternative management strategies for three different rates-of-spread scenarios. They considered it realistic to reduce infestations by 99% over 10 years only for infestations of less than 10 ha, and to reduce infestations by 90% for areas up to 500 ha.

The vast majority of information on *N. neesiana* control and management relates to agricultural areas (e.g. Bourdôt 1988, Bourdôt and Ryde 1986 1987a 1987b, Duncan 1993, Gardener 1998, Gardener *et al.* 1996a 1996b 2005, Grech 2007a, Grech *et al*. 2004 2005 2007, McWhirter *et al.* 2006, Slay 2001 2002b 2002c, Snell *et al.* 2007) and the National Strategic Plan for *N. neesiana* (ARMCANZ *et al.* 2001) did not detail an integrated management approach for native grasslands (Downey and Cherry 2005). To date the best guide for *N. neesiana* management in grasslands and grassy woodlands is that of Beames *et al.* (2005), although Snell *et al.* (2007) provided useful guidance. Various options for conservation areas have been suggested, with the aim of generally reducing populations while maintaining existing native species and managing to advantage the native plants (Bedggood and Moerkerk 2002). Spot spraying is the favoured method of eradication, using non-persistent herbicides (Beames *et al.* 2005). Snell et al. (2007) recommended use of flupropanate, but warned that it can be very damaging to many native grass species. Regular biomass reduction by burning or grazing is widely used in the south-eastern Australian grasslands (see below under grassland management) to maintain plant diversity and has been suggested as useful in reducing *N. neesiana* biomass and fuel load (Bedggood and Moerkerk 2002). Use of fire to reduce seeding and destroy fallen seed has also been recommended (Snell *et al.* 2007). Resowing with native grasses is recommended when more than three tussocks are removed or an area >0.5 m diameter is treated, either with the 'spray and hay' method (see below) or other techniques (Bedggood and Moerkerk 2002, Snell *et al.* 2007). Annual grazing and burning of native pasture was listed as a successful management option by Bedggood and Moerkerk (2002). The pasture is grazed heavily until *N. neesiana* enters the reproductive phase, stock are then removed and the area is burnt late, i.e. in autumn or winter, so as not to kill *T. triandra*.

Hand removal

Isolated plants and small infestations can be grubbed out (Bourdôt 1988), although Slay (2002a) considered this impractical. Liebert (1996) recommended using a mattock. Slay (2002c) recommended digging to at least 15 cm depth and 40 cm diameter and disposal of bagged material by incineration or deep burial. Snell *et al.* (2007) considered manual chipping a preferred method because the potential for regeneration from basal cleistogenes is eliminated if chipped plants are removed from the site.

Herbicides

According to Slay (2002a), who reviewed herbicidal management of *N. neesiana*, twenty five herbicides have been used in documented control attempts. The most frequently used in Australia have been glyphosate, flupropanate, 2,2-DPA, atrazine, hexazinone and simazine; the first two being the main chemicals used in Australian native grasslands (Lunt and Morgan 2000). The herbicides with soil residual properties, particularly flupropanate, are valued for the ability to prevent seedling emergence.

Use of herbicides on *N. neesiana* in Australia was severely inhibited for many years by the failure of herbicide manufacturers and retailers to include the plant on herbicide labels. None of the chemicals mentioned by Duncan (1993) were at the time registered for use against *N. neesiana* in Australia, nor were those mentionded by Liebert (1996). This situation remained unchanged in October 2004, although State Government agencies, funded by the Australian Government, were undertaking detailed trials in order to achieve appropriate herbicide registrations (Iaconis 2004). Thus chemical control relied on 'off-label' use for a very long period. Lack of label recommendations in some cases meant that State Government officers could provide no recommendations or advice on *N. neesiana* herbicidal management (Iaconis 2004). In Victoria, a government 'Code of Practice for Provision of Chemical Advice to Clients' (DNRE 2000) prohibited any mention of off-label uses by government officers involved in recommending herbicides for weed control. Interpretation of the Victorian Code was complicated by the listing of broad weed categories such as 'perennial grasses' on some herbicide labels. In New South Wales and the Australian Capital Territory label directions were able to be overridden byAustralian Pesticides and Veterinary Medicines Authority (APVMA) permits (Michelmore 2003). NSW recommendations relied on a series of temporary APVMA permits, for pasture spraying with glyphosate and flupropanate, spray-topping with glyphosate, and use of fluazifop-P in legume pasture and lucerne (listed in

Storrie and Lowien 2003). However under Victorian legislation governing pesticide use these permits did not legalise use: off-label use, with certain provisions, not being illegal.

Label registration for all *Nassella* species was finally achieved for a flupropanate product in 2004 (McLaren *et al.* 2005). Label recommendations were for application to actively growing plants, by boom or spot spraying, once per year, in urban open space, woodlands, roadsides, nature reserves and pastures. Other products with on-label uses soon followed. As of October 2007 the only other herbicide with specific label recommendatons for *N. neesiana* was glyphosate, registered only for spot spraying, although a number of minor use permits were in operation (Snell *et al.* 2007).

Glyphosate

Glyphosate prevents synthesis of essential aromatic amino acids. It is probably the world's most widely used herbicide. It is a non-selective, systemic, water soluble herbicide, absorbed by foliage, rapidly translocated throughout the plant and non-residual, being inactivated on contact with soil (Tom.lin 1997). It has relatively rapid activity, kills all plants, and creates bare ground, so when there is a soil seed bank of *N. neesiana* the plant quickly re-establishes (Liebert 1996). Pritchard (2002) found it gave excellent initial control, preventing seed formation when applied at the boot stage, but that 10 months after application many tussocks showed new growth.

Off-target damage from glyphosate can be high, but depends on the selectivity of the application method. There is no withholding period for livestock grazing or other agricultural activity although stock grazing should not be undertaken for 7 days after application (Snell *et al.* 2007)..

Flupropanate

Flupropanate (flupropanate-sodium, formerly called tetrapion) is an halogenated (fluorine) alkanoic acid which functions as an inhibitor of fat sysnthesis. It is a water soluble, systemic herbicide with low contact activity, taken up mainly by roots, and used only for control of perennial and annual grasses in pastures and uncultivated areas (Tomlin 1997). It is moderately selective and slow acting, with soil residual effects that kill emerging seedlings (Parsons and Cuthbertson 1992, McLaren *et al.* 2005). Recommended rates for control of mature *N. neesiana* are 1.5-3 L ha^{-1} (Grech *et al.* 2009a). Effects on target plants may be noticeable after 3-5 months but it may take upt to 12 months for plants to die (Snell *et al.* 2007). Pritchard (2002) found only slight foliage death 15 weeks after treatment but recorded 92-95% kill of tussocks after 45 weeks. The residual effects are increased at higher application rates and their duration is dependent on rainfall, which leaches the herbicide from the soil (Michelmore 2003). Fluporanate activity and behaviour is dependent on soil type – higher rates are used on fertile basalt soils and in higher rainfall areas, lower rates on infertile soils derived from sedimentary and granitic rocks and in lower rainfall areas (Snell *et al.* 2007). Flupropanate provides some selectivity: *Austrodanthonia*, *Austrostipa* spp. and *Microlaena* are killed, especially at higher applications rates, while *T. triandra*, *Bothriochloa macra* and *Poa labillardieri* Steud. are generally tolerant at label rates. *Phalaris aquatica* L., *Dactylis glomerata* L. and *Festuca arundinacea* are affected but recover, while young *Trifolium subterraneum* L. are severely affected (Michelmore 2003). In Australia, a withholding period for grazing stock or cutting for stock food of 4 months minimum after blanket application is mandatory, and 14 days for spot application, along with some other restrictive provisions for production agriculture (McLaren *et al.* 2005).

Flupropanate has been the preferred herbicide for spot spraying in agricultural areas and on land lacking significant native cover (Liebert 1996). An infestation in Geelong, originally with 80% cover, was reduced to 10% cover after spraying in 3 consecutive years and the broadleaf weeds that initially colonised were short-lived and some native grasses began to establish (Liebert 1996).

Grech (2007a) found that set-stocking combined with flupropanate spraying resulted in more bare ground and an increase in infestations. Of the range of herbicide and stocking options examined, flupropanate combined with strategic grazing and pasture rehabilitation provided the best control. Grech *et al.* (2009b) found that low rate treatments with flupropanate (0.25 and 0.75 L Ha^{-1}) we ineffective in controlling *N. neesiana* seedlings. Grech *et al.* (2009a) found that flupropanate at 2 L Ha^{-1} effectively controlled *N. trichotoma* in pot trials, but not *N. neesiana*, and that a range of native and exotic grasses was unaffected apart from a transient decline in growth.

A major disadvantage of flupropanate is the creation of bare ground that persists for long periods (Snell *et al.* 2007). These areas may be prone to subsequent reinvasion.

2,2-DPA

2,2-DPA is an halogenated alkanoic acid which acts by precipitation of protein (Tomlin 1997). It is a systemic herbicide absorbed by leaves and roots, used mostly for control of annual and perennial grasses (Tomlin 1997). It is selective for some grasses at low rates, and at high rates provides non-selective control of monocots (Parsons and Cuthbertson 1992). It is generally considered to be less effective and useful than the two most favoured herbicides, and does considerably more damage to non-target species than flupropanate (Michelmore 2003). Pritchard (2002) found it quickly killed foliage, but 45 weeks after application had only reduced the number of tussocks by 40%. Hartley (1994) found that 2,2-DPA reduced seed production by 90-99%, but detected resistance to 2,2-DPA in New Zealand after 2 years of annual or biannual application.

Hexazinone

Hexazinone is an inhibitor of photosynthesis and is a non-selective contact herbicide, absorbed by leaves and roots (Tomlin 1997), mainly the latter (Parsons and Cuthbertson 1992). It has a long residual life in soil (Parsons and Cuthbertson 1992) and maintains bare ground for long periods, and is available commonly in granular preparations.

Triazines

Atrazine is a triazine chemical which acts by inhibiting photosynthesis. It is a water soluble, selective systemic herbicide, absorbed mainly through the roots but also through foliage, mainly used to control broadleaf weeds and annual grasses (Tomlin 1997). It is relatively rapid acting and has pronounced residual effects for 6 months or more after application (Parsons and Cuthbertson 1992). Simazine is another triazine compound that acts by inhibiting photosynthesis. It is mainly root-absorbed and provides selective pre-emergence control of grasses and broad-leaved weeds, with long residual control at high application rates (Parsons and Cuthbertson 1992). Pritchard (2002) found that both atrazine and simazine application at the boot stage resulted in a small reduction in seedhead production but no other useful control. Atrazine was used against *Nassella* spp. by Philips and Hocking (1996) and Mason and Hocking (2002). Mason (2005) reported reductions from c. 20 to 7 plants m^{-2} two months after application of atrazine at an unstated rate.

Other herbicides

Paraquat dichloride ("Gramoxone"), a non-selective contact herbicide, has some activity against *N. neesiana* but is not as good as glyphosate in limiting seed production (Bedggood and Moerkerk 2002). Grass selective herbicides such as fluazifop-P are reportedly effective on *N. neesiana* seedlings but require excessively costly high application rates to control larger plants (Bedggood and Moerkerk 2002). Fluazifop-P is a relatively fast acting and selective systemic herbicide absorbed by foliage, is not residual and usually kills *N. neesiana* in 3-5 weeks (Snell *et al.* 2007). Slay (2001, 2002c) found in spray topping treatments that haloxyflop was superior to glyphosate in reducing seed production and subsequent seedling emergence but was more than ten times as costly.

Mason (2005) reported that acetic acid (4% acetic acid vinegar) and surfactant solution applied at 0.5 L m^{-2}gave close to 100% control of above-ground *N. neesiana* two months after application and reduced plant density from c. 20 to 8.6 plants m^{-2}.

Soil fumigants

Hurrell *et al.* (1994) examined the efficacy of three soil fumigants to kill buried seed. They found that dazomet and methyl bromide were highly effective, killing 98% of viable seed, while metam-fluid was less effective (83% of viable seed killed). Cleistogenes and panicle seed appeared to be similarly susceptible. Soil treated with these fumigants can be resown within 7 days of application, in contrast to residual herbicides such as hexazinone that create bare ground for long periods. However soil fumigation is expensive, and may be hazardous and difficult. Small patches have been successfully treated with Dazomet (Slay 2002c).

Wick wiping

Hocking (2009) demonstrated that mechanised wick wiping using glyphosate prior to flowering achieved major reductions in density and cover of *N. neesiana*, but was less effective when the height differential between with other plants was small and when active *N. neesiana* growth was limited. Mature tussocks density was reduced by up to 95% when wiping was undertaken in two successive years. Wick wiping was viewed as a valuable approach to integrate with mowing to reduce roadside infestations to a density at which subsequent spot spraying could be cost-effective (Hocking 2007 2009), but the technique may have wider applicability.

Grech *et al.* (2009c) examined the effects of wick wiping with glyphosate, flupropanate and a tank mix of the two herbicides in exotic pasture grassland and found that wiping was no more effective in achieving control than boom spraying, although it used less herbicide. The tank mix was ineffective, indicating antagonistic responses of the two herbicides.

Agricultural areas

Early recommendations for control in agricultural areas were for spraying of glyphosate to kill established plants, and of 2,2-DPA (dalapon) to control seedlings in pasture (Bourdôt and Ryde 1986 1987a 1987b, Bourdôt 1988) and to prevent flowering and reduce plant density (Hartley 1994). Duncan (1993) recommended glyphosate application in autumn and flupropanate in spring or autumn and noted that paraquat could be mixed with the flupropanate "to provide a quicker dessication and eliminate seed production". Storrie and Lowien (2003) recommended a glyphosate/flupropanate mix for this latter purpose, but research by NSW Agriculture found that glyphosate reduces the effects of flupropanate and it is better not to mix them, except when a quick marker is required for the treated area.

Bourdôt and Hurrell (1987a) found that hand-held wiper application of glyphosate in spring lead to higher rates of tussock survival (56% of plants with some surviving tillers) than boom spray application, which killed all plants (as assessed 9-18 months post-treatment), except when applied under drought conditions. 2,2-DPA was less effective, but suppressed the plant except when applied in winter. Other herbicides tested were ineffective. Wick wiper application was suggested but not experimentally examined. Storrie and Lowien (2003) reported that wiping with glyphosate between flowering and the milky-dough stage of the grain prevented panicle seed set, but killed <60% of plants. Hocking (in Iaconis 2006b) reported that wiping of roadside infestations in November killed 50-60% of plants and resulted in regeneration of native species. Britt (2001) found that glyphosate at 360 g/L (application rate not recorded) eradicated adult plants in a long-infested pasture, but did not significantly alter the number of adult plants when applied at concentrations of 180 and 7.2 g/L. McWhirter *et al.* (2006) found flupropanate to be superior to glyphosate for control in established pastures in New South Wales because it caused a smaller reduction in basal cover of desirable plants. Glyphosate was considered more suitable for spraying prior to pasture renovation. However use of both herbicides led to significantly higher cover of broadleaf weeds than in untreated areas.

Pasture topping (spray-topping) with sub-lethal rates of glyphosate is effective in reducing seed production (Storrie and Lowien 2003). Slay (2002b) found that chemical topping with glyphosate or haloxyflop in early seedhead stage, before anthesis, resulted in 91% and 97% suppression of seeding respectively in dense infestations, but markedly less success on scattered plants. The number of seedlings in the following winter were 81% and 21% respectively (Slay 2001). Dense populations did not produce new reproductive tillers but a scattered population with larger plants produced a second flush of tillers. Gaur *et al.* (2005) found that glyphosate applied in early-mid spring, prior to full panicle emergence, was the most effective treatment, able, if appropriately timed, to prevent production of filled, germinable panicle seed. Increasing application rates decreased or prevented the production of stem seeds and viable panicle seeds but did not prevent basal cleistogene formation, which was already completed. 2,2-DPA was much less effective.

Slay (2002c) reported that glyphosate or haloxyfop treatment at the early seed head reduced basal cleistogene development by 20%.

Bourdôt and Hurrell (1987b) tested a range of herbicides for control in lucerne. Hurrell and Bourdôt (1988) tested granular formulations of three herbicides and found that hexazinone at 16 kg ha^{-1} killed plants and prevented seedling establishment for at least 7 months. Bourdôt (1988) recommended hexazinone for infestations on roadsides and waste places.

Establishment of competitive plants (pasture species or fodder crops) is generally recommended after herbicidal control on agricultural land (e.g. Bourdôt 1988, Liebert 1996).

Natural areas

Herbicidal treatment of *Nassella* spp. in native vegetation has often had devastating effects on native vegetation, killing native plants or whole populations and facilitating irreversible weed invasions (Hocking 1998). Non-selective herbicides and non-selective application measures constitute one aspect of the problem. Uncritical adoption of recommended agricultural applications is another. A consistent complicating factor is the low level of knowledge of the resistance and susceptibility of native plants to particular herbicides across a range of seasons. Little detailed information appears to be available about off-target effects in native grasslands, perhaps because there is reluctance to admit that good intentions can produce bad results.

McDougall (1989) established that atrazine had "no direct effect" on *Themeda triandra* establishment and growth and suggested it could be used to reduce weed competition in *T. triandra* grassland sites lacking native species that are sensitive to it. Harris (1990) recorded that this herbicide would be a major component of *N. neesiana* control programs in native grasslands in the Melbourne area, including Derrimut and Laverton North, and that trials were to be undertaken comparing high volume spot spraying with low volume application methods such as 'Micro-Herbi', 'Splatter Gun' or 'Gas Gun'.

Flupropanate at low rates (1.5-3 kg active ingredient ha^{-1}) can be used to selectively remove *Nassella trichotoma* from pastures with little effect on native grasses including *T. triandra*, *Botriocholoa macra* and *Poa labillardieri*, but *Austrodanthonia* spp. and *Microlaena stipoides* are killed at less than half this application rate, and legumes may be damaged (Campbell 1997 1998). Hocking (1998) warned that atrazine, simazine and flupropanate were likely to be highly toxic to native grassland forbs. Bedggood and Moerkerk (2002) stated that atrazine killed *N. neesiana* in native grasslands with little effect on *T. triandra*.

Dare and Hocking (1997) tested glyphosate, atrazine, flupropanate and simazine at unspecified rates for control of *N. neesiana* in Melbourne area native grasslands and found that atrazine and flupropanate provided effective kill when applied in winter, as assessed 11 months later. Atrazine was found to act fast, providing effective kill within 10 weeks, and treated plots remained weed free. Glyphosate and simazine were slower acting (12 weeks) and glyphosate plots were reinvaded by weeds.

Brereton and Backhouse (2003 p. 3) observed that herbicides used to control grass growth in native grasslands to reduce fire fuel loads "usually" promoted "the establishment of exotic grasses to the detriment of the native flora", and Williams (2007) found that herbicide application as an alternative to burning for fuel reduction has wiped out a number of remnant native grasslands in western Victoria. Significant herbicide damage to desirable native species has been noted in the ACT. To address this the ACT Weeds Working Group (2002) recommended promotion of glyphosate spraying at the correct time and use of low rates of flupropanate for seedling control, as well as the use of alternative control techniques and greater concentration on control in buffer zones to restrict spread to conservation areas. Muyt (2005) suggested the use of either grass-selective or non-selective herbicides from autumn to late spring in one ACT grassland. McDougall (1989) argued that fluazifop would have advantages since is has no direct effects on establishment and growth of *Themeda triandra*, although it inhibits flowering, and is ineffective at reducing competition by annual forbs.

Puhar (1996) tested the impact of glyphosate, flupropanate and atrazine on *N. neesiana* by measuring the root and shoot lengths of seedlings germinated on agar plates impregnated with herbicide at various rates. Germination of dehulled seeds (i.e. lemma removed) was unaffected by any of the herbicides at any concentration. Glyphosate had significant negatives effect on root and shoot elongation. Atrazine had a lesser, but still significant effect, while flupropanate also caused significant negative impact, but with higher root growth rates than for glyphosate. All four herbicides were judged to be able to kill emerging seedlings at 0.25 of the label rate for grassland spraying, but the rapidly acting glyphosate was more damaging. Similar tests were undertaken for *T. triandra*, but the susceptibility to off-target damage of the remainder of the grassland flora remains largely unknown.

Disadvantages of herbicidal management

Whatever the herbicide used, cleistogenes that have already matured but remain attached to the plant, concealed beneath leaf sheaths are not killed (Hurrell *et al.* 1994). Furthermore, when a large *N. neesiana* seed bank is present, baring the ground with herbicides encourages seedling recruitment and may lead to rapid re-establishment, and an ultimate increase in density and cover (Hartley 1994, Gardener *et al.* 1996b, Gardener *et al.* 1999, Lunt and Morgan 2000, Slay 2002a, Storrie and Lowien 2003). Herbicidal management has often resulted in the expansion of populations and exacerbation of spread due to the elimination of competition (Slay 2001 2002a 2002c). When herbicides are applied in spring, for example, the basal cleistogenes are already mature, there is a greater effect on potential competitor plants and the bare areas created allow for more *N. neesiana* seed to germinate (Slay 2002c).

However if the seed bank is small, herbicial control may not simultaneously provide conditions for seedling establishment. Britt (2001) found no seedling growth 6 months post-treatment. Hocking (2005b) reported on the seed bank at infestations managed by repeated herbicide applications, mainly of glyphosate, in south-central Victoria and Hobart. In all cases the density of filled seeds (i.e. seeds containing a grain and embryo) in the seed bank was <10 m^{-2} and the vast majority of seed in the seed bank consisted of empty lemmas (unfilled seed) or dead seed. No filled seeds were found at Hobart.

Management of infestations and regeneration in non-agricultural areas by annual herbicide applications to kill seedlings can effectively reduce infestations, including soil seed banks, to very low levels, and could be used to achieve eventual eradication if persistently applied over a long period (Hocking 2005b). But in general the effect of these herbicides on native plants, and the impact of such spray regimes on the biota of the sprayed areas as a whole, have not been studied. *N. neesiana* might be controlled, but the control activites may themselves have significant biodiversity impact.

Liebert (1996) provided estimates of the costs of herbicidal control using flupropanate, glyphosate, 2,2-DPA and fluazifop-P ("Fusilade"). Slay (2002c) considered glyphosate to be the most economical.

Slashing and mowing

Slashing can reduce the production of panicle seed and stem cleistogenes but has little other benefit, apart from stimulating regrowth that is more palatable to grazing livestock (Snell *et al.* 2007). Britt (2001) found that plants slashed to 1 cm in early May at Greenvale had failed to produce flowering stems by late October, whereas 60% of unslashed plants had produced flowering heads by that time. Hocking (2005b) found that mowing in spring had no major effect on the number of mature tussocks and failed to significantly reduce tussock size. Slay (2001) incorrectly attributed to *N. neesiana* the findings of Mulham and Moore (1970) about mowing *Austrostipa* swards. Those authors found that mowing in late September prevented seed maturation and that late mowing could allow seed maturation on cut stems. Slay (2001) found that mowing twice at early seed head emergence (Feekes stages 10-10.4) totally prevented the formation of viable panicle seed and stem cleistogenes and resulted in regrowth acceptable for livestock grazing. Grech (2007a) also studied slashing impact in pastures and quantified some benefits in terms of palatable regrowth that could be exploited by grazing. Mowing before emergence of the panicle may result in the growth of more reproductive tillers, so repeated treatments are generally required. The best time to slash or mow is before flowering when 25-75% of the heads have emerged from the flag leaf sheath (Slay 2002c), or at the flowering stage (Grech 2007a, Snell *et al.* 2007). Slay (2002c) noted that the resultant reduction in shade may facilitate the survival of seedlings.

Mowing can encourage the formation of prostrate swards, so may also reduce the production of stem cleistogenes (Snell *et al.* 2007).

Fire

Published information on the value of fire as a managment method are equivocal. According to Bourdôt (1989) the New Zealand experience was that repeated fires favour the grass, and when tried as a means of control in Marlborough appeared to have "eliminated other species resulting in pure stands". Muyt (2001 p. 73) stated that fire "stimulates vigorous regrowth", often promotes spread, but is useful for improving access and effectiveness of herbicide application by removal of litter and dead material. However he also noted that fire "generates bare ground and reduces immediate competion, conditions that are ideal for seed germination" (Muyt 2001 p. 73) so should therefore should be followed by herbicide application (Muyt 2005). In pastures, Slay (2002c) recommended spraying with glyphosate to dry out the grass before burning and follow-up herbicidal control to kill seedlings that grow from cleistogenes in burnt tussocks.

Snell *et al.* (2007) advocated the use of fire to prevent seed set, burn off standing seed and to stimulate growth of seed from the soil seed bank, but advised integration with other selective control techniques. They also noted its usefulness in enabling a clearer indication of intensity and pattern of infestations.

In *T. triandra* grasslands burning in spring is recommended, so competing cover establishes quickly (Muyt 2001). Hocking (2005b) found that burning in spring in a native grassland under drought conditions resulted in major reduction of large, mature tussocks and proliferation of small tussocks, probably derived from the large. The total area occupied by tussocks was decreased by >75% without decreasing the density of the population. Late spring burns reduced seed production by half, and did not lead to major seedling recruitment. He suggested that fire was therefore useful to weaken the stand, making it more susceptible to subsequent control activities of a different type and in limiting seed production, and could play a role in a containment strategy and integrated management. Hocking (2007) noted that fires kill few plants and that seed production resumes within a year. Snell *et al.* (2007) agreed that burning usually does not result in much kill of mature plants. However reductions in density of c. 90% have been reported after annual November burning for 5 years at Plenty Gorge Parklands, Victoria, however *N. neesiana* was replaced by *Phalaris aquatica* (Snell et al. 2007 p. 34), which may have even worse biodiversity impacts.

The effects of repeated periodical burning and of fires in autumn do not appear to have been adequately assessed by scientific tests. In particular better knowledge of the effects of fire on the litter and near-surface soil seed banks would be desirable.

Cultivation and cropping

The objective of cultivation and cropping is too reduce the soil seed bank before re-establishment of a vigorous pasture that can suppress any seedlings that may subsequently appear. Cultivation stimulates seed germination and shallow cultivations are supposedly superior in depleting the seed bank because most of the seed is close to the surface (Snell *et al.* 2007). Herbicides applied by boom spray are recommended as the intitial treatment, followed by a series of shallow cultivations interspersed with dense, uniform sowing of annual fodder crops (Bourdôt 1988, Duncan 1993, Slay 2002a 2002c). Shallow cultivation (no greater than 5 cm) is recommended so that seed will not buried and the maximum amount will germinate. Slay (2002a) warned that the cultivation technique and timing were critical to minimise dispersal of cleistogenes. Duncan (1993) recommended winter cropping for two years followed by pasture establishment, and in less arable areas herbicide spraying, direct drilling of fodder crops, and fertiliser application. Bourdôt (1988) recommended three years of such management before sowing of 'permanent' pasture. Storrie and Lowien (2003) broadened the range of recommended crops to include summer forage species and summer grains, and the aerial application of herbicide, seed and fertiliser to treat steep, rocky, inaccessible areas. Establishment of lucerne after glyphosate spraying, with residual grass herbicide application and winter spraying with grass-selective paraquat and metribuzin is an alternative approach (Bourdôt 1988).The best methods, including crop and pastures to sow, depend on the specific characteristics of the infestation, regional agronomic factors, etc. (Slay 2002c).

Grazing

Overgrazing is likely to favour *N. neesiana*, due to its lower palatability (Bourdôt 1988) at least during its reproductive period (Grech 2007a). Crude protein, metabolisable energy and digestible dry matter contents of *N. neesiana* peak in winter and early spring and decline markedly from September to December, corresponding with the onset of reproductive phase (Grech 2007a). Strategic grazing in pastoral ecosystems to best utilise the green feed produced by *N. neesiana* in winter and spring has been intensively studied (Gardener 1998, Grech 2005a 2007a). Intense grazing pressure over a short period is required to suppress seed production (Storrie and Lowien 2003) but in practice is very difficult to achieve and probably not feasible in most grazing enterprises (Slay 2002a, Grech 2007a). In addition there is a risk that overgrazing will encourage further *N. neesiana* establishment (Slay 2002a). Set stocking with sheep exacerbates the problem by reducing the cover of desirable pasture grasses and creating more bare ground suitable for further *N. neesiana* establishment (Grech 2007a, Snell et al. 2007). Preliminary results of grazing trails reported by Grech (2005a) at Greenvale, Victoria, showed that cattle reduced the amount of panicle seed produced in comparison to ungrazed paddocks by 95%, and in comparison to sheep grazed paddocks by 77%, when stocking at a normal rate for the district, at 12 Dry Sheep Equivalent ha^{-1}. Both sheep and cattle continued to gain weight over the spring. Strategic grazing can be combined with spray-topping and/or wiping before flowering. Grazing management is predicated on acceptance of *N. neesiana* as an ineradicable pasture component and making best use of the feed it offers. In pasture situations it is a weed one can 'learn to love' (Storrie 2006).

Shade

Establishment of *Pinus radiata* to shade out *N. neesiana* is being investigated by Hawkes Bay Regional Council in New Zealand (Slay 2002a). Five years after plantation establishment, *N. neesiana* was "weaker, rotting and forming a dense thatch" (Slay 2002a p. 33).

Quarantine and restriction of dispersal

Bourdôt (1988) recommended a range of measures to restrict seed dispersal: restricting livestock access to seeding plants, appropriate mangement for contaminated stock, not harvesting fodder from infested land, cleaning of contaminated vehicles, machinery and clothing, and eradication from flood-prone land. Additionally Liebert (1996) mentioned the use of only weed-free fodder and seed, and not moving contaminated soil. These measures can be implemented by strategically timed slashing and mowing, restricted grazing (including droving of livestock along infested roadsides), fodder harvesting (Liebert 1996, Frederick 2002), and vehicle movement, signage to alert people to *N. neesiana* presence, particularly on roadsides (Liebert 1996, Frederick 2002), machinery hygiene programs (Frederick 2002, Moerkerk 2006a), State-wide quarantine (DPIW 2007) and other measures. The presence of stem cleistogenes requires that fodder harvested from infested swards at any time should not be fed out in uninfested areas.

To minimise seed movement on livestock the Tasmanian Department of Primary Industries and Water has prescribed measures in Regulations under the *Weed Management Act 1999*. The length of hairs on the coat is not to exceed 25 mm, seeds are not to be adhering to the animal, a permit for importation is required and the animals must be imported to an approved facility or slaughterhouse. Suggested actions include liaison with suppliers and confinement of the animals in holding pens until they have been thoroughly inspected and have completed "bowel evacuation" (DPIW 2007 p. 3). Similar hygiene activities are recommended for clothing, machinery, soil and other materials. Persons wishing to dispose of contaminated materials must contact a government officer who shall determine whether removal to a quarantine place or destruction *in situ* is most appropriate (DPIW 2007).

Integrated management in native vegetation

Spot spraying with glyphosate is the usual management method in natural or semi-natural areas (e.g. at Organ Pipes National Park, McDougall and Morgan 2005). Repeated herbicide treatments are commonly required to kill mature plants (Muyt 2001) and several cycles of treatment and monitoring are required for long-term control (Liebert 1996, Frederick 2002). Liebert (1996) considered the residual activity of flupropanate made it unsuitable for use in native vegetation. Bedggood and Moerkerk (2002) noted that investigations were underway in the ACT to determine spraying times when the native plants were dormant and thus less likely to be impacted. However native C_3 grasses probably generally have similar growth periods to *N. neesiana*, so the scope for such temporal selectivity appears very limited. Victorian experience is that native species are always damaged (Bedggood and Moerkerk 2002, citing C. Hocking).

Liebert (1996) suggested that burning before November could help to kill seeds and promote germination of cleistogenes, which could be sprayed with glyphosate the following autumn.

Lunt and Morgan (2000) recommended maintenance of dense swards of the dominant grass as the most efficient means of limiting the establishment and density of *N.neesiana* in *T. triandra* grasslands, and re-establishment of dense *T. triandra* after herbicidal control of *N. neesiana*. They reported slower and comparatively little invasion where *T. triandra* cover exceeded 50%, and in one invaded grassland, proximity to large infestations did not appear to be a significant factor in determining the presence of the weed in particular quadrats (Lunt and Morgan 2000). Oversowing of *T. triandra* does not appear to reduce the soil seed bank of *N. neesiana*, possibly because the growing periods of the two species has little overlap, however *Austrostipa* or *Austrodanthonia* spp. may be more suitable (Beames *et al.* 2005). Direct drilling of *T. triandra* seed after spraying has been found to provide effective control (Liebert 1996 citing Craig Bray).

Current best practice management in invaded *Themeda*-dominated grasslands has been detailed by Beames *et al.* (2005) and Hocking (2005b) and involves finely targetted biannual or more frequent glyphosate spraying before flowering, followed by establishment of *T. triandra*. Fire can be integrated into these programs both to improve germination of native and *N. neesiana* seeds and open up the landscape, and the broadcasting of native seeds is recomended. A brief case study of such an approach was provided by Snell *et al.* (2007).

Muyt (2005) recommended selective mowing with catcher mowers at the edges of dense stands, but the scale and irregular distribution of patches in most infestations make this approach impractibable.

In uninvaded grasslands, best practice management is focused on minimisation of major disturbance, and the maintenance of existing native grass sward density and cover. Many herbicides used to control *Nassella* spp. have severe impacts on native vegetation and can result in major weed invasion similar to those which occur after ploughing (Hocking 1998). As noted in more detail above, when the dominant native grass dies or is killed by disturbance, the N and P held in the plant is released into the soil, creating a nutrient flush which enables successful establishment of *Nassella* spp. (Henderson and Hocking 1997, Wijesuriya and Hocking 1997, Hocking 1998).

A range of techniques have been developed for re-establishment of native grasses and replacement of *N. neesiana* in native grasslands (McDougall 1989, Stafford 1991, Hocking 2005b) and have been recommended for use for paticular areas (e.g. Muyt 2005). However the development of effective techniques requires much improved understanding of the underlying ecological processes (Hocking and Mason 2001).

Themeda re-establishment

McDougall (1989) reported the results of detailed experiments to determine suitable methods for the re-establishment of *Themeda triandra*. The most effective method involved application of *T. triandra* thatch immediately after harvest in January, followed by burning of the thatch in September when dry enough. This provided seedbed conditions favourable for *T. triandra* germination and seedling establishment. A mulch of brown coal greatly improved seedling establishment from surface-sown seed. Hebicide spraying prior to *T. triandra* seed germination indicated that establishment was not inhibited by low-growing weeds. Spring burning promoted germination of *T. triandra* seed in the soil seed bank.

Stafford (1991) reported on long-term investigations of techniques to establish *T. triandra* to restrict weed invasion in secondary grassland and woodlands. The ability to burn established *T. triandra* swards in spring/early summer and its tolerance to herbicides used to control woody weeds provided the weed management advantages. His technique can be characterised as 'hay/spray/burn': haying with *T. triandra* culm thatch, spraying to suppress weeds and burning to remove the thatch and dry weeds. Herbicidal control of weeds was critical to success, but the effective herbicides are widely active against a range of plants, both exotic and native. High labour inputs to obtain sufficient seed were identified as a major problem. A vehicle-mounted reel-stripper was developed, but proved to have limited efficiency in gathering undamaged, chaff-free seed. It also damaged the sward. Modification of the stripper, including addition of wire flails to the rotor, enabled harvesting of the panicles at high efficiency. However germination of the material harvested was only 10% of that with hand-cut material. Harvesting sufficient seed for the areas requiring rehabilitation remains an ongoing problem.

'Spray and hay' techniques have been developed and modified to a point where *N. neesiana* swards in *Themeda* grasslands can be selectively removed and replaced with *T. triandra* when seasonal rainfall is adequate (Dare and Hocking 1997, Hocking 1998, Mason 1998, Mason and Hocking 2002, Mason 2004, Hocking 2005b). The method, first developed for *N. trichotoma* (Phillips and Hocking 1996, Mason 2004) involves mowing in late spring to reduce *N. neesiana* biomass, spraying of *N. neesiana* plants with glyphosate the following autumn, application of seed-bearing *T. triandra* grass hay in winter and allowing the seeds to bury themselves in the ground, then removal of the hay thatch by hand or by burning in early spring (Hocking 2005b). Tested variations on the technique have involved tilling of the soil and use of other herbicides (Mason 1998 2004). Dense patches of *N. neesiana* have been controlled in this way in dry and average rainfall years, with *N. neesiana* cover reduction from >65% to c. 10% and *T. triandra* cover increase from c. 5% to >85% over 3 y with c. 17 *T. triandra* and c. 6 *N. neesiana* plants m^{-2} established in the most successful trials (Mason and Hocking 2002, Hocking 2005b). A very similar ratio of *T. triandra* to *N. neesiana* tussocks was found in these trial plots 5 years later, adding weight to the finding of Lunt and Morgan (2002) that invasion of *N. neesiana* is restricted when there is a healthy cover of *T. triandra* (Hocking 2005b).

Atrazine has also been used as the herbicide in the 'spray and hay' method (Mason 1998). Both atrazine and acetic acid vinegar were tested in a small trial by Mason (2005) but acetic acid treatments resulted in much reduced *T. triandra* seedling establishment and control of *Nassella* spp. that was less than, or approximately equivalent to that provided by atrazine, 10 months after treatment.

Dare and Hocking (1997) reported an unsuccesful trial of the method, blamed on very low rainfall during summer. Appropriate timing of the stages of the treatment is critical, and abundant, high quality seed is required (Mason and Hocking 2002). The best time to spray when using the spray and hay method was determined by Phillips and Hocking (1996), who found that late autumn to winter herbicide application resulted in a 3 month weed-free window, whereas February and September spraying resulted in rapid invasions by a suite of weeds.

'Spray and hay' methods have generally had poor effectiveness under drought conditions (Dare and Hocking 1997, Hocking 1997, Hocking pers. comm.) and are subject to the same general constraints on rehabilitation of native grasslands as other methods, notably the difficulty of harvesting and very limited supplies and low quality of native seed or thatch (McDougall 1989, Bedggood and Moerkerk 2002, Muyt 2005) and high labour inputs.

To circumvent some of these problems Muyt (2005) recommended sowing of other native perennial grasses at the same time as *T. triandra*, including *Austrodanthonia*, *Austrostipa*, *Microlaena stipoides* and *Elymus scabra*.

Biological control

No succesful biological control programs against grass species have been undertaken and programs targetting grasses are all of recent origin (Witt and McConnachie 2004). Grass species were once thought to lack specific arthropod herbivores because they very rarely produce toxic secondary metabolites as defenses, and are too simple and similar in structure, physiology and ecology for specific herbivores to have evolved (Evans 1991). However secondary metabolites that function as defensive compounds are common in many cereals and grasses, including hordenine in barley (McDonald 1991), a specific invertebrate herbivores have gradually begun to be discovered. Gross similarities and close taxonomic relationships between grass weeds and valuable crop and pasture species was also thought to provide little scope for development of biological control (Witt and McConnachie 2004). The potential for biological control of *Nassella* spp. in Australia was also initially considered to be low due to their close relationship to Australian Stipeae (Wapshere 1990 1993).

An Australian project with Argentine and New Zealand collaborators to biologically control *Nassella* spp. with fungi has been pursued since 1999: see below under "Pathogens". Anderson *et al.* (2006) presented a recent update on progress in host specificity testing and production of potential agents. One reason biological control remains difficult is because the geographical source of Australian populations has not been identified: effective predators and parasites in the area of origin cannot therefore be identifed. Another reason for slow progress is the need to demonstrate that the large number of endemic Australian Stipeae will not be affected. Biological control using insects may be worth further consideration in the future, given increasing recognition of the existence of host specificity amongst invertebrate grass herbivores and overemphasis of the role of plant chemical defenses as an evolutionary driver for monophagy (Witt and McConnachie 2004) (see discussion below under 'Predators and Pathogens').

Predators and pathogens

Evans (1991 p. 60) considered that the natural enemy complexes (invertebrates and fungal diseases) of all the world's worst grassy weeds to be "largely unknown". This paucity of information extended to grasses in general, in part as the result of failures to consistently identify grasses found to be under attack (Evans 1991 p. 53).

Wapshere (1990) found natural enemy species-specificity to be rare amongst grasses, compared with genus-specificity. He considered it likely that Australian grass genera with many species would have large groups of specific or near-specific predators and parasites. The corollary of this is that *Nassella*, with many South American species, should have a large herbivore fauna and a a wide variety of diseases.

Wapshere (1990) determined from published records the main invertebrates and fungi that attack grasses in Europe: Noctuidae (cutworms, armyworms, etc., Lepidoptera), microlepidoptera (various families), Cecidomyiidae (gall midges, Diptera), Brachycera (flies, Diptera), Aphididae (aphids, Hemiptera), Ustilagines (smuts) and Uredinales (rusts). As an indication of host specificity, he also determined the number of species in each group recorded from a single grass species, a single grass genus, 2-3 genera and 4 or more genera. Cecidomyiidae and Ustilagines showed the highest levels of species- and genus-specificity amongst these groups. High levels of specificity was also apparent with leaf-miners (insects) and particularly with gall makers (arthropods, nematodes and fungi).

Predators

Very little appears to be known about the animals that attack *N. neesiana*, a similar situation to that for *N. trichotoma*, for which Wapshere (1990 p. 71) noted an absence of "any readily available knowledge concerning the arthropods … in its home range" and (1993 p. 344) no arthropods recorded from it in Australia. Herbaceous monocots have often been viewed as having relatively impoverished invertebrate faunas compared to other groups of plants. Their simple architecture and decreased structural complexity (hence lower niche diversity) is often cited as the cause (e.g. Lawton and Schroder 1977). However, as Waterhouse (1998 p. vi) noted in relation to the paucity of grasses as targets for classical biological control, "it would be surprising if co-evolution and co-adaptation have never led to effective and highly specific natural enemies of at least some individual species in the Poaceae, as it has in members of other plant families".

Molluscs

Published information about slug and snail utilisation of grasses indicates they may often be avoided in preference for other plants, but the data is equivocal and it is clear that some species are recognised pests of cereals and grass fodder, and that grasses in general are not unpalatable (Barker 2008). Holland *et al.* (2007) found that *Milax gagates* Draparnaud (Milacidae) consumed two native grasses including *T. triandra* in laboratory tests and that the palatibility of the grasses was within the palatibility range of native dicot species tested. Newly emerged seedlings appear to be at most risk of damage by molluscs. No information appears to be available on mollusc attack on *N. neesiana*.

Insects

Evans (1991 p. 52) referred to a seeming "general absence of host specific insects associated with grassy weeds". He found from a literature survey that insects specific to grass species were unknown, and that grass-feeders were generally polyphagous, attacking a range of grasses, often including cereals. The relatively uniform structure of Poaceae supposedly "promotes polyphagy" (Evans 1991 p. 53) and reduces the evolutionary pressures for monophagy (Briese and Evans 1998).

Evans' (1991) generalisation was largely, but not entirely correct, as presaged by Waterhouse (1998) and demonstrated by the studies of Wapshere (1990), Witt and McConnachie (2004) and others. Wapshere (1990) found host-specificity at species or genus level for grasses in Europe to be particularly common in Elachistidae (Lepidoptera), Chloropidae and Cecidomyiidae (Diptera), and *Tetramesa* (Hymenoptera: Eurytomidae). He noted that all *Tetramesa* spp. in the USA are relatively monophagous, being recorded only from single grass genera. In Australia the genus is represented by three species that are phytophagous in grass seeds or internodes, according to Naumann (1991), although Boucek (1988) stated that no Australian host records were known. *Tetramesa* spp. "develop as phytophages feeding on the inner tissues of the internodes or of the seeds and places attacked, specific for each species, swell some to some degree, sometimes considerably, so that a characteristic gall is formed" (Boucek 1988 p. 95). De Santis and Loiácono de Silva (1981 1983) found that the stem-boring *Tetramesa adrianae* De Santis was the main natural enemy of the stipoid *Amelichloa brachychaeta* in the provinces of Buenos Aires, La Pampa and Entre Rios, Argentina, and discussed programs to breed and disperse it more widely as part of an integrated control program. This species causes gall-like stem deformations that affect seed production (De Santis and Loiácono de Silva 1983). Possibly this wasp also affects *N. neesiana*: Gardener *et al.* (1996b) reported that botanical specimens in the Instituto Darwinion Herbarium had galls of undetermined origin on the flowering stems which appeared to prevent flowering. The Palaearctic species *T. cylindrica* (Schlechtendal) and *T. punctata* Zerova attack the flowers of *Stipa capillata* L. and *S. lessingiana* Trin. and Rupr. (De Santis and Loiácono de Silva 1983). *A. brachychaeta* is also attacked by a cecidomyiid, *Contarinia* sp. (De Santis and Loiácono de Silva 1983).

Some *Eurytoma* spp. "can complete their development feeding solely on the plant tissues in stems of grasses, but because their eggs are laid only in places where a genuine phytophagous eurytomid of the genus *Tetramesa* is developing (and causing growth of plant tissues), they normally devour the larva of *Tetramesa* before reaching maturity" (Boucek 1988 p. 107). Australian *Eurytoma* are poorly known and no grass hosts were mentioned by Boucek (1988). The Australian eurytomid genus *Giraultoma* Boucek is also associated with grasses, while the biology of some other Australian genera is unknown (Boucek 1988, Systematic Entomology Laboratory USDA 2001).

Because Australia has a wide diversity of *Austrostipa* species, closely related to *Achnatherum*, Australian species from these insect taxa may be the most likely candidates amongst the host-specific or narrowly-oligophagous species to 'host shift' on to *N. neesiana* in Australia. Exchange of insect species ("acquisition of a herbivore guild on an evolutionary timescale") between closely related plants is hypothetically more likely because of closer biochemical and structural similarities between related species (Lawton and Schroder 1977 p. 138). Lawton and Schroder (1977) found evidencefor this relationship for monocot species (not including grasses) but not other plant groups they analysed in Britain.

No published records have been located of invertebrates feeding on *N. neesiana* in Australia although a few species are known to feed on *Nassella trichotoma*. A most interesting recent development is the finding by Braby and Dunford (2006) of empty pupal cases of the endangered Golden Sun Moth *Synemon plana* Walker (Lepidoptera: Castniidae) protruding from *N. neesiana* tussocks, from which it was inferred to be a probable larval food plant (see further discussion below).

Zimmerman (1993) recorded *N. trichotoma* and "some other grasses" as hostplants of the ground weevil *Cubicorhynchus sordidus* Ferguson (Coleoptera: Curculionidae: Amycterinae: Amycterini), evidently an identification of Howden's (1986) "*Cubicorrhynchus* sp." observed near Yass, NSW (see also May 1994), and noted that B.P. Moore had found both larvae and adults of the NSW species *Phalidura abnormis* (Macleay) (Amycterini) feeding on *N. trichotoma*, the native host plants being unknown. Larvae of *P. elongata* (Macleay) feed on underground parts of *N. trichotoma*, and other grasses (Zimmerman 1993), while adults consume *N. trichotoma* and pupae are also found in association with it (Howden 1986). Howden's (1986) listing of *Phalidura assimilis* Ferguson feeding on *N. trichotoma* near Yass are treated by Zimmerman as *P. abnormis* and May (1994) listed *P. abnormis* as the only known *Phalidura N. trichotoma* feeder. Adults and a larva of *Cubicorhynchus calcaratus* Macleay of eastern and southern Australia have been found in a clump of "*Stipa*" in South Australia, while *Austrostipa nitida* and *A. nodosa* along with other grasses are hosts of another eastern and southern species *C. taurus* Blackburn, with larvae found in the crowns and root masses (Howden 1986, Zimmerman 1993, May 1994). Other species in the genus also have grass hosts including *Microlaena stipoides* and "*Stipa*" for the Western Australian *C. bohemani* (Boheman) (Zimmerman 1993) and unidentifed grass for *C. crenicollis* (Waterhouse) (May 1994). Howden (1986 p. 100) noted that all *Cubicorhynchus* species "collected to date have been associated with either native or introduced species of Poaceae". Larvae "collected from the crowns of grass plants often regurgitated green material, indicating that they fed on underground stems and not the roots" (Howden 1986 p. 100). *Sclerorinus* spp. (Amycterini) have been recorded from undetermined "*Stipa* sp." (May 1994 p. 495). Amycterini are flightless ground-dwellers and most are confined to grasses, or other monocots, most larvae living underground in the root crowns and the adults eating leaves, evidently including, unusually, dry grass (Zimmerman 1993). Larvae are free living in the soil and eggs are deposited directly into the substrate, rather than a prepared site (Howden 1986, May 1994). Adults of the species that feed on wiry stems have stout, blunt mandibles and gular roll ('lip'), while species that feed on soft tissues have a different mouthpart morphology (Howden 1986). *Themeda triandra* and *Austrodanthonia* are not known hosts (not mentioned in Zimmerman 1993 or May 1994). Zimmerman (1993) considered the tribe to be Gondwanaland relics with no known closely related group in South America. "Over vast areas of the country the Amycterinae have been nearly exterminated by the clearing of vegetation, cultivation and the grazing of livestock, especially by the destructive activities of millions of sheep" (Zimmerman 1993 p. 176).

Gardener *et al.* (1996a) suggested that *N. neesiana* seed predation by ants appeared to be lacking, possibly due to the impenetrability of the lemma providing good protection to the edible caryopsis. However Gardener (1998) set up experiments in pasture in which de-awned seeds were placed on the soil surface or buried in soil at 1.5 cm depth and exposed for six weeks from late January to early March, or offerred, along with de-awned *Themeda triandra* seed, in dishes arranged to prevent access by larger animals for 4 weeks in May. In the first experiment 99.5% of buried *N. neesiana* seeds were recovered but significantly fewer (71%) of the unburied seeds. In the second experiment 97.5% of the seeds of both species were recovered ("no seeds ... taken" Gardener 1998 p. 53). The experimental results were considered inconclusive: seeds in the first experiment may have been removed by other organisms, ants may have been inactive in the second experiment or not interested in the seeds. No identification was suggested for any ant species that may have been responsible.

Absence of ant predation appears to be unlikely. On a world basis, Formicidae are amongst the most important granivores in desert ecosystems (Saba and Toyos 2003). Ants are the dominant seed predators in the Sonoita Plains grassland of Arizona, where they selectively remove seeds with awns, projections or significant pubescence (Pulliam and Brand 1975). The other main seed predators, sparrows and rodents, consume smaller amounts, selectively favour 'smooth' seeds, and have different seasonal foraging patterns, so have little dietary overlap with the ants. In the Monte Desert of northern Patagonia, Argentina, where the vegetation is a steppe dominated by *Larrea divaricata* Cav. and stipoid grasses, ants are the most important granivores in spring and summer, but remove little seed in other seasons (Saba and Toyos 2003). Ants are the dominant granivores in arid areas of Australia (Morton 1985), although the dominant grasses in these areas rarely include stipoids. The Australian fauna of seed-harvesting ants is rich and the species are capable of causing severe seed losses: up to 90% of weed seeds in crops can be removed (Vitou *et al.* 2004). Ants are the dominant weed seed predators in agricultural landscapes in Western Australia and have preferences for particular weed species (Minkey and Spafford Jacob 2004). The few studies of ants in south-eastern Australian native grasslands show that seed-harvesters are generally present (Coulson 1990 appendix 3, Miller and New 1997), one of them, *Pheidole* sp., being amongst the most abundant ants in Victorian Basalt Plains grasslands (Yen *et al.* 1994a). The seeds of *N. neesiana* are very similar to those of some *Austrostipa* spp., so it appears highly likely that they would be harvested by ants as a matter of course. Ant seed herbivory has been found to be higher for African grasses in Brazil compared to native savannah species (Klink 1996), so in Australia *N. neesiana* seeds may even by preferred.

Apart from ants, Gryllidae and granivorous carabid ground beetles are the most important post-dispersal seed predators in temperate agro-ecosystems (Lundgren and Rosentrater 2007) and no doubt the seeds of *N. neesiana* must be destroyed by speices in these groups, although only one example seems to be on record. Slay (2001 p. 33) recorded that "field crickets" consumed shed *N. neesiana* seeds in a New Zealand pasture. The seeds were "hollowed out" and the insect "might well be implicated in reducing the numbers of recently shed seeds". This is almost certainly the Black Field Cricket, *Teleogryllus commodus* (Walker) (Gryllidae), a recognised pasture pest in New Zealand (Heath 1968) and Australia, and a common native insect in south-eastern Australian grasslands.

A wide range of non-specific grass feeders including Orthoptera, Thysanoptera (thrips), Hemiptera (true bugs) and Noctuidae (Lepidoptera) are likely to be found to utilise *N. neeiana* in Australia (see the Appendix to this Literature Review).

Vertebrates

Many stipoid grasses are readily eaten by livestock, including *N. neesiana*. In the Great Basin region of the USA *Stipa* spp. *sens. lat*. are considered "for the most part valuable forage plants" (Hitchcock and Chase 1971 p. 445). *N. neesiana* is readily eaten by sheep, cattle and horses in Argentine pastures in winter and spring, but consumption is much reduced when the plant is flowering and seeding, except under drought conditions or when stocking rates are high (Gardener *et al.* 1996b, Gardener 1998). It has been rated as one of the most valuable winter pasture species in the pampas (Gardener *et al.* 1996b).

Grasses defend themselves against grazing mammals in a variety of ways, including adaptations of form, habit and phenology, presence of indigestible structural compounds and presence of toxic chemicals. Very few grass species contain toxic secondary metabolites that deter grazing and herbivory: less than 0.2% contain alkaloids, and the presence of noxious terpenoids and cyanogenetic compounds is rare (Tscharntke and Greiler 1995, Witt and McConnachie 2004), although McDonald (1991) claimed that defensive metabolites are common in cereal and other grasses. Records of toxic effects of stipoids on livestock are scarce. According to Quattrocchi (2006 p. 1361) "Some" *Nassella* species "have caused poisoning to mammals". Randall (2002) stated that *N. neesiana* has been recorded as toxic, and the US Food and Drug Admimistration Poisonous Plants Database (USFDA 2006) lists *N. neesiana*, citing Kellerman *et al.* (1988).

Probably most cases of toxicity attributed to grasses are the result of grass fungi. Possibly the best known example is ergot, *Claviceps purpurea*, which infects cultivated *Secale cereale* L., other cereals, and other grasses, the toxic effects of which have resulted in mass human poisonings (Gair *et al.* 1983, Wink and Van Wyk 2008). However none of the many *Claviceps* species affect Stipeae (Wink and Van Wyk 2008). The Mexican and southwestern USA *Achnatherum robustum* (Vasey) Barkworth (= *Stipa vaseyi* Scribn. = *Stipa robusta* (Vasey) Scribn.), known as Sleepy Grass, allegedly acts as a "narcotic", especially on horses (Hitchcock and Chase 1971) due to infection with endophytic *Acremonium* fungi. The active principles were identified by Petroski *et al.* (1992), the dominant one, lysergic acid amide, likely being responsible for a reportedly extreme "sedative" effect on animals. However lysergic acid and its derivatives are generally considered to be hallucingens, producing delerium but not sedation (Wink and Van Wyk 2008). *Achnatherum inebrians* (Hance) Keng of China and Mongolia, known as Drunken Horse Grass, probably affects animals by ergot alkaloids produced by the endophytic *Neotyphodium gansuense* Li and Nan (Clavicipitaceae) (Moon *et al.* 2007). The ergot alkaloids consist of two main series, clavine alkaloids and the lysergic acid amides (Wink and Van Wyk 2008). Such fungal endophytes occur widely in grasses (see section on "Other biotic relationships" below) and produce a variety of poisonous secondary metabolites that effectively deter pathogen attack and grazing, and sometimes poison mammals (Tscharntke and Greiler 1995, Jallow *et al.* 2008), and are thus generally considered to be symbionts, rather than pathogens (Wink and Van Wyk 2008).

Grass poisoning can also be caused by organic acids, which irritate skin and mucous membranes (Wink and Van Wyk 2008). *Stipa capensis* contains glycosides producing a strong acid that can harm cattle (Tsvelev 1984).

Specialist granivorous birds, of which the most important are finches, parrots and pigeons, probably commonly consume stipoid seeds, however there appear to be few relevant records. Twigg et al. (2009) found from anyalysis of stomach contents that seeds in the diets of Australian finches (two *Emblema* spp.) and Alcedinidae (three dove and pigeon spp.) were predominantly <6 mm long, so seeds of *N. neesiana* may be less favoured than those of smaller seeded grasses.

Birds are the dominant granivores in the Monte desert of northern Patagonia, Argentina (Saba and Toyos 2003), but information on their role in areas occupied by *N. neesiana* in South America is not readily available. *Nassella* spp. are not recorded in the diet of birds in Australia (Barker and Vestjens 1990) except for the Red-rumped Parrot, *Psephotus haematonotus*, which has been recorded consuming *N. trichotoma* (Conole 1994). Small groups of this bird were observed feeding on seed on roads in the northern Brisbane Ranges, Victoria, where large quantitities of seed-bearing panicles had accumulated in wind drifts (Conole 1994). Several bird species are known to consume the seed and other parts of unidentified *Austrostipa* spp. (Barker and Vestjens 1989 1990), and *Austrostipa tenuifolia* (Steud.) S.W.L. Jacobs and J. Everett seed has been recorded in the diet of the Red-rumped Finch (Read 1994). Finches also attack cereals in Australia (Irrigation Research and Extension Committee 1975) and may perhaps also occasionally feed on *Nassella* seeds.

The seeds of exotic grasses are likely to be presented in a similar manner to those of native species, so birds that are adapted for consuming seeds of native are preadapted for consuming similar exotics (Loyn and French 1991 p. 137), Since seeds of *Austrostipa* species are eaten, consumption of *N. neesiana* seeds by birds in Australian possibly occurs widely. Many Australian parrots are important grass seed eaters and several species are recognised as pests of cereals. Cockatoos *Cacatua* spp. and galahs *Cacatua roseicapilla* damage green grain of cereals, cockatoos cut off heads of summer crops, galahs damage young shoots, parrots "pick up any available grain", eating large quantitities, with the smaller species, particularly budgerigars and cockatiels *Nymphicus hollandicus*, attacking seed in the soft dough stage (Cole 1975 p. 136).

However granivorous birds tend to avoid awned seeds (Mares and Rosenzweig 1978). Campbell (1975 p.134) advocated the use of less susceptible "bearded rather than poorly awned wheats or 'birdproof" [high tannin] grain sorghum" to reduce crop damage by Galahs and Cockatiels in Australia. The seeds of barley and awned wheats are relatively protected against bird predations (Dale 1975). Long, robust awns probably deter a wide range of potential vertebrate seed-predators. A sharp callus, as found in most *Austrostipa* species and *N. neesiana*, probably provides an additional strong predation defence.

As well as consuming seeds, birds may eat the vegetative parts of grasses. *Austrostipa pubescens* (R.Br.) S.W.L. Jacobs and J.Everett foliage has been recorded in the diet of Tasmanian Native Hen *Gallinula mortierii* (du Bus de Gisignies) (Barker and Vestjens 1989) and ducks attack cereal grasses in Australia (Irrigation Research and Extension Committee 1975). These and other water birds may consume suitably soft foliage of *Nassella* species.

Granivorous rodents are also important predators of grass seeds. They are significant granivores in the Argentine Monte Desert (Saba and Toyos 2003, contra Mares and Rosenzweig 1978) but not in the arid zone of Australia (Morton 1985). Mares and Rosenzweig (1978) found that birds were relatively unimportant granivores in the Monte and the Arizona (USA) desert and argued that extinction of the specifically adapted marsupial granivores of the Argyrolagidae of South America in the late Pliocene (1-2 mybp) left a niche for granivorous mammals that has not subsequently been filled, but has been compensated for by increased importance of ant granivory. Specific information on mammal granivory in areas where *N. neesiana* is native appears to be lacking and no information is availabe about rodent granivory in Australian native grasslands.

Pathogens

A wide range of pathogenic fungi attack grasses. These are often highly host-specific, notably head smuts and rusts, with specificity often being confined to particular host biotypes (Witt and McConnachie 2004). Wapshere (1990) mentions, in addition, the genera *Phyllochora* (Ascomycetes), *Cercospora* (Hyphomycetes) and *Stagonospora* (Coelomycetes) as having, on a world basis, a high proportion of their species known from only a single grass genus.

N. neesiana has a rich pathogenic fungal flora in South America (Briese *et al.* 2000, Anderson *et al.* 2004), including the following taxa:

Powdery mildew (Anderson 2002b)
Septoria leaf spot (Anderson 2002b)
Teliomycetes (Rusts)
Puccinia digna Arth. and Holw. (Greene and Cummins 1958)
Puccinia graminella Diet. and Holw.- damaging infestations in central Argentina (Briese *et al.* 2000)
Puccinia nassellae Arth. and Holw. var. *platensis* Lindquist (Briese and Evans 1998, Briese *et al.* 2000, Anderson *et al.* 2004 2008)
Puccinia saltensis var. *saltensis* (Briese *et al.* 2000)
Puccinia aff. *avocensis* (Anderson *et al.* 2002)
Uromyces pencanus Arth. and Holw. (Greene and Cummins 1958, Anderson 2002a, Anderson *et al.* 2006 2008)
Uredo sp. (Briese *et al.* 2000)
Ustomycetes (Smuts)

Tranzscheliella hypodytes (Schltdl.) Vánky & McKenzie (= *Ustilago hypodytes* (Schlecht.) Fr., *sensu lato* (Briese *et al.* 2000, Anderson 2002a, Anderson *et al.* 2004), listed as *Ustilago* sp. by Anderson *et al.* (2002).

However some populations in Argentina are free of pathogens including Entre Rios Province where in one survey “many huge and dense populations ... were completely devoid of disease” (Anderson 2002b). Knowledge of these pathogens has been greatly enhanced by studies undertaken for an Australian biological control program for *Nassella* spp., initiated in 1999 (Anderson et al. 2008).

Puccinia graminella is known from western and southern South America and California, and also attacks *N. hyalina* (Greene and Cummins 1958). It was found to be damaging *N. neesiana* populations in central Argentina by Briese *et al.* (2000). During one survey *P. graminella* was found at 12 of 14 sites and was killing *N. neesiana* leaves at 4 sites (Anderson *et al.* 2002). It was initially thought to cause little damage to *N. neesiana* (Anderson 2002b) but can cause mortality under wet conditions (Anderson *et al.* 2004) and severe damage in the field (Anderson *et al.* 2008). It appears to have restricted host-specificity, is autoecious and completes its lifecyle on *N. neesiana*, with both uredina and telia having been recorded on the plant (Anderson *et al.* 2004 2006). However *N. neesiana* appears to have qualitative resistance to infection and a pure culture has not been established (Anderson *et al.* 2008).

Puccinia nassellae is known from Argentina, Bolivia and Chile (Greene and Cummins 1958). Two strains have been investigated as potential biological control agents, specific to *N. neesiana* and *N. trichotoma*. The strain on *N. neesiana* commonly forms telia and produces pustules that are plain to see on open leaf lamina. It is virulent (Anderson *et al.* 2008), easy to rear, probably host-specific, hemicyclic (urediniospores and teliospores on *N. neesiana*, but possible other stages unknown), but probably not autoecious (Anderson 2002a) with *Clematis montevidensis*, *Solidago chilensis*, *Cestrum parqui*, *Verbesina* sp. and *Morrenia* sp. found with aecial rust infections, although none appear to be solid candidates as alternate hosts (Anderson 2002b). It has not infected *Austrostipa* spp. and *Stipa* spp. that have been tested, but of the strains collected in the wild, only one has been able to infect 3 of 6 Australian *N. neesiana* accessions, so there is high specificity at the subspecific level (Anderson 2002a, Anderson *et al.* 2002 2006). Trap plants of *N. neesiana* obtained in the Australian Capital Territory became infected with strain NT27 in Argentina (Anderson 2002a).

Puccinia digna is known from Bolivia and Chile (Greene and Cummins 1958) and has not been studied for biological control purposes.

Uromyces pencanus is known from Argentina and Chile (Greene and Cummins 1958), appears to be host-specific and can be very damaging to *N. neesiana* in Argentina, but its lifecyle on the plant is incompletely understood (Anderson *et al.* 2006 2008). It is easy to rear and has infected 5 of 6 Australian accessions of *N. neesiana*. Isolate Up27, virulent against most Australian accessions of *N. neesiana*, has been found not to infect *N. hyalina*, *Austrostipa aristiglumis* (F. Muell.) S.W.L. Jacobs & J. Everett and a range of economically important agricultural grasses (Anderson *et al.* 2008).

Mixed species rust infections are not uncommon in Argentina and appear to be particularly damaging to the plant (Anderson *et al.* 2006).

The smut *Tranzscheliella hypodytes* is a cosmopolitan species (Vánky and Shivas 2008) and infects a number *of Austrostipa* species (Briese and Evans 1998) in south-eastern Australia and *Dichelachne crinita* (L.f.) Hook. in NSW and Victoria, but does not appear to have been recorded on Australian *N. neesiana* (Vánky and Shivas 2008). It infests upper culm internodes of *N. neesiana* in Argentina, preventing most seed production when plants are severely attacked, and infection occurs at germination (Anderson *et al.* 2002). It is not known if strains found on *N. neesiana* can infect *N. trichotoma* and vice versa (Anderson 2002a). Conditions for infection appear to be uncommon in nature (Anderson *et al.* 2004) and the species has been found only at very low incidence in Argentina (Anderson 2002b).

Knowledge of the fungal flora of *N. neesiana* in its introduced ranges is limited. Slay (2002a) summarised results of a Landcare Research survey of *N. neesiana* fungi at five sites in New Zealand. Fourteen species were identified, of which six were potentially pathogenic: *Alternaria* sp., *Colletotrichum* sp., *Drechlera* spp., *Phoma leveilli* Boerma and Bollen and *Phoma* sp. Britt (2001) conducted a fungal pathogen survey at eight sites in Victoria and found four possible species of *Alternaria*, and one each of *Aspergillus*, *Fusarium* and *Epicoccum* on leaves, none of which was precisely identified. Leaf discoloration, spotting and necrosis was common in the field. Cultures on agar plates were distinguished by colour and form (downy/woolly/cottony/powdery). Testing showed that the fungi aided seed germination of *N. neesiana* but only *Epicoccum* sp. had a statistically significant effect, probably due to the small sample sizes. No seeds germinated in the absence of fungi. The effect could be due to fungal production of plant hormones, such as gibberellin, that break dormancy or stimulate germination, or to fungal digestion of the lemma. Growth substrates other than *N. neesiana* seed may be preferred by the fungi,so the effect may not occur under field conditions.

As of 1998, none of the 27 species of fungi recorded from *Austrostipa* in Australia were recorded on *Nassella* spp. in Australia, nor do South American and Australian Stipeae have any rusts in common (Briese and Evans 1998).

Greene and Cummins (1958) recorded a single rust species on *Austrostipa*, *Puccinia flavescens* McAlp., with two known hosts, *A. flavescens* (Labill.) S.W.L. Jacobs and J. Everett, *A. semibarbata* (R.Br.) S.W.L. Jacobs and J. Everett. Vánky and Shivas (2008) recorded three smuts from *Austrostipa* in south-eastern Australia in addition to *T. hypodytes*: *Fulvisporium restifaciens* (D.E. Shaw) Vànky, *Tranzscheliella minima* (Arthur) Vànky and *Urocystis stipeae* McAlpine. The latter also occurs on *Achnatherum* spp. in south and east Asia (Vánky and Shivas 2008).

Other biotic relationships

Fungal and bacterial symbionts of *Nassella* spp. appear to be poorly known, apart from the observations of Britt (2001) (see “Pathogens” section, above). Higher plants in general have fungal endophytes that live within their tissues without causing damage, and plant roots are always inhabited by mutualistic fungi, usually classed as arbuscular mycorrhizal fungi, ectomycorrhizae or dark septate fungi (Khidir *et al.* 2009). Presence of these organisms can greatly affect the invasiveness of a plant and influence its ability to modify soil properties (Rout and Chrzanowski 2009).

Grasses harbour large and diverse communities of root-associated fungi, including arbuscular mycorrhizal fungi (AMF), the colonisation of which appears to be strongly effected by climatic conditions and nutrient availability, and dark septate fungi, which are the main colonisers of grasses in semiarid environments (Khidir *et al.* 2009). No mycorrhizal relationships have been recorded for *N. neesiana* but vesicular arbuscular mycorrhiza have been reported for *N. leucotricha* and other stipoid grasses (Clark and Fisher 1986, Wang and Qiu 2006) and a dark septate fungus of the genus *Paraphaeospheria* sp. has been recorded from *Achnatherum hymenoides* (Roemer & J.A. Schultes.) Barkworth (Khidir *et al.* 2009). 80% of surveyed land plant species are mycorrhizal (Wang and Qiu 1996) so the possibility that *N. neesiana* lacks these root fungi seems remote.

Root associated fungi appear to be generalist species that inhabit a range of species in a community and across large areas (Khidir *et al.* 2009). Khidir et al. (2009) found that co-occuring grasses had a common flora of non-AMF groups from the Pleosporales, Agaricales and Sordariales, with *Paraphaeospheria* spp. (Pleosporales), *Moniliophthora* spp. (Agaricales) and *Fusarium* spp. (Hypocreales) most common, but AMF fungi (*Glomus* sp.) were also present. The dark septate fungi may enable the plant host to access nutrients, including N and P, and may play a role in drought and heat tolerance (Khidir *et al.* 2009).

N fixation by free-living bacteria associated with grass roots has been recorded (Clark and Fisher 1986) and several African grasses are known to fix significant levels of N in their native habitats (Rossiter *et al.* 2003). Rout and Chrzanowski (2009) found that *Sorghum halepense* harboured a range of bacteria in its rhizomes known to fix N, and almost certainly able also to chelate iron and mobilise phosphorus.

Species of *Neotyphodium* Glenn and their teleomorphic relatives *Epichloë* Tul. (Balansieae, Clavicipitaceae) are endosymbiotic non-pathogenic fungi found in an estimated 20-30% of graminoid species, mainly in grasses of the subfamily Pooidae (Moon *et al.* 2007, Rudgers *et al.* 2009). They are closely related to the ergot fungi, *Claviceps* spp., and are commonly called ‘grass endophytes’ (Aldous *et al.* 1999). Each sexual species of *Epichloë* is associated with a particular grass tribe in North America or Europe, but the many asexual species, transmitted via seeds, are hybrids resulting from crosses between *Epichloë* species or between *Epichloë* and *Neotyphodium* species, that bear no such direct relationship with their range of hosts and may have ‘jumped’ between tribes (Moon *et al.* 2007). Endophytes transmitted vertically (inherited) are more likely to evolve to be symbiotic than those that spread vertically by contagious spread, which are more likely to retain pathogenicity (Rudgers *et al.* 2009). Some grass endophyte species, including some affecting *Achnatherum* species, cause poisoning in livestock, and many produce chemicals that deter attack by insects (Moon *et al.* 2007). Tests with the mollusc *Deroceras reticulatum* Muller indicate that the different secondary metabolites produced by *Neotyphidium* can deter or enhance feeding (Barker 2008). Other documented benefits from endophyte infection include drought tolerance, increased vigour and higher nutrient content.

Within Stipeae, species of *Neotyphodium*/*Epichloë* are known to infect only *Achnatherum* species (Moon *et al.* 2007, Rudgers *et al.* 2009) except for an unknown species infecting *Nassella viridula*. Those currently known are *Neotyphodium chisosum* (White and Morgan-Jones) Glenn *et al.* and probable *Epichloë amarillans* from *A. sibiricum* (L.) Keng (Wei *et al.* 2007, Ren *et al.* 2008, Moon *et al.* 2007), *N. chisosum* from *A. eminens* (Cav.) Barkworth, *N. gansuense* Li and Nan and its morphologically and geographically distinct variety *inebrians* C.D. Moon and C.L. Schardl from *A. inebrians* (Hance) Keng, *N. funkii* K.D. Craven and C.L. Schardl from *A. robustum* and an undescribed species from *A. sibiricum* (Moon *et al.* 2007). Undetermined species are also known from *A. lobatum* (Swallen) Barkworth, *A. purpurascens* (Hitchcock) Keng, *A. splendens* (Trinius) Nevski and *A. viridula* (Rudgers *et al.* 2009). The last has been classified as *Nassella viridula* by Barkworth (2006) who suggested it may be an alloploid between *Nassella* and *Achnatherum*.

No evidence appears to be available on the presence or absence of endophytes in *N. neesiana*. But given their importance to plant fitness, endophyte presence should be investigated. In the USA endophyte infection of the non-native *Festuca arundinacea* Schreb. increases its invasiveness and impact on biodiversity (Rudgers et al. 2009).

BIODIVERSITY

“Biodiversity ... one of the best descriptors of ecosystem condition”
(Aguiar 2005 p. 262)

This section explores the concept of biodiversity and aspects of its assessment, discusses the range of impacts that invasive plants, and grasses in particular can have on biodiversity, and evaluates existing knowledge of the impact of *N. neesiana* on biodiversity in temperate Australian grasslands.

Definitions

The United Nations Convention on Biodiversity concluded at Rio de Janeiro on 5 June 1992 defines biological diversity as “the variability among living organisms from all sources including, *inter alia*, ... ecosystems and the ecological complexes of which they are a part: this includes diversity within species, between species and of ecosystems.” Biodiversity has elsewhere been defined as “the number, variety and variability of living organisms at genetic, population, species, community and ecosystem levels” (Giles 1994). It is present at every heirarchical level within the purview of biology (Mayr 1982): molecular, genetic, chromosome, organelle, cellular, tissue, organ, organism, taxon, association, etc. At each level, diversity varies spatially and temporally, in historical origin, functional role and evolutionary significance (Mayr 1982). In broader terms, biodiversity encompasses not just the biological taxa, but the processes and functions in which the organisms participate (Saunders 2000). It therefore includes the range of interactions organisms have with one another and the physical environment, and the associations they form, including mutualisms, competitive relationships, guilds, functional groups, successional dynamics and patterns, trophic relationships and foodwebs (Woods 1997, Saunders 2000). Indeed, “there is hardly any biological process or phenomenon where diversity is not involved” (Mayr 1982 p. 133), so understanding the impact of an invasive species on biodiversity requires understanding this broader context. Since all individuals differ in their history and precise chemical makeup, and in sexually reproducing populations in many other ways, every individual of every population is a unique part of biodiversity (Mayr 1982).

Biodiversity enables ecosystem services, provides direct economic benefits and creates the distinctive milieu in which human cultures flourish (Saunders 2000, Mansergh *et al.* 2006b). The concept of ecosystems services provides a framework for the economic quantification of chemical and biological reserves and cycles in areas including soil stabilisation and fertility, water quality and quantity, biological production, etc. (Mansergh *et al.* 2006b). Biodiversity can also create ecosystem “dis-services”, including, in general, exotic invasive species (Mansergh *et al.* 2006b p. 300). However many processes alter ecosystem functioning, not just alterations to biodiversity, and its contribution to ecosystem services has not been adequately resolved (Aguiar 2005). Less diverse anthropogenic systems may in some circumstances provide similar levels of service to those provided by diverse natural ecosystems.

Contracting parties to the Convention on Biodiversity, which include Australia, are required to identify components of biodiversity important for conservation and sustainable use, monitor them through sampling and other techniques, identify processes and categories of activities that have or are likely to have significant adverse impacts on the conservation and sustainable use of biological diversity and monitor their effects. Parties are also required to prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species (United Nations 1992).

Quantification and indices

Full quantification of biodiversity requires enumeration of diversity at each heirarchical level, both in terms of taxonomy (classes to subspecies) and levels of biological organisation (molecular to ecosystem). Understanding of the processes and mechanisms that alter or maintain biodiversity requires study and measurement of the interactions on and between each level (Giles 1994).

Numerous authors caution against the over-reliance on species richness as an index of biodiversity (e.g. Aguiar 2005), but biodiversity assessment must start somewhere, so there has been long historical emphasis on species, and their intrinsic worth, novelty, or ‘uniqueness’. The dependence of eccological processes on biodiversity is a more recent concern, that has come to be included under the moniker of “sustainability”. Fuller capturing of these multidimensional attributes of biodiversity requires a series of indicators (Aguiar 2005). Biodiversity attributes for which such indicators exist or can be measured include composition (the identity and variety of the component elements at each heirarchial level from gene to landscape), structure (physical, chemical, biological and geographical organisation of these elements) and function (ecological and evolutionary processes that organise the systems) (Aguiar 2005). Consideration of the biodiversity attributes within such a framework enables a much fuller appreciation and understanding of system functioning.

As a general rule, the number of species present increases as the total area under consideration is increased (Londsdale 1999). Assessment of biodiversity must therefore standardise for spatial scale. Exotic fraction, the ratio of exotic species to native species, has been widely used as an indicator of invasibility, but does not control for scale (Lonsdale 1999).

The most basic measure of diversity is species richness, a simple count of the number of species present. Species richness indices can be compiled from species richness data. All more complex diversity measures rely on determining the number of individuals of each species. When population numbers are known the heterogeneity of the community can be determined, and a community with only two species that are equally abundant is supposedly more heterogeneous than when one species is more abundant than the other (Krebs 1985).

Species abundance models often indicate that there are few common species and many rare ones, i.e. the relationship between the abundance of individuals of the species in a sample and the number of species in a sample is logarithmically related. This relationship results in the alpha diversity index, which gives an indication of diversity that is independent of sample size:

$S = \alpha \log_e(1+N/\alpha)$

where S = the number of species in the sample and N = the number of individuals.

However the logarithmic model is applicable only to a limited set of communities with few species. A larger number of communities are better represented by a log normal distribution, which is the generally expected statistical distribution (Krebs 1985). Determining the total number of species present in a community takes a large amount of sampling effort. But if such a distribution is assumed, it is possible to predict the total number of species present without having to sample intensively to detect the rare species.

The Shannon-Wiener index is based on information theory and incorporates the concept of evenness in the population size of the species. The more even the numbers of the species the higher the diversity. Other indices include Simpson's index and Margalef's index (Krebs 1985).

The usefulness of various indices is debatable (Adair and Groves 1998). They often rely on assumptions that remain untested and provide few benefits in terms of enabling ready interpretation of comparitive data. In practice the basic information on the number of species in a sample and abundance of each summarises most of the diversity information (Krebs 1985). Indices assume fixed relationships between numbers of individuals and numbers of species, but the number of insect individuals is so temporally and spatially variable that the indices may only become meaningful after prohibitively extended sampling efforts (Farrow 1999). The same arguments apply to plant sampling, where the number of individuals may be prohibitively large when the species is of small size, or the determination of what constitutes a single individual may often be difficult. Farrow (1999) therefore argued that simply enumerating the species present by extending sampling over a longer period was a superior approach for grassland invertebrate biodiversity assessment because of the major effort involved in counting what may often be superabundant organisms, and that simple presence/absence assessments are appropriate in some circumstances.

Diversity indices also tend to perpetuate the emphasis on species richness, which they all require for their computation, and divert attention from the structural and functional attributes of biodiversity that may be more important and valuable, and from the compositional attributes at other heirarchical levels – genetic, association, community, etc.

Diversity studies also require that important and unimportant species be identified, that exotic species are distinguished from natives (Greenslade 1994), pest from beneficials, etc., i.e. the identification and appropriate weighting of desirable and undesirable elements (Driscoll 1994). Proper contextualisation also requires precise identification of all taxa.

Assessments of overall biodiversity of a diverse ecosystem or community is always difficult, and beset with temporal and spatial scaling problems. Simple species richness assessments based on very few higher taxa (e.g. mammals or vascular plants) are of little value because no high level taxon appears to adequately indicate biodiversity in any other high level taxon (Melbourne 1993). Furthermore, the biodiveristy significance of a particular area can only be adequately assessed in the context of other similar areas and overall regional biodiversity (Melbourne 1993).

Impacts of weeds on biodiversity

General considerations

An impact is "a disruption to a particular set of ecosystem services or functions" (Mathison 2004), or more simply, any change in the diversity or abundance of one organism that is caused by another. Impacts of invasive species may be predicted by introvert and extrovert measures (Williamson 2001). Introvert assessments are made from study of the invasive organism, its range, abundance and ecology, to predict likely effects. Gardener and Sindel (1998) predicted impact on Button Wrinklewort *Rutidosis leptorrynchoides* F. Muell. and Kirkpatrick ***et al.*** (1995) on Sunshine Diuris *Diuris fragrantissima* D.L. Jones and M.A. Clements using this approach (Ens 2002a). Extrovert measures involve direct quantification of impact on affected organisms, processes or communities.

In the trivial sense, any invasive species initially increases the biodiversity of the area it invades. Many invasive plants "integrate smoothly" (Woods 1997) into the invaded ecosystem and are recognised as having minimal impact (Kirkpatrick ***et al.*** 1995, Woods 1997, Grice 2006). Most Australian temperate grasslands have large inventories of alien vascular plant species and all areas have at least some exotics (Kirkpatrick ***et al.*** 1995). Invasion by multiple weed species, together or sucessively, is usual, particularly in southern Australia (Adair 1995). A relatively small number of native plant species have largely disappeared, but on the broad scale the overall vascular plant species diversity is much higher than before European occupation. 'Xenodiversity' is the richness of a community in exotic species and of new communities dominated by, or assembled from alien species (Cox 2004). Xenodiversity of plants in general increases total species biodiversity, and on a world basis, the rate of new aliens entering communities much exceeds the rate of extinction of native species. A central problem is that similar sets of alien species are entering all the world's biogeographical regions, so the world flora is being homogenised (Cox 2004). Invasions are "blurring the regional distinctiveness of Earth's biota" (Vitousek ***et al.*** 1997 p. 6) and grasslands everywhere are being invaded by similar sets of species.

The minimum impact of an exotic plant that integrates smoothly into a native community might possibly be very small: conceivably it might use resources that would not otherwise be used by the native plants and space that they would not occupy. In general however resource must be used and displacement is usual. Larger impacts involve displacement of more species over wider areas. Major impact may involve preemption of the niche of a community dominant. The highest levels of impact involve alteration to the community properties – the invader is a so-called 'transformer species' (Henderson 2001). Typically these dominate by forming a high proportion of the biomass in the community or stratum or have disproportionate influences on ecosystem function (Grice 2006). In order to measure the impact of an invasive species on biodiversity it is necessary to examine the effects on native biota and ecosystem functioning, determine any threshold below which impact is minimal and determine the management factors that influence the degree of impact (Adair and Groves 1998). The interactions between the invader and the invaded system are complex, and of many types, and are often indirect (Groves 2002).

According to Woods (1997 p. 61) “there have been few cases where competition from invaders has been shown unambiguously to be responsible for significant alteration of communities. Most of the extensive literature suggesting such effects is based on correlative studies, historical records, or anecdotes”. Byers *et al.* (2002) considered that much of the research purportedly demonstrating detrimental impacts fails to clearly demonstrate that the invasive organism is the cause of supposed effects. The presence of weeds where native plants once grew may be due to their ability to invade without disturbance, or be a consequence of damage to the native species by disturbance. Correlations between weed density and reduction in cover and abundance of a native plant implies a direct negative interaction. However the affected species could be reacting in an opposite way to some independent environmental factor such as an altered disturbance regime resulting from human activity. It is generally difficult to determine if the invading species or the altered conditions are the cause of such changes (Weiss and Noble 1984, Huenneke *et al.* 1990, Woods 1997). If anthopogenic disturbance is the cause, management should address the disturbance, rather than the weed.

Despite such difficulties there is wide consensus that “introduced alien species are the most rapidly growing cause of extinction and extirpation of endemic, native species” worldwide (Cox 2004 p. 220) and currently “a significant cause of global biodiversity decline” (Downey and Coutts-Smith 2006 p. 803). Environmental weeds apparently cause fragmentation of habitat, disintegration of plant communities and extinctions, but the details of how this occurs and what is impacted have been scanty (Adair 1995) and little quantitative information of effects on native species and ecosystem functioning has been published (Byers *et al.* 2002). The severity of impact generally increases with the extent of weed cover (Carter *et al.* 2003).

In Australia, even the simplest data on the proportion of the landscape or habitat invaded and the relationship of weed density to impact has been lacking for most weeds (Adair 1995). “Remarkably few” studies have attempted to quantify the impact of weeds on biodiversity, in part because the effects are viewed as “obvious” (Adair and Groves 1998 p. 3). Groves (2002 p. 18) considered it “surprising” that the impacts of some of Australia’s worst invasive plants on species richness was “still unknown” and noted only “few well-documented” studies of biodiversity impact. Most published statements about impact “are based on more or less casual observations” (Grice 2006 p. 28) and this reliance on anecdotal and subjective information is a worldwide problem (Byers *et al.* 2002).

Overall in Australia the mechanisms by which weeds impact on ecosystem structure and function - “how” weeds affect biodiversity - have not been widely quantified (Grice 2004a, Grice *et al.* 2004), although a few studies have examined land use and environmental factors associated with invasion (Adair and Groves 1998). There is little data specifically dealing with the effects of weeds on the biodiversity of Australian rangelands (Grice 2004a 2006). Most studies have focused on vascular plants and some on vertebrates (Grice 2006) but there are much fewer studies of the effects on animals than on plants (Grice 2004a 2006) and very few on invertebrates and soil biota (Grice 2006). However most fauna studies indicate marked reductions in diversity and abundance of vertebrates and invertebrates (Adair and Groves 1998).

In general, information has not been readily available on the species and communities acually impacted in Australia, nor has there been an adequate compilation of the weeds causing the impacts (Downey and Cherry 2005, Downey and Coutts-Smith 2006, Downey 2008). As with the worldwide information (Byers *et al.* 2002), causal relationships between invasion and impact have “generally [been] implied but not demonstrated” (Grice 2004a p. 54). For example, Chejara *et al.* (2006) claimed that *Hyparrhenia hirta* “greatly reduced the species richness of native flora”, although they only compared sites where the grass was present or absent, and undertook no manipulative experimentation. McArdle *et al.* (2004 p.50), studied the same species using “matched plots” with “similar ... apparent disturbance history”, and reached a similar conclusion: “demonstrated impacts on plant diversity” (p. 54), despite little attempt to determine the mechanisms that enabled the invasion or its history at invaded study site.

Impact on threatened species and communities

Leigh and Briggs (1992) compiled data on the proportion of threatened plants in Australia that were threatened by “weed competition” and found that alien plants had been dentified as a threat to 69 species. Adair and Groves (1998) found that weeds had been cited as a major cause of extinction of four plant species and an endangering process for 57 nationally endangered plant species. They also found that 23 entities listed under the *Victorian Flora and Fauna Guarantee Act 1998* were at risk from 22 exotic weed species. Groves and Willis (1999) found that environmental weeds have been implicated in the extinction of four native species.

In terms of detailed data on the impact of weeds on threatened species or communities in Australia 19 of the 20 studies of environmental weed impact on plant communities in Australia examined by Adair and Groves (1998 p.7) “demonstrated a decline in either species richness, canopy cover or frequency of native species”. A brief review by Vidler (2004 p. 652) found a general absence of quantitative information, but concluded that weeds are “a major threat to at least 41 threatened plant and animal species”. A much more thorough review (Coutts-Smith and Downey, 2006, updated by Downey and Coutts-Smith 2006) found negative impacts on 283 plant species (including algae and fungi), 63 animal species, 15 threatened populations and 71 endangered ecological communities (90% of all officially recognised endangered communities) in NSW alone. Weeds threatened 45% (or 44% according to Downey 2008) of the 970 entities listed under the NSW *Threatened Species Conservation Act 1995*. 127 weed species were on record as biodiversity threats. Unspecified weed species accounted for 51% of the threats and 43% of threats comprised multiple weed species. Of the major animal groupings, invertebrates had the highest proportion of listed ‘threatened entitites’ at risk from weed invasions. Competition (as opposed to habitat degradation by weeds and weed control activity) was determined to be the main threatening factor, and accounted for 81% of the threats. The number of native species at risk from alien plants in one State alone was found to be an order of magnitude larger than previous estimates for the whole of Australia (Downey 2008). Furthermore, these assessments only considered threats to species formally listed by the State, so considerably underestimated the real threat (Downey 2008).

Downey(2008) applied similar methodology as used in NSW by Coutts-Smith and Downey (2006) and by Downey and Coutts-Smith (2006) to the biodiversity listed under the national *Environment Protection and Biodiversity Conservation Act 1999*, and found that alien plant invasions were a threat to 291 theatened species. Specific weed species were identified for only 33% of the threats, and these totalled 57 species.

Invasion of native vegetation by environmental weeds is recognised as a threatening process under the Victorian *Flora and Fauna Guarantee Act 1988* (Department of Sustainability and Environment 2009b) but no action plan has been developed. The negative impacts mentioned include limitation or prevention of recruitment of native taxa, alteration to fire regimes, hydrological cycles, nutrient cycling and other processes, increased soil erosion, genetic pollution, alterations to structure and floristics of native vegetation communities, competition, and niche modification.

Approaches to impact assessment

Assessments of the biodiversity impacts of weed are of four main types (Downey and Cherry 2005): 1. scientific studies of individual weed species and the systems they have invaded; 2. reviews or meta-analyses of such studies; 3. reviews of threatened species databases, and 4. detailed consultation with biodiversity stakeholders as part of a process of threat assessment and abatement planning. The former two methods approach the problem primarily from the individual weed perspective, the latter two more from the perspective of the impacted biodiversity.

In terms of scientific studies, knowledge is particularly poor about how the biodiversity impacts of weeds vary in space and time (Grice 2004a). Assessment is complicated by communities and systems being in disequilibrium or being dependent in their evolution or dynamics or historical factors, rather than having a single stable state or successional pathway (Woods 1997). In general very little is known of the impact of invading species at different stages of community succession, or of the permanence of the occupation, i.e. the potential for community recovery if the factors initially permitting invasion are mitigated (Woods 1997). Furthermore, the balance of negative and positive impacts can shift dramatically over time and across habitats (Groves 2004). Knowledge about how weeds alter fire regimes and other ecological processes, and scientific understanding of the responses of a range of different taxa in the same area to a weed invasion is also very limited (Grice 2004a). Impacts on fauna are more complex than those on vascular plants and are therefore more difficult to determine (Grice 2006). In addition, the impact of measures to control the weed upon biodiversity is rarely known or investigated, although Coutts-Smith and Downey (2006) found that 7% of species threatened by alien plants were at risk from inappropriate control measures.

A simple example representing a combination of the metanalysis/review approach to impact assessment is that of Carr *et al.* (1992), who identified 166 taxa threatened by environmental weeds in Victoria, including many found in grasslands. A slightly different approach identified the communities at risk: FFG SAC (1996) listed numerous communities threatened by weed invasion in Victoria, including Northern Plains Grassland, Plains Grassland (South Gippsland) and Western Basalt Plains Grassland.

Much information about specific impacts is available but has never been adequately compiled and mobilised. Coutts-Smith and Downey (2006) demonstrated the great utility of a more comprehensive review of such existing threat information. The authors found that weeds posed a threat to 45% of threatened species, populations and communities in New South Wales and were the most important single threat after land clearing. However details of the specific biodiversity threatened by particular weeds, including Weeds of National Significance, in Australia was found to be almost entirely lacking, and only a very small proportion of the threat information obtained came from scientific studies.

Downey and Cherry (2005) demonstrated the utility of the consultation approach in assessing weed impact for the coastal dune weed *Chrysanthemoides monilifera* subsp. *rotundata* (erroneously called subsp. *monilifera* by the authors). They found the number of species threatened by it to be 25 times higher than previously suggested.

Types of impact

Weed impacts can be harmful or beneficial (Adair and Groves 1998, Williams and West 2000, Low 2003, Richardson and van Wilgen 2004). Weeds can provide food, fodder, building materials, nectar, shade and numerous other benefits (Richardson and van Wilgen 2004). Weeds can contribute to conservation of biodiversity, for example by protecting other plants from herbivores and acting as refuges. Invasive plants may become food for native fauna, which ‘host-shift’ to feed on them, or already have wide host preferences. The possibility of host range expansion is one of the most important hazards in classical biological control of weeds (Hopper 2001): the deliberately introduced invader may prefer a non-target plant. Shapiro (2002) documented the case of the city of Davis, California, where a diverse, highly valued urban butterfly fauna is largely dependent on naturalised and cultivated alien plants, and where, in consequence, efforts to control the alien species conflict with biodiversity goals. Low (2002) provided numerous Australian examples of native animals, including endangered species, benefitting from alien plant invasions.

In evolutionary time, the interactions of invasive species with other species in the invaded community changes selection pressures and ultimately results in evolutionary change, with new species arising (Cox 2004). Thus invasive species eventually tend to “become integrated into the new biotic community in such a way that their initial impacts are softened. Integration occurs through the processes of coevolution and counteradaptation” with the ecological adjustments tending to precede the evolutionary (Cox 2004 pp. 246-247).

Food webs are one conceptual basis for comprehending the interactions of invasive species on the invaded community (Strong and Pemberton 2002 p. 59). Those that develop around animals introduced for biological control “are simpler than in natural communities” (Strong and Pemberton 2002 p. 57) and similar simplified systems may be expected around invasive plants. Unfortunately there is a general lack of detailed information about the food webs of even the most abundant native plants in Australia and the complexities of such interactions greatly complicate scientific assessment.

Further complications are usually provided by weed management activities, since the weeds most worthy of study for biodiversity impact are generally those that are subject to control activities. Weed control activities themselves may impact negatively on biodiversity. In native grasslands herbicidal control in particular can have detrimental effects on native flora and lead to proliferation of non-target weeds (Lunt 1991, Slay 2002c, Brereton and Backhouse 2003). Such impacts are, by default, attributable to the particular weed that is being targetted, but little quantitative information on off-target damage is available. The effects of weed management activities on native invertebrates is unkown (Yen 1999).

Specific threats posed by weeds to biodiversity

Invasive plants potentially influence the structure, function and composition of ecosystems by impacting on growth, recruitment and survival (Grice 2004a Vidler 2004). These impacts are “ovewhelmingly negative”, but positive impacts also occur (Groves

2004, Richardson and van Wilgen 2004). Complex, simultaneous negative and positive effects are probably usual. For example Lenz *et al.* (2003) found that the presence of annual exotic grasses on a hillside in one South Australian grassland facilitated native perennial grass growth on upper slopes but impeded it at the lowest elevations.

Feedback processes, in which the invasive plant modifies the invaded environment or habitat for other organisms are doubtless frequently important. The invader may increase temporal or spatial resource fluctuations and may increase the heterogeneity or homogeneity of the area invaded in a wide variety of ways (Melbourne *et al.* 2007).

Impact on the invaded systems may include changes to:

1. Competitive interactions with other plants for light, nutrients, water, pollinators and other resources - resulting in changes in species composition, niche displacement, or replacement of another species (Weiss and Noble 1984, Adair 1995, FFG SAC 1996, Woods 1997, Prieur-Richard and Lavorel 2000, Williams and West 2000, Levine *et al.* 2003, Vidler 2004).
2. Species richness or dominance patterns (Adair 1995, FFG SAC 1996,Woods 1997).
3. Physical structure and chemistry of the habitat (Adair 1995, FFG SAC 1996, Woods 1997, Williams and West 2000).
4. Alterations to animal health, habitat, food chains and trophic structure of communities (Williams and West 2000, Groves 2002, Low 2002, Levine *et al.* 2003).
5. Phenology of native species (Woods 1997).
6. Facilitating or allowing invasion of other species, including other plant or animal pests, or pathogens (Groves 2002).
7. Genetic changes, including rates and details of evolutionary interactions, introduction of foreign genes, hybridisation and gene swamping (Carr 1993, FFG SAC 1996, Williams and West 2000, Cox 2004).
8. Disturbance regimes and successional pathways (Woods 1997, Vitousek *et al.* 1997, Mack and D'Antonio 1998, D'Antonio *et al.* 1999, Prieur-Richard and Lavorel 2000).
9. Ecosystem function and ecosytem services (Versfeld and Van Wilgen 1986, Adair 1995, FFG SAC 1996, Prieur-Richard and Lavorel 2000, Levine *et al.* 2003, Richardson and van Wilgen 2004) including nutrient cycling (Vitousek *et al.* 1997, Rossiter *et al.* 2006), hydrological processes (Vitousek *et al.* 1997, Versfeld *et al.* 1998, Williams and West 2000), geomorphological processes including soil erosion and landform (Adair and Groves 1998, Williams and West 2000), fire cycles (D'Antonio and Vitousek 1992) and C storage (Seabloom *et al.* 2003).
10. Management regimes, resulting from altered management directed against the weed (Groves 2002).

More detailed explanations and examples of each of these rather arbitrary categories are provided below.

Competitive interactions

Competition by invasive plants is by far the most frequently invoked cause of invasive plant impact on biodiversity (Levine *et al.* 2003). 'Weed competition' with native plants had been identified as by far the most important cause in NSW, however in approximately half of the instances the competing weeds were not identified, and only rarely have competitive mechanisms been investigated (Downey and Coutts-Smith 2006). Mechanisms of competition between plants include sequestering of resources (space, water, nutrients, light), and alterations to the pathways and rates of cycling of energy, water and nutrients (Levine *et al.* 2003, Grice 2004a, Vidler 2004). In general, the more resources an invasive plant obtains, the fewer are available for the invaded community, and invaders that dominate resources can reasonably be expected to have high biodiversity impacts (Grice 2006).

The foliar cover achieved by successful invasive plants is a useful general indicator of their potential impact. Canopy dominance reduces light availability to subsidiary species and clearly reflects biomass dominance, which ultimately indicates the extent to which the plant monopolises available resources. A 'canopy dominant' environmental weed can totally or largely alter the nature and functioning of an ecosystem by dominating, overtopping or replacing the natural canopy, while a subcanopy dominant can have similar effects in a lower stratum (Swarbrick 1991). Woods (1997) argued that few experimental studies had demonstrated that competition for light by invasive plants is a causal factor of community change and there was similarly little support for the contention that competition for other limiting resources is important. This may largely be due to the lack and difficulty of adequate study, rather than the unimportance of such effects. Multi-factor competition may well be usual (Levine *et al.* 2003). Hautier *et al.* (2009) clearly demonstrated that competition for light causes losses of understorey species in experimental grassland communities.

Asparagus asparagoides L. Druce (Liliaceae) has a strong negative impact on the endangered *Pterostylis arenicola* M. Clements and J. Stewart (Orchidaceae) probably because both grow from tuberous roots in autumn and winter and senesce in spring and summer (Groves 2002 2004). Root competition of this species has also been demonstrated to significantly reduce germination of the endangered *Pimelea spicata* R.Br. (Thymelaeaceae) (Groves 2002 2004).

Competitive superiority of the invader to an ecologically similar native has been partially demonstrated for *Chrysanthemoides monilifera* subsp. *rotundata* (DC.) Norl. which directly displaces *Acacia sophorae* (Labill.) R.Br. on coastal dunes in New South Wales (Weiss and Noble 1984). Similarly a species may replace an ecological guild - Woods (1997, citing Chilvers and Burdon 1983, etc.) cites the example of *Eucalyptus* spp. replacement by *Pinus radiata* D. Don. in Australia.

Successful invasion resulting from superior competitive abilities may not result in any functional changes in ecosystem properties, the invasive species essentially functioning like the displaced native (Adair and Groves 1998), but the examples cited have, or will likely lead to more profound shifts in dominance patterns and the conversion of ecosystems to new types.

Species richness and dominance patterns

A consistent negative relationship has been found between the abundance or presence of invasive plants in Australian and that of native species (Grice 2006). Invasive plants are recognised threats to whole communities, e.g. the aforementioned *Chrysanthemoides monilifera*, which ultimately suppresses seedling establishment by most native species in some of the ecosystems it occupies, including canopy trees (Groves 2004). In Australia, *Mimosa pigra* has replaced native sedgelands with tall shurbland, *Annona glabra* L. has replaced wet grassland with closed forest, *Acacia nilotica* (L.) Willd.ex Del. has replaced dry grassland with tall shrubland, rainforest has been converted to vine thickets by *Thunbergia grandiflora* Roxb., *Mcfadyena unguis-cati* (L.) A. Gentry and *Andredera cordifolia* (Ten.) Steenis in Queensland (Panetta and Lane 1996), and *Tamarix aphylla* (L.) H. Karst. Had replaces *Eucalyptus camaldulensis* woodland in the inland (Groves 2002). Amongst the invasive Poaceae, *Glyceria maxima* (Hartman) Holmb and *Brachiaria mutica* (Forrskal) Stapf convert shallow water aquatic systems to wet grassland (Panetta and Lane 1996). Weeds that convert one ecosystem to another, changing its major functional characteristics have been termed transformers (see above) and are usually 'canopy dominants' (Panetta and Lane 1996).

Most invasive plants are not transformer species but are are functional analogues of native species in the invaded systems. Few invasive grasses have the potential to change a grassland into any other ecosystem, but they frequently appear to simplify the system by reducing species richness and becoming dominant. For instance *Hyparrhenia hirta* was found to dominate areas it occupied, which also had reduced native plant species richness (McArdle *et al.* 2004).

Weed invasion "can affect invertebrates adversely by elimination of native plant species, habitat alteration and ... the spread of exotic invertebrates" (Yen 1999 p. 63).

Physical structure and chemistry

Alterations to the biotic structure and composition of a community by an invasive plant affects the spatial and temporal patterns of resource flow within that community (Grice 2006). Altered soil chemistry can result from allelopathy, pH changes or changes in the availability of minerals, particularly major nutrients and salts (Woods 1997, Levine *et al.* 2003).

Legumes (Fabaceae, Caesalpineaceae, Mimosaceae) such as *Lupinus arboreus* Sims, may increase soil N levels (Adair and Groves 1998) and have a direct effect on soil fertility. On young volcanic soils in Hawaii, the invasive tree *Morella faya* (Aiton) Wilbur (Myricaceae) and its microbial symbionts increased soil N fixation to levels 90 times that of all native plants combined and increased the rates of N mineralisation, which created a cascade effect through the system and altered its subsequent development (Vitousek *et al.* 1987, Vitousek and Walker 1989). Bacterial symbionts in *Sorghum halepense* enable it to invade N-poor soils, partly explain its ability to form dense near-monocultures that exclude other plants, and are largely responsible for its ability to significantly alter soil biogeochemistry (Rout and Chrzanowski 2009).

Other plants can deposit salt on the surface, e.g. *Mesembryanthemum crystallinum* L. (Aizoaceae) (Woods 1997). In Argentine grasslands *Pinus* spp. alter the pH and other properties of soils to the detriment of some native grasses (Amiotti *et al.* 2007). Alterations to the soil chemistry in turn commonly result in alteration to nutrient cycles.

Many weeds were introduced to combat soil erosion. *Chrysanthemoides monilifera* was widely planted and became a major weed because it is an efficient sand binder (Groves 2004). McIlroy *et al.* (1938) advocated the use of three now severely invasive grasses *Paspalum dilatatum*, *Pennisetum clandestinum* Hochst. ex Chiov. and *Cynodon dactylon* L. for erosion control in Victoria.

The many physical, chemical and biotic effects of the production and deposition of litter by invasive plants can impact markedly on biodiversity. Presence of litter can reduce seedling establishment (Lenz *et al.* 2003). Litter alters the microclimate, surface conditions and soil properties including temperature, water infiltration, retention and evaporation, and may produce chemical leachates. These changes in turn can modify competitive interactions between organisms, alter rates of seed and seedling predation, favour proliferation of fungal pathogens, etc. (Lenz *et al.* 2003). *Avena* litter at 400 g m^{-2} was found to significantly reduce maximum soil temperature (by c. 3ºC in early November) but not minimum temperature or soil moisture (Lenz *et al.* 2003). Ens (2002a) found that dense litter mats produced by *N.neesiana* altered the species composition and activity levels of invertebrate communities with flow-on effects through the system. Dense grass litter in grasslands generally results in reduced plant biodiversity (Lenz et al. 2003). Buildup of perennial *native* grass litter in the higher productivity temperate south-eastern Australian grasslands, paticularly *T. triandra* grasslands, has the same effect, so regular biomass reduction through fire, grazing or other management is necessary to maintain vascular plant diversity (Stuwe and Parsons 1977, McIntyre 1993, Morgan 1997, Henderson 1999, Lunt and Morgan 2002). For example Morgan (1995a 1995b) found that seedling establishment of *Rutidosis leptorrhynchoides* in dense *T. triandra* grassland required large canopy gaps, mortality of young seedlings in smaller gaps being due to shading and increased herbivory. In contrast, litter experiments in Dry *Themeda* grasslands in the ACT by Sharp (1997) found that retention of the *T. triandra* litter resulted in higher native forb richness and cover than when litter was removed, with the opposite effect for exotic forbs. The effects of grass accumulation on plant productivity differs seasonally and from site to site and species to species (Lenz *et al.* 2003). Generally plants with smaller seeds are inhibited more by litter because the germinants have inadequate energy reserves (Lenz *et al.* 2003). Annuals are thus more likely to be negatively impacted.

In pot experiments using soils from native grassland in South Australia Lenz *et al.* (2003) found that *Avena arbata* litter at different densities had complex, time-dependent effects on the emergence and biomass of seedlings, that varied between taxa. The establishment or growth of some exotic dicots was reduced by dense litter, but after 4 months the biomass of annual grasses was positively affected , and total biomass fell markedly in the dense litter treatment, mainly due to suppression of *Trifolium* spp.. Medium and high litter levels had little effect on the only native plants that emerged in sufficient numbers to assess, *Austrodanthonia* spp., but after 4 months all had died due to fungal disease. Field experiments, in which all standing biomass was removed and dry *Avena* litter added, demonstrated similar complex effects. In winter, c. 4 months after treatment, growth of annual grasses was increased by dense litter and there were significant suppressive effects on *Austrodanthonia* spp., and some exotic herbs, but no effect on *Austrostipa eremophila* (Reader) S.W.L. Jacobs and J. Everett. After c. 9 months, the biomass of exotic annual grasses was slightly increased by high litter levels, there was no siginficant effect on native perennial grasses, but the biomass of all other species combined (mostly exotic forbs) was significantly decreased.

Invasive plants can severely modify hydrological cycles (Vidler 2004). *Tamarix* in inland Australia lowers the water table, alters stream flow and flooding regimes and ultimately salinity levels (Griffen *et al.* 1989). *Andropogon virginicus* L., develops a high biomass of dead shoots that reduce evaporation rates from the soil and also passes through an inactive senescent phase during which transpiration is reduced (Mueller Dombois 1973). In rainforest communities this results in excess water in the soil, increased runoff and accelerated erosion.

Altered microclimates (Vidler 2004) are probably commonplace, particularly through increased shading.

Alterations to animal health, habitat, food chains and community trophic structure

Invasive plants frequently have impacts on consumers and decomposers, including their community composition, diversity and behaviour (Levine *et al.* 2003). The impacts of invasive plants on fauna are more complex than on plants, and can be positive or negative depending on the particular animal group or species (Grice 2006). Invasive plants may be utilised by animals in the same wide range of ways as native plants and can degrade or enhance the habitats of animals (Low 2002, Vidler 2004). Weeds provide food and shelter for vertebrates (Low 2002) including vermin such as rabbits and foxes (Parsons and Cuthbertson 1992) and native and introduced birds (Loyn and French 1991). Peter (2000) for example provided details of shelter and nest site provision by *Lycium ferocissimum* Miers, and utilisation of its fruit by native and exotic birds. Fruit and seeds are widely eaten, along with foliage, while nectar, pollen, roots and other plant parts may be exploited. Invasive plants may be used when nothing else is available. Loyn and French (1991 p. 138) noted that weeds used as food by birds "may be better than nothing, but not as good as the native plants they displace". Grice (2004a) noted that existing studies provide little indication of the importance of the plant for the diet of the animal utilising it, nor the impact of the feeding on the plant.

Invaded habits may be less suitable for animals in many ways. Habitat degradation in invaded areas may mean loss of food or shelter or alteration to physical conditions that make the site unsuitable for habitation. Much of the literature has focused on how the behaviour and ecology of individual native animals is altered by different characteristics of the invasive and native plants (Levine *et al.* 2003), Valentine (2006) found that areas invaded by *Cryptostegia grandiflora* Roxb. ex R.Br. (Asclepiadaceae) were less suitable for lizards. Invasive plants may simply out-compete food plants of endangered animal species (Vidler 2004). In general they can be expected to support a different suite of primary consumers to the plants they displace (Grice 2004a).

Weeds may be toxic to animal species. Groves (2002) discussed impacts on animal health, but mentioned only livestock related cases. Little appears to be known about poisoning of native animals by invasive plants in Australia but some examples are on record. The decline of the Richmond Birdwing, *Ornithoptera richmondia* (Gray) (Lepidoptera: Papilionidae) in Australia is partly due to the introduced Dutchman's Pipe vine *Aristolochia elegans* Mast. (Aristolochiaceae), a close relative of the native food plants. *A. elegans* is highly attractive to ovipositing female butterflies but the young larvae are poisoned and do not survive (Sands and Scott 1996, Braby 2000). Another vine, *Cryptostegia grandiflora* is possibly toxic to reptiles (Valentine 2006).

Environmental weeds can also reduce access to breeding, nesting or feeding sites (Vidler 2004). Vertebrates that consume the fruit and seeds of exotic plants can in turn can become important dispersers of propagules. Dispersal of fleshy-fruited weeds by birds is particularly important in this respect (Loyn and French 1991). Carr (1993) provided a list for Victoria of some naturalised plants and the indigenous and exotic animals which disperse their seed following ingestion of fruit or seed. The complexities of impact may take many years to run their course. Synergistic effects, e.g. when a bird dispersed weed facilitates invasion by other bird dispersed weeds (Grice 2004a) may continue almost indefinitely in environments where new adventives are always appearing.

Impacts on detritivores and decomposers have been much less investigated (Levine *et al.* 2003).

Phenology of native species

Phenology is the study of the relationship between climate and the temporal variation of the lifecycle of an organsim. Any modification of microclimate caused by an invasive plant may affect a range of other species. Increased shade due to riparian invasions of the exotic Siam weed *Chromolaena odorata* (L.) R.M. King and H. Rob. (Asteraceae) in South Africa have reduced soil temperatures and altered the sex ratio of locally breeding Nile crocodiles (Leslie and Spotila 2001). Any plant examples?

Facilitating other invasions

Invasive plants can facilitate the invasion of other plants. Fixation of N by legume weeds can profoundly alter soil conditions to the detriment of native species and potential benefit of new invaders (Levine *et al.* 2003). Australian *Acacia* species invasive in South African fynbos make the environment far less suitable for fynbos plants (Versfeld and van Wilgen 1986) and thus more suitable for other species. As previously mentioned the attraction of furit eating animals to a weed food source may facilitate consumption of the fruit of other weed species and dispersal of their seed.

Genetic changes

Loss of genetic diversity in particular plant species or populations resulting from weed invasion are probably widespread, but have rarely been investigated, in part due to the lack of or difficulty of appropriate techniques (Adair and Groves 1998). Probably the most common impacts occur where weed invasion destroys small, isolated or remnant populations that often possess more extreme geneotypes than core populations. Invasive perennial grasses have played a role in reducing the genetic variance of *Rutidosis leptorhynchoides* in temperate Australian grasslands by contributing to the extinction of local populations (Groves 2004).

On a world basis genetic diversity information for grasslands is entirely inadequate and the genetic composition of only a very small proporrtion of species has been investigated. Aspects of genetic diversity requiring investigation include its spatial distribution, structural and functional attributes and processes under various disturbance regimes (Aguiar 2005). Inadequate baseline data makes assessment of genetic biodiversity impacts very difficult.

Hybridisation is another threat. Hybridisation of indigenous species with exotic garden escapes, accidentally introduced exotics and other indigenous species established outside their native range have all been reported in Australia, along with exotic-exotic hybrids (Carr 1993). For example hybrids or possible hybrids between the Argentinian *Nicotiana glauca* Graham (Solanaceae) and the natives *H. suaveolens* Lehm. and *N. velutina* H.-M. Wheeler have been found in Victoria (Carr 1993, Jeanes 1999a). The likelihood of hybrid vigour and the possibility of hybridogenic speciation are particular concerns (Carr 1993). The presence in Australia of a set of *Nassella* species from different areas of the Americas and their introduction into an environment inhabited by a large set of native stipoids provides unique circumstances that may allow novel gene flows, with unpredictable effects.

Disturbance regimes and successional pathways

Invasive plants may act directly as disturbance agents but they can also modify the response of the community to disturbance. The literature survey of Mack and D'Antonio (1998) found numerous studies in which plant invasions led to subsequent alteration of disturbance regimes. Such changes included alteration of physical or biological attributes of the disturbance (e.g. enhancement or suppression of fire and erosion) and changes in the responses of other plants. Invasion by species that interact strongly on disturbance regimes can often produce "discrete state changes in ecosystem structure and function" (Mack and

D'Antonio 1998 p. 195). Alterations to fire regimes are the best documented (Versfeld and van Wilgen 1986, D'Antonio and Vitousek 1992, Grice 2006), along with invasions by woody weeds (Adair and Groves 1998).

Altered disturbance regimes are less likely when the invasive species differs little from the natives, but subtly different organisms can produce subtle changes (Mack and D'Antonio 1998). Permanent changes to disturbance regimes and successional pathways eventually result in conversion of the system to a new state.

Ecosystem function and ecosytem services

Weeds that significantly modify ecosystem function affect the living conditions of all the other species in the system, and thus have the most profound effects on biodiversity (Adair and Groves 1998). Most studies of these impacts have involved comparison of invaded and uninvaded areas and require cautious interpretation because the mechanisms that enable one system to be invaded and not the other are usually poorly understood (Levine *et al.* 2003).

Woody weed invasions of South African fynbos have resulted in major declines in stream flows and water yield (Versfeld and van Wilgen 1986, Versfeld *et al.* 1998). Mechanisms of impact include increased interception of rainfall, increased transpiration and changes in infiltration and erosion rates (Versfeld and van Wilgen 1986). Invasive species impacts can also result in reductions in water use (Levine *et al.* 2003) and thus increased flooding and habitat change. The replacement of native perennial bunchgrasses by annual exotic grasses in California grasslands has decreased the amount of C they store (see references in Seabloom *et al.* 2003), and consequently the amount of atmospheric CO_2 and the extent of global warming. Impacts on nutrient cycling have been widely investigated with a focus on nitrogen (particularly in grasslands) and leguminous plants (Levine *et al.* 2003).

In the most extreme cases weeds threaten whole ecosystems or ecosystem units, either by creating a new vegetation stratum or by altering major ecosystem properties (Adair and Groves 1998). *Acacia nilotica* (L.) Delile thickets threaten Mitchell Grass grasslands in the Northern Territory and northern Queensland by creating a dense overstorey, with over 1 million ha infested by 1992 (Parsons and Cuthbertson 1992). The grass-fire feedback cycle (D'Antonio and Vitousek 1992), where the biomass of an invasive grass enhances fire (see below) is transforming ecosystems around the world.

Impacts on the delivery of ecosystem goods and services may be evident, but few studies have quantified the effects at regional or wider scales (Richardson and van Wilgen 2004).

Management regimes

Management activities are targetted at significant weeds and often have unintended consequences. Attempts to reduce the prevalence of *Nassella trichotoma* in Victoria by establishment of trees have attracted criticism that they will also eliminate the native grassland remnants in which the weed is growing. Similarly, herbicidal control of exotic stipoid grasses in Melbourne area grasslands has been criticised for its severe impact on native plants.

Invasive grasses - impacts and threats

Useful grasses have been widely introduced as forage plants for livestock and for other purposes, and many grasses of less forage value have dispersed widely without deliberate human intervention. In many cases they have replaced native grasses, being the agents, the beneficiaries, or both agents and beneficiaries of ecosystem transformation. These transformations have taken place in many of the major temperate grassland regions of the world. North American grasslands have been subjected to massive changes through the deliberate introduction of a wide range of grasses considered superior for livestock production including *Bothriochloa* spp. (Schmidt et al. 2008). The grasslands of the Llanos, Venezuela, and savannah-forest in the Cerrado, Brazil, both supported cattle grazing, but the Spanish and Portuguese immigrants considered the native grasses inferior and by the late 18th century had intoduced African species such as *Brachiaria mutica* (Forrsk.) Stapf, *Melinis minutiflora* P. Beauv. and *Panicum maximum* Jacq., which are now the dominant species in huge areas of tropical and subtropical Latin America (Mack and Lonsdale 2001). Similar transformations have occurred in Australia.

Poaceae is one of few plant families that consistently provides a high proportion of invasive species relative to its total taxa (Rejmánek 2000). Poaceae is probably the dominant weed family in Australia in terms of areas occupied and species diversity. Poaceae represent about 14% (375 spp.) of all naturalised vascular plant species in Australia, and 141 spp. (37.6%) are considered major weeds (Grice 2004b). There are more species and infraspecific taxa of Poaceae in the exotic flora of Victoria than any other family (Carr 1993).

Invasion of native plant communities by exotic perennial grasses is listed as a key threatening process under the NSW *Threatened Species Conservation Act 1995*, based on the impact of five species, *Hyparrhenia hirta, Cenchrus ciliaris*, *Eragrostic curvula*, *N. trichotoma* and *N. neesiana* (NSW Scientific Committee 2003, Downey in Virtue *et al.* 2004). Perennial grasses are one of the major groups threatening biodiversity in NSW (Downey and Coutts-Smith 2006). *N. neesiana*, *N. trichotoma* and *E. curvula* are among the major species recognised as threats in temperate grasslands (Kirkpatrick *et al.* 1995, Groves 2004). More cautiously, Adair and Groves (1998 p. 9) suggested that *N. neesiana* invasion of temperate *Themeda* grasslands is "perhaps" an example of simple species displacement, causing no significant functional changes in the ecosystem.

McArdle *et al.* (2004) investigated the impact of *H. hirta* by comparison of the botanical composition of matched invaded and uninvaded areas in Kwiambal National Park, northern NSW, and demonstrated reduced native plant richness and projective foliar cover in the ground strata of invaded areas. Exotic components of the system were not affected. The tendency of this plant to dominate was quantified, with infested sites being more homogeneous. Chejara *et al.* (2006) further investigated the impact on vascular plant diversity of this species on a travelling stock route near Manilla NSW. Where it was present it was the dominant species. Invaded areas had native plant species richness significantly reduced by half or more, as determined by spring and autumn surveys in 2003 and 2005, and native cover was significantly less in infested plots. A major fault with this study was that the areas lacking *H. hirta* had been spot sprayed with glyphosate to control the plant from 2001 to 2004. These plots were found to contain significantly greater numbers of exotic weed species in 2005. Another problem was that the invaded and uninvaded areas were 1 km apart and were "similar in respect to soil, landform, drainage and apparent disturbance history", but there was no way to tell whether the vegetation prior to invasion had been similar (Chejara *et al.* 2006 p. 208)

Competition with native plants

Competition with other plants is a widespread general expectation for invasive grasses (Evans and Young 1972, Newsome and Noble 1986, D'Antonio and Vitousek 1992, Lonsdale 1999, Grice 2004). 'Unequal competition' is widely assumed where grasses are invasive, but the mechanisms by which it operates are rarely demonstrated (Seabloom *et al.* 2003). Release from natural enemies is one contributing factor often suggested (e.g. Schmidt *et al.* 2008). *Phalaris aquatica* and *Ehrharta calycina* J.E. Sm., for example, are associated with major habitat degradation on roadsides on Kangaroo Island, threatening a range of endangered plants, imputedly the result of their superior competitive abilities (Vidler 2004, citing Davies 1996 and Taylor 2003).

Competitive superiority of invasive species was demonstrated for Old World *Bothriochloa* species over native Kansas bunchgrasses by Schmidt *et al.* (2008). In pot experiments, the exotics reduced one or more of three productivity attributes of native species, either vegetative tiller height or above or below ground biomass, while two of three native species tested failed to inhibit growth of the exotics.

Demonstable competition has been recorded where the invasive grass has higher rates of N uptake and higher N use efficiency (Rossiter *et al.* 2006). This is thought to be the case with exotic *Bothriochloa* inavsion of native tallgrass prairie in the USA (Schmidt *et al.* 2008). Increasing N levels in one American grassland created dramatic shifts in grass species dominance, with *Bromus hordeaceus* becoming a superior competitor to grasses including *Aira caryophyllea* and *Briza minor*, in the presence of adequate P. *B. mollis* has also been demonstrated to be an inferior competitor to *Erodium botrys* (Cav.) Bertol. (Geraniaceae) when the S status of soil is low, *E. botrys* having more rapid root growth. But when nutritional conditions were favourable, *B. mollis* outcompeted the herb for light because of its greater size and more erect habit (Evans and Young 1972). Competitive shifts in the flora resulting from changed nutrient status of the soil may be altered by a range of other environmental factors, including weather, grazing regime and the interaction between rainfall, temperature and grazing (Evans and Young 1972). N enrichment of soils in Californian grassland in dry years resulted in the almost complete elimination of the native bunchgrass *Agropyron intermedium* (Host) Beauv. by *Bromus tectorum* L., depletion of soil moisture by the superior competitor being thought to be the main mechanism (Evans and Young 1972).

Monocultures of invasive *Bothriochloa* species in the USA are more structurally homogeneous than native grassland and have reduced forb species richness (Schmidt *et al.* 2008).

There are relatively few studies that document the effects of exotic grasses on species diversity in Australia in any detail (Chejara *et al.* 2006), but numerous introduced species are implicated in decline of native vegetation via competition. These include *Cortaderia* spp. (Harradine 1991). Threats to small populations of endangered plants by competition from introduced grasses, include *Nassella* spp. on *Amphibromus pithogastrus* S.W.L. Jacobs and Lapinpuro "by reducing potential bare areas for establishment of seedlings" (Ashton and Morcom 2004 p. 2), and *Phalaris aquatica* L. on *Prasophyllum fosteri* D.L.Jones (Coates 2003a), *P.* sp. aff. *suaveolens* (Western Basalt Plains) (Coates 2003b) and *Thelymitra gregaria* D.L. Jones and M.A. Clem. (Coates 2003c).

In Queensland, *Brachiaria mutica* Para grass and *H.amplexicaulis* are a threat to the aquatic *Aponogeton queenslandicus* H.Bruggen (Vidler 2004 citing Williams pers. comm.). Kikuyu, *Pennisetum clandestinum*, is a threat to *Pimelea spicata* R.Br. in NSW (Vidler 2004 citing Groves and Willis 1999). *Ehrharta calycina* is a threat to Blue Gum woodlands (*Eucalyptus leucoxylon* F. Muell.) and Metallic Sun Orchid *Thelymitra epipactoides* F. Muell. in South Australia (Vidler 2004 citing Mercer pers. comm.) and to *Eucalyptus incrassata* and *E. fasiculosa* woodland associations and the Sandhill Greenhood *Pterostylis arenicola* (Virtue and Melland 2003). *E. calycina* frequently establishes on bare ground. Native vegetation "subject to disturbances such as livestock grazing, fire or soil movement [is] particularly prone to invasion" although "certain 'naturally open' vegetation types on sandy soils appear susceptible to invasion in the absence of major disturbance" (Virtue and Melland 2003 p. 111, citing pers. comms. of B.Bartel and D. Ancell) or the plant "may be mainly establishing in gaps (e.g., on lichen crusts) where there is no competing vegetation" (Virtue and Melland 2003 p. 112). *E. calycina* "can have a major effect on the diversity and regeneration of native plants, particularly understorey species" (Virtue and Melland 2003 p. 112) and can form 100% groundcover (G.Carr pers. comm. cited by Virtue and Melland 2003).

Grasses collectively, or particular categories of grasses, have also been regularly listed as threats to particular native plants. Introduced grasses are a threat to Shiny Peppercress *Lepidium aschersonii* Thell. in NSW (Vidler 2004 citing Ayers *et al.* 1996). In NSW exotic annual grasses are a threat to Red Darling Pea *Swainsona plagiotropis* F. Muell. while exotic grasses are a threat to *Swainsona recta* A.T. Lee (Vidler 2004 citing Ayers *et al.* 1996). Grasses are a threat to Ironstone Grevillea *Grevillea elongata* Olde and Marriott in WA (Vidler 2004 citing Stack and English 2003a). Annual grasses are a threat to *Acacia aprica* Maslin and A.R.O. Chapm. blunt wattle in WA (Vidler 2004 citing Bayliss 2003). Wild Oats *Avena fatua* and other "grasses" are a threat to Pinnate-leaved Eremophila *Eremophila pinnatifida* Chinnock MS in WA (Vidler 2004 citing Stack and Brown 2003) and introduced grasses are a threat to Spreading Grevillea *Grevillea humifusa* Benth. in WA (Vidler 2004 citing Stack and English 2003b). African Lovegrass *Eragrostis curvula* (Schrad.) Nees is a threat to Narrow-petalled Featherflower *Verticordia plumosa* (Desf.) Druce var. *pleiobotrya* A.S. George in WA (Vidler 2004 citing Phillimore and Evans 2003). Weeds associated with irrigation crops are a threat to Menindee Nightshade *Solanum karsense* Symon, in NSW (Vidler 2004 citing Ayers *et al.* 1996). Quaking Grass. Tall wheatgrass *Thinopyrum ponticum* (Podp.) Z.-W. Liu and R.R.-C. Wang "has been observed invading native *Themeda triandra*, *Austrostipa* and *Austrodanthonia* grasslands" in Victoria (Virtue and Melland 2003 p. 127) but is most successful at sites with high soil moisture levels and water tables and saline or alkaline soils, particularly winter-wet, saline sites (Virtue and Melland 2003).

Competition from grasses have been listed as a threat to a wide range of plants in basalt plains grasslands, including, introduced grasses on *Carex tasmanica* Kuk. (Morcom 2004) and *Comesperma polygaloides* F. Muell. (McIntyre *et al.* 2004), annual grasses on *Senecio macrocarpus* Belcher (Hills and Boekel 1996 2003) and 'dense grasses' on *Rutidosis leptorrhynchoides* (Humphries and Webster 2003), although this probably refers to *T. triandra* more than exotic species (cf. Morgan 1995a).

In comparison to annual grasses, perennial grasses have relatively low seedling vigour and slow early growth (Evans and Young 1972). The outcome of competition between perennial grass species is therefore highly dependent on the timing of germination and differential rates of early growth.

Impacts on animals

Invasive grasses may provide or fail to provide resources for a wide range of other organisms. They are used by birds in nest construction e.g. *Nassella trichotoma* by Yellow-rumped Thornbill *Acanthiza chrysorrhoa* (Quoy and Gaimard) (Peters 2000). Naturalised grasses provide food for various animals. Many birds eat the seeds of exotic grasses in Australia, including the Stubble Quail *Coturnix pectoralis* Gould and Plains Wanderer *Pedionomus torquatus* Gould in native grasslands (Loyn and French 1991). Most cockatoos and parrots consume exotic grass seeds and some species have become largely dependent on the resource, paticularly in cereal growing areas (Cole 1975, Loyn and French 1991, Barker and Vestjens 1989). In Victoria kangaroos eat and disperse the seed of *Aira elegantissima* Schur, *Briza minor* L., *Hordeum marinum* Huds., *Lolium rigidum* Gaudin and *Vulpia bromoides*, while feral horses and sambar eat and disperse the seed of *Anthoxanthum odoratum* and *Holcus lanatus* L. (Carr 1993).

Significant negative impacts on native fauna appear to be commonplace where extensive, dense infestations of exotic grasses occur, but have rarely been investigated in any detail in Australia. Compared to habitats dominated by native grasses, monocultures of invasive *Bothriochloa* species in central Texas have been found to have reduced rodent species richness and in Kansas had significantly reduced bird species richness, and reduced abundance and biomass of arthropods (Schmidt *et al.* 2008). The suppression of native psammophilous grasses by invasive *Cynodon dactylon* (L.) Pers. in Germany has impacted on the native leafhopper fauna of these grasses, and two exotic leafhoppers associated with *C. dactylon* now occur (Biedermann *et al.* 2005). The advent of New World-Old World hybrid *Spartina* in Europe appears to have resulted in the establishment of an American planthopper that attacks the European native *Spartina maritima* (Curtis) Fern. (Biedermann *et al.* 2005).

Some recorded negative impacts on fauna in Australia include those of Aleman Grass *Echinocloa polystachya* (Kunth) A.S. Hitchc., and Olive Hymenachne *Hymenachne amplexicaulis* (Rudge) Nees, which “can choke out waterways used by ... pygmy geese” (Vidler 2004, citing Garnett 2003). In Queensland, *Brachiaria mutica* Para grass and *H.amplexicaulis* are a threat to the Jabiru *Ephippiorhynchus asiasticus* Latham (Vidler 2004 citing Williams pers. comm.). *Briza maxima* L., is considered a threat to the Eltham Copper butterfly *Paralucia pyrodiscus lucida* Crosby (Vidler 2004 citing DPI/DSE 2003b).

Hydrology

Invasive grasses can modify hydrological cycles in a range of simple and complex ways. They can modify the rate and timing of evapotranspiration, infiltration and overland flow of water, and of the nutrients, minerals and soil particles in the water (Levine *et al.* 2003, Grice 2004).

Alterations of soil water usage, in total, seasonally and at different levels in the soil may occur. Replacement of native summer-growing grasses with annual spring-growing grasses results in wetter autumn soils, higher water tables and increased drainage flows (Sinclair 2002). Replacement of deep-rooted perennials by shallow rooted annuals may reduce water use and concentrate water use to a particular season (Levine *et al.* 2003). In Californian native grassland, annual grasses reduced the reproduction and seedling growth of native perennial Poaceae through competition for soil moisture (Lenz *et al.* 2003). Absence of summer growth due to prior depletion of soil water may also result in higher erosion during intense summer rainfall events (Sinclair 2002). Markedly increased rates of soil drying by high densities of the annual invasive *Bromus tectorum* adversely affect seedlings of a native perennial grass when the two were germinated simultaneously (Evans and Young 1972).

Disturbance regimes

Exotic grasses can change the nature and timing of disturbances through feedback effects (Woods 1997). Alterations to fire regimes and the frequency and intensity of flooding, erosion or herbivory may occur.

The most dramatic and best documented of feedback disturbance effects involve increases in fire (D’Antonio and Vitousek 1992, Woods 1997, Mack and D’Antonio 1998, Levine *et al.* 2003, Vidler 2004). Changes to evapotranspiration may lead to altered soil and vegetation dryness patterns, while changes in timing and density of biomass production can alter the fuel load and its temporal and spatial (vertical and areal) distribution (including continuity and curing rates), leading to changes in the the frequency, severity and timing of fires. Grass invasions commonly result in increased grass biomass production (Rossiter *et al.* 2006). Grass leaves have a high surface area: volume ratio and grasses commonly accumulate large amounts of dead biomass (Mack and D’Antonio 1998) with some species producing much more poorly biodegradable, inflammable bulk than others. But in most cases where increased biomass production occurs, the specific reasons are unknown (Levine *et al.* 2003). More frequent and hotter fires result in higher rates of nutrient loss and alterations in microclimate, and may stymie succession processes; thus altered fire regimes can result in major shifts in the composition and functioning of ecosystems, including dramatic alterations to biodiversity. In northern Australia, Gamba grass, *Andropogon gayanus* (Kunth), a South African species, produces up to seven times as much fuel as native grasses, resulting in a fire regime that is more frequent and much more intense (Rossiter *et al.* 2003, Ferdinands *et al.* 2006). If the changed fire regime leads to greater abundance of the responsible grass a ‘grass-fire cycle’ is initiated that reinforces the impact of the invasion (D’Antonio and Vitousek 1992, Hobbs and Heunneke 1992). Invasion by *A. gayanus* has led to reduced tree cover in open woodlands by this mechanism (Ferdinands *et al.* 2006).

Mission grass *Pennisetum polystachion* (L.) Schultes and buffel grass *Cenchrus ciliaris* L., two other high biomass invasive species in northern Australia also effect fire regimes (Rossiter *et al.* 2003, Grice 2004). Fire enhances growth of *C. ciliaris* which in turn enables more intense fires (Puckey and Albrecht 2004). A large range of short lived native grasses and forbs disappear when the density of *C. ciliaris* reaches a certain threshold. The number of native ground cover species declines significantly, there is very little germination of native seed and total invertebrate diversity and abundance of most inverterate groups is reduced (Puckey and Albrecht 2004). It is a specifically identified as a threat to the skipper butterfly *Croitana aestiva* E.D.Edwards (Vidler 2004 citing Wilson and Pavey 2002). Increased cover of *C. ciliaris* has been correlated with a decline in the numbers of Carnaby’s skink *Cryptoblephrus carnabyi* and delicate mouse *Pseuodmys delicatulus* in central Queensland (Puckey and Albrecht 2004 - see their references). *C. ciliaris* cultivar populations have low genetic diversity because of the dominance of asexual seed production, so local fungal epidemics can damage whole populations, increasing the likelihood of further ecological damage (Puckey and Albrecht 2004).

Temperate Australia appears to be less susceptible to an invasive species grass-fire cycle, in part because climatic conditions mitigate against very high biomass production. Milberg and Lamont (1995) inferred increased fire susceptibility due to invasion by *Ehrharta calycina* and *Eragrostis curvula* on roadsides in Western Australia. *E. calycina* was also implicated as a cause of more frequent fire by Virtue and Melland (2003), as were *Cortaderia* spp. in Tasmania by Harradine (1991). McArdle *et al.* (2004) suggested that *Hyparrhenia hirta* has the potential to induce a positive feedback fire cycle because of its dense tussock form that may protect the growing points from fire damage. Stoner *et al.* (2004) demonstrated that invasive *Phalaris aquatica* produced approximately three times the fine fuel biomass of *T. triandra*, the grass it replaced in their study area of southern Victoria, and argued that the increased fire intensity and flame residency and burnout times would be more likely to irreversibly damage native plant communities.

Invasive plants may also decrease the intensity or frequency of fire. Succulent plants or mesic species can have this effect (Carr 1993). However, as with *Pittosporum undulatum* in south-eastern Australian it may be difficult to tell whether the plant is reducing the fire-proneness of the vegetation or invading as a result of a pre-existing reduction of burning (Carr 1993). *N. neesiana* might reduce the incidence or severity of fire in spring in *Themeda triandra* grassland by increasing the ratio of green to dry vegetation in the standing crop (*N. neesiana* being a spring grower and *T. triandra* a summer grower), or it might possibly reduce fire in general by producing a smaller amount of flammable material than the plants it displaces.

Impacts on nutrient cycling

Several African grasses are known to fix significant levels of N in their native habitats (Rossiter *et al.* 2003). Invasive grasses can also alter N fixation rates by displacing legumes or by reducing the litter of other plants that support non-symbiotic N fixers (Rossiter *et al.* 2003). Invasive grasses may produce litter with different physical and chemical properties which accumulates and decays at altered rates and seasons (Grice 2004a). Higher C:N and lignin:N ratios in the foliage and litter may reduce nitrogen mineralisation rates (Levine *et al.* 2003). The decomposition rates of invasive grass litter was lower than that of native grasses in three of six cases reviewed by Rossiter *et al.* (2003).

Where invasive grasses displace summer growing species there is reduced uptake N mineralised in summer, so more is lost by leaching after autumn and winter rains (Sinclair 2002).

Other effects

Another class of feedback effects include erosion and soil stabilisation. According to Heyligers (1986) the introduced coastal dune grasses *Ammophila arenaria* and *Thinopyrum junceiforme* are more efficient at trapping sand and better colonisers of the backshore zone than native dune grasses. The dunes they build are larger and have a different shape. They also build foredunes in areas where the native grasses would be ineffective sand stabilisers. Changes in erosion patterns resulting from substrate stabilisation are also caused by *Spartina* (Gray *et al.* 1997) and *Cynodon dactylon* (Mack and D'Antonio 1998).

More complex alterations to disturbance regimes occur with grazing. Caldwell *et al*.(1981) found that invasive *Agropyron repens* (L.) Beauv. had greater photosynthetic capacity in its new growth and recovered more quickly after grazing than a dominant native species *Agropyron spicatum* (Pursh) Scribn. and J.G. Sm., and that these factors were driving species replacement over large areas. Thus invasive grasses have the potential to alter successional dynamics (Grice 2004).

Impacts of *N. neesiana*

Hocking (1998 p. 86) argued that the biodiversity impact of *N. neesiana* in Australia was "likely to be major" in part because it was known to be "actively invading high quality grassland remnants at much higher rates than serrated tussock and to have a greater potential for invasion of grassy woodlands, over a wide range of climatic conditions" (Hocking 1998 p. 89). Earlier, Morgan (1994 p. 88) considered it to be"one of the most troublesome grassy weeds of grasslands". However major biodiversity impacts are more likely to arise from weeds with "growth forms that are novel to the invaded ecosystem [rather] than growth forms for which there is a native ecological analogue" (Grice 2004a p. 55). Such weeds are more likely to be 'transformer species'. *N. neesiana* has a growth form similar to a number of native species that are commonly dominant or subdominant in temperate native grasslands in south eastern Australia. Various *Austrostipa* and *Austrodanthonia* species have similar tussock forming habits and stature, have similar cool-season growth periods and probably a markedly similar phenology. Hocking (1998 p. 86) also observed that "some well-managed" native grassland remnants have shown resistance to invasion "but further documentation is needed".

Exotic stipoid grasses including *N. neesiana* have been identified as "one of the most significant issues ... threatening nationally important remnant grasslands in Australia" (McLaren, Stajsic and Iaconis. 2004). *N. neesiana* has been identified as a particular threat to numerous grasslands, e.g. notably by Craigie (1993) as a "very serious threat to the integrity" of the Laverton North Grassland, because few native plant species survive beneath dense infestations. According to Craigie (1993) "prior disturbance" did "not seem to be necessary" for *N. neesiana* invasion and it was "invading the margins of swamp depressions and spreading out from those" with most infestations in areas where *Themeda* cover was sparse. She observed that "It grows back more quickly than other perennials after burning and [cleistogenes] ... may partially escape burning", that it "aggressively colonise[d] the inter-tussock spaces" and initially "grows faster than native species". Liebert (1996 p. 8) noted that it "quickly invades disturbed soils" resulting from revegetaion programs, while a report by Bob Bates (Jessop *et al.* 2006 p. 108) observed that it wa: "able to become established on even the hardest bare sites on disturbed ground".

Despite inclusion amongst the few exotic perennial grasses listed as a key threatening process in NSW, *N.neesiana* is not listed by Coutts-Smith and Downey (2006) as posing a threat to threatened biodiversity in NSW. However this indicates a failure both of their literature review technique (for Ens (2005) had previously stated that *N. neesiana* "threatens the ecological integrity of affected natural ecosystems") and the administrative process of threat identification in NSW, and also reflects the general lack of integration of weed impact literature. A poor historical linkage between biodiversity conservation and invasive species management is also to blame (Downey and Cherry 2005).

The greater height and density of *N. neesiana* swards than those of native grasses has been considered to make it a fire hazard (Liebert 1996), although no directly comparative quantitative data appears to have been published. Grasslands dominated by *T. triandra* are green in summer, while *N. neesiana* ceases to grow in summer after producing a large quantity of stems in spring and early summer. There are therefore good *a priori* reasons to suggest that *N. neesiana* might alter fire regimes by changing the seasonal distribution of fuel. Comparisons of total biomass of invaded and natural *T. triandra* grasslands during a range of seasons could easily determine this.

Four threatened plant species are listed by ARMCANZ *et al.* (2001) as threatened by *N. neesiana*: Sunshine Diuris *Diuris fragrantissima* D.L. Jones and M.A. Clem., Small Milkwort *Comesperma polygaloides*, Plains Riceflower *Pimelea spinescens* and Button Wrinklewort *Rutidosis leptorhynchoides*. More details for *D. fragrantissima* are provided by Webster *et al.* (2004) and Vidler (2004) and for *R. leptorynchoides* by Humphries and Webster (2003). However the national strategic plan (ARMCANZ *et al.* 2001) fails to “identify the biodiversity at risk in a manner that can be used to deliver effective management” and contains no specific section on impact minimisation (Downey and Cherry 2005 p. 42).

In summary, very little is known about the impact of *N. neesiana* on biodiversity and what little is ‘known’ appears to be largely based on simple correlative observations without adequate scientific study. Suggestions that the impacts are major or catastrophic appear to be founded on the rapid proliferation and high cover of the plant in native grasslands under conditions that have been poorly documented and in which the supposed impacts may be due to disturbance. Possibly *N. neesiana* is basically similar to a native grass and replacement of native grasses by *N. neesiana* may have little biodiversity impact. In the following section the atttributes of the temperate native grasslands of south-eastern Australia are examined and the effects of a range of disturbances on *N. neesiana* and the native grasses are discussed in more detail.

GRASSLANDS

Grasses: “... the most important single family of ogranisms in the world of life ...”

G. Ledyard Stebbins (1986 p. 360).

This section provides general descriptions of Australian temperate grasslands and their biodiversity, including their palaeoecology and historical and current disturbance and management regimes, and the features and attributes that make them vulnerable to *N. neesiana* invasion

Definitions of grassland

Grasslands are plant communities structurally dominated by grasses and without trees (Mott and Groves 1984, McDougall 1999). One criterion for a grassland that is widely used in Australia is <10% projected foliage cover of trees, shrubs and sedges in the tallest stratum (McDougall and Kirkpatrick 1994). Another is that the formation supports <1 tree or shrub ha^{-1} (Carter *et al.* 2003). In south-eastern Australia, natural grassland was often bounded by grassy woodlands, defined by a tree cover exceeding 10% or >1 tree ha^{-1}. Defined by structure alone, grasslands cover a very large proportion of south-eastern Australia, but most is sown pasture of exotic plants or secondary grassland developed after the clearing of trees or shrubs from other vegetation types (Yen, Horne, Kay and Kobelt 1994 citing Stuwe 1986, Moore 1993, Benson and Redpath 1997). Native grasslands of course are dominated by native grasses, and grasslands dominated by exotics, whether sown or volunteer, are often classed as exotic grasslands or pastures (Moore 1993).

Evolution of grasslands

The earliest grasslands around the world were probably formed in the Miocene (25-13 mybp) (Tsvelev 1977) and may have been dominated by Stipeae and Arundineae (Jones 1999a). Grasses from most of the major tribes were probably present in Australia before the break up of Gondwana (Jones 1999a). Grasslands dominated by C_4 grasses appeared simultaneously and abruptly c. 7-8 million years ago (late Miocene) in the Americas, Asia and Africa and spread rapidly from equatorial regions due to falling levels of atmospheric CO_2 or climatic change to form “novel grassy ecosystems where forested systems had prevailed” (Bond *et al.* 2008). Low CO_2 at the Oligocene-Miocene boundary may have driven the evolution of C_4 grasses or been a precondition for it (Bouchenak-Khelladi *et al.* 2009). The temperate south-eastern Australian grasslands, dominated by the C_4 *T. triandra*, may well have formed at the same time, but clear evidence of this appears to be currently lacking.

The Tertiary period

Forests covered the vast majority of Australia throughout the Tertiary period (c. 70-2 mybp), including rainforests dominated by *Nothofagus* (‘wet’ rainforest) or gymnosperms (‘dry’ rainforest), and sometimes Cunoniaceae and Proteaceae, and in the late Tertiary by drier, scleropyllous forest (Kershaw *et al.* 1994, Martin 1994, Macphail *et al.* 1994). The first probable *Eucalyptus*, and Cyperaceae pollen indicative of low open vegetation is recorded from the early Eocene (c. 57 mybp) (McGowran *et al.* 2000). Grass pollen first appears in the Australian fossil record in the late Paleocene (58-50 mybp) (Macphail *et al.* 1994, Keith 2004). In south-eastern Australia, fossil Poaceae pollen is first recorded in the early Eocene (Martin 1994). According to McGowran *et al.* (2000) Poaceae first appeared in the Murray-Darling Basin in the mid to late Eocene (c. 43-36 mybp) and in northern Australia in the Miocene (c. 25-13 mybp), but Martin (1994) illustrated early Miocene pollen assemblages from Lake Menindee, Mallee Cliffs, Hillston and Deniliquin, all within the Murray-Darling Basin, that contained c. 20% or more grass pollen, and Macphail *et al.* (1994) noted that Poaceae comprsies up to 2% of pollen assemblages in the Murray Basin during the early-late Oligocene. The early Tertiary palynomorphs are classified as *Graminidites* spp. (Macphail et al. 1994). Grasses present during much of the early Tertiary may have been species found in swamp communities and possibly saltmarsh (Macphail *et al.* 1994).

Grass pollen has been found in the Oligocene (36-25 mybp) (Jones 1999a) and in the probable early-Miocene in Tasmania (Macphail *et. al.* 2004), but until the mid Miocene (c. 19 mybp) is present in quantities too low to suppose the existence of true grasslands (Jones 1999a). Herbaceous communities dominated by Asteraceae and Chenopodiaceae expanded in the inland in the Pliocene (13 mybp +) (Jones 1999a). True grassland vegetation probably began to develop in the inland by the end of the Miocene, c. 5 mybp (Benson and Redpath 1997), following intensifying aridity (Jones 1999a). In the late Miocene to Pliocene “low/open communities dominated by Asteraceae, Chenopodiaceae, Gyrostemonaceae and/or Poaceae communites” existed in northwestern Australian and inland areas (McGowran *et al.* 2000 p. 450). In south-eastern Australia there were “local increases” of grass pollen at this time (Martin 2004 p. 108) suggesting grass presence in open forest formations, but “it is uncertain whether they were dryland or swamp grasses” (Martin 2004 p. 126). Coal and overburden sequences from the Latrobe Valley of Victoria show low values of Poaceae pollen in the late Miocene (c. 15 mybp), then dramatic change in the late Pliocene – early Pleistocene (c. 3-2 mybp) to very high levels of Asteraceae, w ith some Poaceae and little tree pollen except eucalypts, indicating open vegetation, and finally in the Holocene, high eucalypt levels and increased Poaceae (Kershaw *et al.* 1994).

The Tertiary-Quaternary boundary

Dramatic increases of Poaceae pollen through the late Pliocene and earliest Pleistocene were widespread, indicating general opening of the vegetation and the rise to dominance of true grasslands, possibly throughout Australia, but more likely with chenopod dominated herbfields in north-east Australia (Martin 2004). Pollen records show fluctuating abundance, but a general increase of Poaceae and Asteraceae in the Pliocene (13-2 mybp) and very marked increases in the Pleistocene and Holocene epochs (2m -10 kybp), corresponding with a general drying trend, and charcoal in the cores indicates increasing frequency of wildfire, long before aboriginal people occupied the continent (Benson and Redpath 1997, McGowran *et al.* 2000). Sharp increases in charcoal particles, indicative of increasing fire, occur in the Latrobe Valley coal deposits at approximately the

Oligocene-Miocene boundary, c. 36 mybp, while in the eastern Murray-Darling basin fire appears to have been present through much of the Tertiary although markedly increasing in the late Miocene (Kershaw *et al.* 1994). In the south-east, grassland became more dominant during the Pleistocene (3 mybp +), and may have been as widely developed as today by the late Pleistocene (Jones 1999a).

Fossil grass pollen has been identified only to family level (Martin 2004). The fossil record in Australia for the period of greatest interest from the Miocene through the Pleisocene is "very fragmentory" and often difficult to interpret (Kershaw *et al.* 1994 p. 299).

The Quaternary period

Grassland has dominated much of Australia during much of the last 2 million years (the Quaternary period), expanding during long, cooler, relatively dry periods and contracting during warmer, wetter interglacial periods (Kirkpatrick *et al.* 1995, Benson and Redpath 1997, Keith 2004). On the western plains of Victoria more substantial rainforest occurred during interglacials in the mid-late Pleistocene than in the early Pleistocene, the formation expanding from refugia such as the Otway Ranges (Kershaw *et al.* 2000). Glacial-interglacial oscillations occurred throughout the Quaternary and selected for taxa tolerant of drier, cooler climates and repeated climatic change, "linked to disturbances including wildfires prior to and coincident with the arrival of humans" (McGowran *et al.* 2000 p 449). Little speciation of all terrestrial taxa is believed to have occurred in the Quaternary – instead species shifted their distribution in response to the dramatic climate changes (Kershaw *et al.* 2000), and grasslands as a whole would have undergone wide geographical shifts in their extent and location (Jones 1999a), and probably in their composition, since "it is very clear" from the Tertiary fossil record "that taxa, not communities, migrate" (Martin 1994). Hope (1994) however argued that the repeated, rapid destruction of ecosystems due to climate shifts caused extinctions, range fragmentation and rapid speciation, e.g. of *Acacia* spp.

An "extensive grassland steppe vegetation" with Casuarinaceae as the tree component occurred from the late Pliocene-early Pleistocene (c. 2.5 mybp +) and has "no identified modern analogue" (Kershaw *et al.* 2000 p. 494). This inland vegetation had high levels of Poaceae and Asteraceae (Hope 1994) and a major Asteraceae component, with the form taxon name *Tubulifloridites pleistocenicus*, does not correspond with any extant Australia daisy and may have been similar to North American *Ambrosia* and African *Stoebe* (Kershaw *et al.* 1994). Evidence of the dominance of Asteraceae, probably woody, c. 1 mybp has been obtained from a site on the edge of Port Phillip Bay, Victoria, and pollen data from the Pejark Marsh volcano in western Victoria covering the period 1-0.7 mybp indicates Poaceae and Asteraceae co-dominance with Casuarinaceae as the main trees (Kershaw *et al.* 2000). Extensive grasslands existed in north-western Australia and possibly in central Australia in the early Pleistocene (Kershaw *et al.* 2000). Late Pleistocene data from north-eastern Queensland indicates a major increase in Poaceae c. 175 kybp indicates "a major expansion of grassland prior to substantial increases in eucalypts and charcoal" (Kershaw *et al.* 2000 p. 500). A number of currently dominant taxa, notably Pooidae (*Poa* spp.) and *T. triandra* entered Australia from the north during the Pleistocene, but the number of recent migrant taxa is small (Jones 1999b).

The Holocene (Recent)

Lower rainfall and temperatures associated with the last ice age, which ended about 10 kybp, probably saw much of south-eastern Australia dominated by grasslands and grassy woodlands (Jones 1999a).The many vegetation histories that have been established from the fossil record indicate that at the peak of the last ice age, c. 18 kybp, most of south-eastern Australia was dominated by largely treeless vegetation, a very open, cold, dry steppe of Poaceae and Asteraceae with annuals, perennial geophytes and shrubs, and that open eucalypt woodlands were widespread across the Bassian plain (Hope 1994). Montane grasslands, such as those in the Monaro region of New South Wales and the midlands of Tasmania are the best current analogue for these formations (Hope 1994). The current interglacial is unusally warm compared to 85% of the Quaternary, and the lowland grassland communities present have therefore formed largely from the species set that survived the cooler, drier glacials (Hope 1994).

Australian grassland formations

Four main types of grassland occur in Australia: 1. tropical summer rainfall coastal grasslands dominated by *Sporobolus* and *Xerochloa* spp., mainly in the Northern Territory and north-western Queensland, 2. *Triodia* arid hummock grassland of the continental interior; 3. *Astrebla* (Mitchell grasss) grasslands in areas with 200-500 mm average annual rainfall, mainly in summer, in western Queensland, inland northern New South Wales, the Northern Territory and northern Western Australia; and 4. subhumid grasslands of eastern Australia (Specht 1970, Groves 1979, Mott and Groves 1984, Groves and Whalley 2002, Benson 2004). The latter has been subdivided into three types: 4a. tropical subhumid grasslands of eastern and northern Queensland, dominated by *Dichanthium* and *Eulalia* and sometimes by *Bothriochloa* and *Heteropogon*; 4b. temperate grasslands of New South Wales, Victoria and South Australia, dominated by *Themeda triandra*, *Poa* spp., *Austrodanthonia* and *Austrostipa* and 4c. subalpine tussock grasslands of wet tablelands and montane areas of the south east, dominated by *Poa* spp. and *Austrodanthonia* (Groves 1979, Groves and Whalley 2002).

Moore (1993) described a substantially different set of subhumid grassland types present in south-eastern Australia: Temperate Tallgrass dominated by *Themeda*, *Poa* and *Dichelachne*, Temperate Shortgrass dominated by *Austrodanthonia*, *Austrostipa* and *Enneapogon*, Subalpine Sod Tussockgrass dominated by *Poa*, *Themeda* and *Austrodanthonia*, Xerophytic Midgrass (Southern) dominated by *Austrostipa*, *Chloris* and *Aristida*, and Saltbush Xerophytic Midgrass dominated by *Atriplex*, *Maireana* and *Austrostipa*. The Temperate Shortgrass communities are largely derived from woodlands and consisted mainly of taller warm season grasses: in the wetter areas *Themeda triandra*, *Austrostipa bigeniculata* (Hughes) S.W.L. Jacobs and J. Everett and *Poa labillardieri* Steud. and in the drier areas *Austrostipa aristiglumis* and *Themeda avenacea* (F.Muell.) Maiden and Betche. Temperate Tallgrass is a formation corresponding with disturbed forests and heaths and defined by *T. triandra*, *P. labillardieri* and *Dichelachne* spp. (Moore 1993).

Small areas of other grassland types occur including maritime grasslands (on beaches, headlands etc.) and grasslands associated with river margins and freshwater wetlands (reed beds, meadows, cane grass swamps, etc.) (Moore 1993, Carter *et al.* 2003, Benson 2004). Only the humid, temperate, non-alpine grasslands are considered here, since the others are thought to be less susceptible to *N. neesiana* invasion. For example “few weed species have successfully established and persisted” in the Australian Alps, the number declining with increasing altitude (McDougall and Walsh 2007 p. 44). Excluded formations include aforementioned wetland formations and maritime grasslands, the Western Slopes Grasslands of NSW including Moore’s (1993) Xerophytic Midgrass (Southern) and Saltbush Xerophytic Midgrass, Eastern Victorian highlands grasslands (e.g. Lake Omeo), high altitude grasslands of the Monaro region of NSW, and alpine grasslands and meadows. The grasslands that once existed around the shores of Lake Omeo (Benambra area) were similar to those of the Southern Tablelands and were dominated by *T. triandra* (Lunt *et al.* 1998) or *Austrodanthonia* (Kirkpatrick *et al.* 1995), but show clear affinities with high altitude grasslands (Carter *et al.* 2003). According to Kirkpatrick *et al.* (1995) the Lake Omeo grasslands are probably derived from *Eucalyptus pauciflora* Sieber ex Spreng. woodland.

The natural occurrence of temperate grasslands in south-eastern Australia was determined by relatively low rainfall (in the range of 350-1000 mm mean annual, mainly 500-600 mm), flat to undulating topography, and soils that were poorly drained, heavy-textured and moderately to highly fertile (Mott and Groves 1994, Sharp 1997, Jones 1999b, Lunt and Morgan 2002). The geological parent materials produce soil with a high clay content (Jones 1999b). Heavy clay or clay loam soils, and a relatively dry, cold climate “are prerequisites for grassland vegetation worldwide” (Benson and Redpath 1997 p. 307). South-eastern Australian grasslands generally occur on younger soils that have not been heavily leached or become lateritic or infertile, and thus tend to occur where the parent rocks have weathered *in situ* and there is little erosion, and the soils are relatively fertile (Jones 1999b). Most grassland soils have a high water content but low water availability because the clay minerals bind water, and there is little pore space (Jones 1999b).

Some temperate Australian grasslands occurred in the drier areas down to c. 250 mm annual rainfall on the arid margins of chenopod shrublands (Mack 1989) although these are probably better categorised as semi-arid formations (Carter *et al.* 2003). In the Australian Alps, grasslands are generally found on deep humus soils in valley bottoms subject to cold air accumulation and frosts (McDougall andWalsh 2007).

Causes of treelessness

Heavy-textured clay substrates dry out and crack deeply in summer (c. 13% on an areal basis according to Patton 1935) and this may prevent the establishment of trees and shrubs, as may fire, which occurs ubiquitously (Groves and Whalley 2002). Moore (1993 p 353) explained treelessness to be the result of “shallow penetration of water in environments with relatively low rainfall and high evaporation, where tree seedlings would be subjected to intense competition for surface-rooted grasses and other herbaceous species” and in wetter areas “poor aeration following temporary waterlogging after winter rains”. Patton (1935 p. 175) argued that trees can be established artificially on the Victorian basalt plains by “opening up the ground and ... destroying the native vegetation”, so concluded that the native vegetation itself prevented the establishment of tree seedlings. Elsewhere however he argued that heavy textured soils inhibit free entry of water, have slow percolation and bad aeration, that summer cracking leads to deep drying, and that deep rooting is difficult, so it is the physical characteristics of the soil, accentuated by the evenness of contour in the plains that determines their treelessness (Patton 1930). Barlow and Ross (2001) argue that multiple, confounded, variable factors are responsible, with soil charcteristics, particularly drainage, the most important and subsidiary influences from climate and fire. In a trial in the South American pampas competition from tussock grasses prevented establishment of half the tree species tested (Aguiar 2005). Kirkpatrick *et al.* (1995) more or less concurred: tree seedlings are largely excluded by competition in dense grassland swards, which may use all the available soil moisture, and severe disturbances such a soil digging are required for trees to establish.

In the Volcanic Plains Grasslands of western Victoria, where ever any other geological formation abuts basalt, trees occur. *Eucalyptus camaldulensis* grows, for example, where granodiorite is exposed or eroded out of the basalt (Patton 1930). The granite of the You Yangs provides another notable example. Soil chemistry, as well as structure can determine treelessness: soils dominated by sodium, common in northern Victoria, usually lack trees (Jones 1999b).

Distribution of grasslands in the ACT is determined by accumulation of cold air pockets in valley floors, creating conditions that are too cold to permit growth of trees and shrubs (Chan 1980), but low rainfall, heavy-textured soils and the legacy of aboriginal fire regimes are also important (Sharp 1997). Very low temperatures associated with nocturnal temperature inversions have been invoked as the cause of treelessness in subalpine valleys (Moore 1993).

Lowland grasslands

The term “lowland” grasslands, considered to include those formations at altitudes below 1000 m, has been widely used (Lunt 1991, McDougall and Kirkpatrick 1993, Kirkpatrick *et al.* 1995, Sharp 1994, Lunt *et al.* 1998). Prior to European occupation they probably covered c. 2 million ha, of which “perhaps” 10,000 ha survived in “more or less natural” condition by 1992 (Kirkpatrick *et al.* 1995 p. 8). Classifications of lowland grasslands have varied between authors and government authorities and have not always coincided. The New South Wales classification of Benson (2004) has four classes covering sub-humid grasslands, including the Temperate Montane Grasslands, found in the south-east, which include high altitude formations dominated by *Poa* spp. Such grasslands, including those on the Monaro Plains of NSW, are generally excluded from the ‘lowland’ category by most authors. The change from lowland to montane and alpine grasslands is gradual and clinal, so 1000 m is an arbitrary delimination (see discussion in Carter *et al.* 2003).

Secondary and derived grasslands

‘Secondary grassland’ is derived from other vegetation formations, often in Australia from grassy woodland in which trees have been cleared and on which livestock are grazed (Moore 1993, Mott and Groves 1994, Groves and Whalley 2002). Temperate grassy woodlands are also a threatened vegetation type (Benson 2004, Keith 2004, McIntyre and Lavorel 2007) and their grassy stratum may be indistinguishable, for practical conservation purposes, from that of adjoining natural grassland (Carter *et al.* 2003, Keith 2004). Indeed Moore (1993 p. 343) considered that most of his Temperate Shortgrass communities, including most of the Western Basaltic Plains of Victoria, the NSW Riverina and Gippsland Plains, to be “mostly the understoreys of temperate woodlands modified by clearing and grazing by livestock and rabbits”. The grasslands derived from temperate grassy woodlands are frequently also very similar floristically to natural grasslands (Mott and Groves 1994) and can have the same ecological functioning as natural grassland (Groves and Whalley 2002). In some areas derived grasslands are the only grassland remnants (Kirkpatrick *et al.* 1995).

In the absence of grazing, secondary grassland can revert back to woodland or shrubland (Groves and Whalley 2002, Benson 2004). O'Dwyer (1999 p. 324) suggested that livestock grazing had "prevented regeneration of a shrubby woodland" in many derived Victorian grasslands. Distinguishing anthopogenic grasslands is difficult or sometimes impossible because of continuous human influences over long periods (Wheeler *et al.* 1999, Carter *et al.* 2003), as well as long term climatic fluctuation and large scale natural disturbances which can alter plant dominance patterns. Many grasslands in South Australia are derived formations (Davies 1997), and the Riverine Plains Grasslands of south-west NSW were once dominated by *Acacia pendula* A.Cunn. ex Don. and *Atriplex* spp. (Benson 2004, Keith 2004).

The term 'secondary grassland' is generally used to designate formations that are a product of post-colonisation management, or the lack of it. The extent to which grasslands are cultural landscapes resulting from aboriginal land management has generally been treated as a separate issue in Australia, despite overlap between pre- and post colonisation management regimes and species invasions, and despite the "persistent legacies of past human impact on species composition ... structure, disturbance regimes and soil conditions" (Froyd and Willis 2008 p. 1729).

Grassland distribution

Australian grasslands have mostly been well described botanically, but poorly mapped, in particular in terms of their historical distribution (Groves 1979). Moore's (1993, Fig. 13.1) map, which supposedly shows the distribution of "herbaceous communities", derived from other vegetation communities or not, that were then "used for livestock production" and "composed essentially of native species" (Moore 1993 p. 315), seems particularly defective for south-eastern Australia. For example large areas of continuously forested land in eastern Victoria that have never been managed as grazing land are depicted as "Temperate Tallgrass" grassland. His 1993 and earlier maps have probably caused much confusion over a long period.

Remnants continue to be discovered in areas thought previously to have had no grasslands (Cook and Yugovic 2003, Sinclair 2007). Major vegetation mapping in the last 15 years has greatly improved the situation for current vegetation. The pre-European distribution of temperate grassland in south-eastern Australia was recently mapped by Lunt and Morgan (2002), although Kirkpatrick *et al.* (1995 p. 15) thought it was "no longer possible to map much of the pre-European grassland distribution with any accuracy" because so much was rapidly and completely destroyed. Lunt and Morgan (2002) found that temperate grassland was one of the dominant vegetation classes, covering extensive areas, but noted that the 'grassland' status of some areas, particularly in lower rainfall regions, was in dispute (e.g. the NSW Riverina), mainly on the basis that they were recently derived from other vegetation types as a result of land use. The extent to which these grasslands are 'natural' or derived has been an ongoing area of argument. Kirkpatrick *et al.* (1995) considered that the riverine plains grasslands are more correctly called herblands, being often not dominated by grasses, and Groves (1979) considered that temperate grassland "was never very widespread". Benson and Redpath (1997) argue that too much emphasis on the records of early explorers may have resulted in an exaggerated conception of the extent of open grassy vegetation at the time of European settlement, in part because the explorers were typically tasked with finding new grazing lands and preferentially travelled in country that was easier to traverse on horseback. Carter *et al.* (2003) avoid the problems of interpretation of historical information and speculative argument that characterise the debate, by defining a data cut-off of 1982, which excluded only the most recently derived grassland formations.

The somewhat legalistic definition of Natural Temperate Grassland provided by Carter *et al.* (2003), adapted from McDougall and Kirkpatrick (1993), also overcomes some of the other terminological difficulties and areas of scientific dispute. It is a broad vegetation class defined *inter alia* as being dominated by tussock grasses of the genera *Austrodanthonia*, *Austrostipa*, *Bothriochloa*, *Chloris*, *Enteropogon*, *Poa* or *Themeda* or by *Lomandra* (Xanthorrhoeaceae), with <10% projective foliage cover of trees or shrubs or <1 tree ha^{-1}, not cleared of naturally occurring trees or shrubs within the last 20 years, not inundated for more than one month of the year, not dominated by wetland grasses and not noticeably saline, with <70% of the cover consisting of introduced species in spring or <50% at other times, below 1000 m altitude on the mainland and 600 m in Tasmania and receiving a mean annual rainfall greater than 350 mm which is not summer dominated. The salinity criterion is intended to exclude coastal grasslands. They note however that the precision and detail of the definition should not obscure the fact that vegetation is always characterised by tranistional areas that may be hard to classify. With minor exceptions, natural temperate grassland currently occurs as far north as Northern New South Wales to c. 28ºS, as far west as the western Flinders Ranges in South Australia and as far south as Tasmania.

Current distribution patterns of natural temperate grassland is largely relictual and highly fragmented. On public land it is mostly restricted to small remnants of <10 ha, with most large patches (>100 ha) being native pasture on private land (Carter *et al.* 2003, Williams 2007). Most of the species-rich examples of reference grasslands are very small areas that have never been grazed and consist of narrow linear reserves (roadsides and railway lines), or are in cemeteries (Groves 1965 1979, Mack 1989, Morgan 1998d, McIntyre and Lavorel 2007). Other grassland reserves are larger but have generally been grazed by livestock for long periods and have lost significant proportions of their native plant diversity. The high boundary:area ratio of the small reserves intensifies a range of edge effects and increases their susceptibility to various disturbances and to invasion by exotic plants (Morgan 1998d, Sharp 1997, Byers *et al.* 2002, Mathison 2004, Williams *et al.* 2006). In particular, large edge:area ratios increase invasion opportunities from adjacent, usually weedy habitat (Davies 1997), although small, isolated reserves might also be better insulated from invasion pressures (Byers *et al.* 2002). Small size in itself has serious conservation implications, e.g. small areas are more likely to be insufficient to maintain viable population sizes, etc.(Williams *et al.* 2006). The high proportion of large remnants in private ownership creates particular problems for grassland conservation management (DNRE 1997).

There are a number of popular guides to south-eastern Australian grasslands (Scarlett *et al.* 1992, Wigney 1994, Kirkpatrick *et al.* 1995, Eddy *et al.* 1998, Lunt *et al.* 1998, Marriot and Marriot 1998). These mainly concentrate on the flora, but often give much useful background information, including ecological history, managment aspects and information on the fauna. Wigney (1994) focused on ecological restoration of the original plant communities.

Floristic composition, vegetation structure and ecology

"Unfortunately, there exists no really satisfactory description of the vegetation when the grazier first began to exploit the country" (Wadham and Wood 1950 p. 87). Eighty years after exploitation commenced, Schimper (1903 p. 503) noted that there were "no available descriptions of the extensive savannahs and steppes of the interior of New South Wales and Victoria". Some decades later, McTaggart (1936), as part of an Australia-wide 'survey' of pastures, provided a description of the open grasslands (in which he included "savannah", now grassy woodland) of south-eastern Australia, but it is evident from his text and the listed information sources that no detailed compositional and structural knowledge then existed for most areas.

The earliest detailed studies of Australian grassland vegetation, made in the decades preceding 1950, provide "no guide to the proportions of the various species, or the composition of the vegetation from the standpoint of grazing value" of the areas before grazing commenced, but it is known that "profound" changes had occurred, particularly where rainfall was low or highly variable (Wadham and Wood 1950 p. 87). By 1875, for example, the grasslands of South Australia had "mostly disappeared" by conversion to cereal growing (Schimper 1903 quoting Schomburgk 1875). The "lack of adequate description before alteration occurred" (Jones 1999b p. 29) is an ongoing problem. Lunt (1990a p. 47) thought that an accurate representation was "almost impossible", while Lunt *et al.* (1998) considered "any reconstruction of the original vegetation must be somewhat speculative, particularly at a detailed level". The pre-European composition is still considered to be "poorly understood" (McIntyre and Lavorel 2007) but pre-European grassland was probably more diverse than current reference areas, and many species have presumably been eliminated or greatly depleted in most areas (Sharp 1997).

A similar situation exists with the temperate grasslands of South America. One of the first floristic surveys of pampas vegetation was made by L.R. Parodi in 1930 by which time so-called "virgin grasslands" were rare (Soriano *et al.* 1992 p. 381) and after which agricultural development greatly intensified.

Early historical descriptions

One of the earliest Australian descriptions is Schomburgk's (1875, quoted by Schimper 1903 pp. 504-505) portrait of South Australian grasslands, in which the grasses mentioned are already a mixture of native and introduced species, although the forbs appear to be entirely native: "The plains near the coast ... the soil mostly fertile, extending often to the sea ... The grasses consist of more nourishing kinds ... *Poa*, *Panicum*, *Festuca*, *Agrostis*, *Aira*, *Andropogon*, *Cynodon*, *Stipa*, *Pennisetum*, *Bromus*, *Eriachne*, *Anthistiria* [*Themeda*], *Hordeum* ... The banks of the rivers and creeks, which mostly cease running druing the summer, are lined with majestic gum-trees ... the shrubs extending more or less on the plains, according to the nature of the soil ... the appearance ... has during the dry season, the ... sunburnt yellow character ... destitute of all green herbage ... In the month of May the rainy season generally commences ... a few showers change the aspect ...into a green and beautiful carpet ... in a few days the plains appear clothed with luxiarant verdure ... With the grasses are also recalled to new life *Ranunculus* ... *Oxalis* ... *Hypoxis glabella* ... *Drosera* ...*Wahlenbergia gracilis* ... *Anguillaria* [*Wurmbea*]... *Stackhousia* ... Every week adds new colours to the beautiful carpet ... *Kennedya* [sic] *prostrata*...*Swainsona procumbens* ... and *S. lessertiaefolia* [sic] ... *Thysanotus* ... climbing up the dry grass stalks ... Compositae are seen blooming over the plains in all colours ... But by the middle of November the number of flowering plants already lessens considerably, the annual grasses and other herbaceous plants begin to dry up, droop and disappear, and in January the grass land resembles a ripe thinly-sown cornfield, and we find only ... a few plants of *Convolvulus erubescens*, *Lobelia gibbosa* ... and *Mesembryanthemum australe* [?*Disphyma crassifolium*] ... The seeds of the annual plants have been scattered, perennial herbage returned to its dormant state ... and the plains have during the summer months a dismal, dried-up appearance".

The earliest study of note for Victoria is Sutton's (1916-1917) "Sketch of the Keilor Plains flora" at the drier, eastern end of the Victorian volcanic plains. He provided a valuable census of the vascular flora that included species from neighbouring vegetation associations, but deliberately excluded all of the exotic species. Patton (1935) provided a list of vascular plants for Victorian basalt plains grasslands, discussed their structure, composition and seasonal dynamics and the climate and soils.

Contemporary studies

A much greater range of more detailed studies have taken place in the last fifty years, commencing with investigations such as those of Willis (1964) and Groves (1965). These describe grassland generally dominated by perennial tussock grasses including *T. triandra*, *Poa*, *Austrodanthonia* and *Austrostipa* species, with the latter two genera being more dominant in drier areas (NSW Riverina, Northern Plains of Victoria and Northern Lofty region of South Australia) (Kirkpatrick *et al.* 1995, Sharp 1997, Lunt and Morgan 2002). *Bothriochloa*, *Enteropogon* and *Chloris* may also be dominant grasses, while *Lomandra* is the major dominant in some South Australian formations (Carter *et al.* 2003).

Based on readings of historical records *T. triandra* is thought to have been the dominant species across much of the plains before European occupation, although this is based on the assumption that the vernacular term "kangaroo grass" was applied only to *T. triandra* (Lunt *et al.* 1998). *T. triandra* was almost certainly the most widespread and dominant grass (Groves 1965, Mack 1989, Moore 1993, Kirkpatrick *et al.* 1995) and is considered the major dominant in Victoria, but is replaced by *Poa* spp.,usually *Poa labillardieri* Steud. on wet sites and in higher rainfall areas (Willis 1964, Moore 1993, Entwisle *et al.* 1994). *Austrodanthonia* and *Austrostipa* species were the dominant grasses in drier areas including the Murray River plains grasslands and in parts of South Australia (Kirkpatrick *et al.* 1995). Moore (1993) considered A*ustrostipa bigeniculata* was the principal *T. triandra* associate in drier sites. Sutton (1916-1917) found *Austrodanthonia penicillata* (Labill.) H.P. Linder to often be the dominant in drier areas of the Keilor Plains with *Poa*, *Austrostipa setacea* (R.Br.) Jacobs and Everett, *A. semibarbata* (R.Br.) Jacobs and Everett and *Dichelachne crinita* (L.f.) Hook. f. more prominent in moister areas along with "*Panicum*" spp. Willis (1964) found that *Austrodanthonia* spp. became less prevalent in wetter areas. A large proportion of these grasslands have been modified by grazing and became dominated by shorter grasses such as *Austrodanthonia auriculata* (J.M. Black) H.P. Linder, *A. carphoides* (Benth.) H.P. Linder and *Austrostipa scabra* (Lindl.) S.W.L. Jacobs and J. Everett (Moore 1993). Shrubs are rare and substantially absent (Entwisle *et al.* 1994, Lunt *et al.* 1998). Except for *T. triandra*, the dominant grasses have the C_3 photosynthetic pathway and grow mostly in spring and autumn (Groves and Whalley 2002). Most have seeds with an 'after ripening' period (Groves and Whalley 2002) which presumably acts to prevent germination in the dry season (summer) and delay it until adequate soil moisture is more likely to be available for seedling establishment. Annual native grasses are rare.

Groves (1965) found that a very high proportion of the biomass (62-90% varying seasonally), in a *T. triandra* grassland at St Albans consisted of the dominant grass. Usually the *Themeda* tussocks are mostly widely spaced (10 cm or more apart) and grass cover may be only 30-50% (Lunt *et al.* 1998, Lunt and Morgan 2002), but they can be more closely spaced with a canopy of loosely interlaced leaves (Carter *et al*. 2003). Such cover values of dominant grasses appear typical for mid-latitude grassland: for example McArdle et al. (2004) found that the invasive grass *Hyparrhenia hirta* had an average cover of 65.5% in areas where it dominated in open woodlands on the North West Slopes of New South Wales, and caespitose grasses and Cypreacace accounted for >50% of cover in one southern Brazilian grassland (Overbeck and Pfadenhauer 2007). Projective foliar cover of grasses in fire adapted grasslands is obviously highly dependent on the time since fire. One year after fire in *T. trianda* grassland at Derrimut, bare ground was c. 40%; after 2 years this had reduced to c. 25%; and after 3 years had fallen to <2% (Morgan 1998b). According to McDougall (1989) *T. triandra* can attain 100% cover 3-4 years post-fire. Early historical records across a range of areas in Australia in the 1840s consistently indicated *T. triandra* tussock densities of c. 10 m^{-2} (Scarlett 1994). Patton (1935) indicated c. 14 tussocks m^{-2}, with *Notodanthonia semiannularis* (Labill.) Zotov having the next largest cover. This contrasts with much higher densities of *T. triandra* tussocks in conservation reserves that were formerly grazed for many years: minimum densities of 30 m^{-2} in remnants at Organ Pipes National Park and up to 152 m^{-2} at Laverton North Grassland Reserve (Scarlett 1994). Such differences may be explained by the observations of Soriano *et al*. (1992 p. 392) that cattle grazing resulted in subdivision of larger tussocks into multiple smaller plants. However some of the tussock density data should probably be viewed with scepticism: seedling grasses and smaller specimens perhaps not warranting inclusion as 'tussocks' in some studies.

Plants that grow in the intertussock spaces (gaps) account for most of the floristic diversity. Intertussock space is occupied by forbs, smaller grasses and sedges, 'bare ground' and cryptogam crusts (Lunt 1991, Carter *et al.* 2003). What exactly 'bare ground' means is often unclear in published descriptions: it always indicates absence of a above-ground vascular plant cover at the time of observation, but that ground may be vegetated during a different season or more favourable weather periods, and may or may not have a covering of non-vascular plants or plant litter. The critical point is that the vegetation is often relatively open and lacks a continuous canopy. Sutton (1916-1917 p. 116) observed that the Victorian basalt plains grassland does not form a closed carpet as in a meadow, "bare ground being constantly visible". Patton's (1935) diagram of the cover occupied by species in a typical quadrat clearly emphasises the extent of this 'open ground'. Carter *et al.* (2003) suggested that bare ground may be an indicator of extremely low soil nutrient content, the nutrients having been nearly fully incorporated into the dominant grasses. The studies of Wijesuriya (1999) support the proposition that a high proportion of system nutrient is contained in the biomass, but this question does not appear to have been directly studied, and competition for water may be more important. Bare ground above may be fully occupied below ground, and essentially unavailable for plant colonisation.

Plants of the inter-tussock spaces

A high proportion of the vascular plant diversity of Australian temperate native grasslands consists of forbs growing in the spaces between high biomass grass tussocks (Trémont and McIntyre 1994). This interstitial flora contains many species that have wide distribution in other vegetation types (Willis 1964, Trémont and McIntyre 1994), but the pools of local and regional species combine to produce communities with substantial floristic variation. The inter-tussock native vascular plants as a whole are mostly perennial herbs except in the driest regions, where they are annuals, and the perennials are mostly geophytes or hemicryptophytes, with the exotic species mostly (50-76%) annuals (Morgan 1994, Lunt *et al.* 1998, Lunt and Morgan 2002). Worldwide, post-fire non-sprouting, obligate seeders generally represent a small proportion of the vascular flora of the more mesic temperate grasslands, which in general have species lists consiting of a vast majority of post-fire resprouting forbs (Overbeck and Pfadenhauer 2007). In the Victorian Basalt Plains c. 3-14% of native species are annuals, and in the drier grasslands (including the Northern Plains and Wimmera), c. 17-21% (Morgan 1994). Annuals appear to be more generally more diverse in grasslands that are maintained by climatic factors (soil moisture regimes insufficient to support trees), while perennials dominate in fire-dependent grasslands (Overbeck and Pfadenhauer 2007). The perennials of south-eastern Australian temperate grasslands are mostly geophytes or hemicryptophytes, and the annuals are mostly exotic species (Trémont and McIntyre 1994, Lunt *et al.* 1998, Lunt and Morgan 2002). About 70% of plant frequency in temperate south-east Australian grasslands is comprised by forbs (Sharp 1997).

Early historical records indicate an abundance of lilies, orchids, daisies and other forbs (Lunt *et al.* 1998) and the predominant native families apart from Poaceae in modern times are Asteraceae, invariably the richest family in well preserved remnants, and Liliaceae (Sutton 1916-1917, Patton 1935, Willis 1964, Groves 1965, Kirkpatrick *et al.* 1995, Morgan and Rollason 1995, Carr 1999). Exotic Fabaceae are sometimes respresented by numerous pasture species, notably *Trifolium* (e.g. Groves 1965, Dorrough *et al.* 2004), but native peas have mostly proved to be highly sensitive to livestock grazing and have largely disappeared (Kirkpatrick *et al.* 1995). Orchidaceae, Cyperaceae and Juncaceae are the other important families (Trémont and McIntyre 1994). Myrtaceae, Mimosaceae, Epacridaceae and Proteaceae, dominant families in Australia as a whole, are notably largely absent (Sutton 1916-1917, Patton 1935, Willis 1964), although the former two families are often prominent in other vegetation types along watercourses in grassland areas and Epacridaceae appear in the grasslands floras on the southern tablelands of New South Wales and in the Australian Capital Territory (Eddy *et al.* 1998).

Orchids are a particularly sensitive group (Willis 1964, Jones 1999b), subject to elimination by inappropriate fire regimes and livestock grazing, and numerous grassland species are now endangered (Carr 1999, ACT Government 2005, Smith *et al.* 2009).). Sutton (1916-1917) considered them rather rare in the Keilor Plains flora, with few species present, and Willis (1964) stated that no more than one or two of the 24 spp. known from the Victorian basalt plains were not very rare or localised in their occurrence. Fabaceae, Liliaceae and Rhamnaceae are also disproportionately threatened (Kirkpatrick *et al.* 1995).

A high proportion of vascular plants occur infrequently. McIntyre and Lavorel (1994a) found that slightly more than 50% of species detected in 120 quadrats, each 5 x 6 m, in New England Tableands grasslands occurred at <3% frequency, while a further 21% occurred in <10 quadrats. McIntyre and Lavorel (1994b) using the same criterion (<3% frequency) found 91 of 371 species detected were rare natives. Similarly, a disproportionately large number of threatened plant species occur in these grasslands, many in only one or two known populations (Morgan 1997, Lunt *et al.* 1998, Carr 1999) (see below). The rarity of numerous herbs such as *Swainsona*, *Leptorhynchos* and other daisies, may be the result of repeated range contractions due to rapid climatic changes during the Quaternary with associated shifts in vegetation patterns (Hope 1994). Willis (1964) observed that a high proportion of the flora then present on the Victorian basalt plains (including non-grassland formations) had distributions outside the plains, many being ecological 'wides', with only c. 10 spp. restricted to the region. Similarly many plants of the New England Tablelands grasslands have very wide ranges, with the flora as a whole having low habitat specificity (McIntyre and Lavorel 1994a), and it is generally agreed that only a very small number of vascular species are restricted to Australian temperate grasslands (Kirkpatrick *et al.* 1995). The few native annuals present are often very small plants which tend to occur in wet depressions (Lunt *et al.* 1998) and are ephemeral, growing in early spring (Sharp 1997).

Phenology

Most of the plant species in south-eastern temperate grasslands flower mainly in spring, and a substantial proportion also in autumn, "presumably" responding to day length and day temperatures of c. 20ºC (Groves and Whalley 2002), along with soil moisture. A high proportion of the perennials flower and fruit in spring-early summer and have no living parts above ground for much of the year (Lunt *et al.* 1998). All the Orchidaceae fit this pattern, with no above-ground living material during the warmer months (Smith *et al.* 2009). Patton (1935) considered October-November to be the peak flowering period for grasses and other plants in the Coburg to Melton area of the Victorian basalt plains. He and Willis (1964) noted that the major flowering period corresponds with the time that evaporation begins to exceed precipitation. Sutton (1916-1917) observed that many species were in flower long before the end of winter (31 August). Groves (1965) found that nearly half the species present at St Albans flowered in October and November, with similar patterns for exotic and native species. Most of the grasses in the Victorian basalt plains flower in November (Willis 1964). Yellow-flowered daisies were a prime feature in spring (Sutton 1916-1917) but are now greatly depleted. Chan (1980) recorded the flowering periods of 61 native species at Yarrumundi Reach, ACT, and found that 33 species flowered in September, 51 in October, 49 in November, 32 in December, 28 in January and 7 or fewer species in every other month. Exotic species also showed a marked flowering peak in October and November.

As moisture levels decline the flowering period rapidly ends and "most of the vegetation passes into a resting stage until the following autumn" (Patton 1935 p. 172), being practically dormant from December to April (Willis 1964), with vegetative growth recommencing after autumn rains and continuing slowly during the winter. Summer rains may stimulate growth of many species. Morgan (1995b) for example observed rapid growth of juvenile *Rutidosis leptorhynchoides* after summer rains.

Information on the germination and establishment periods of most species appears to be lacking , possibly because recruitment events are rare. Morgan (1995b) found that *Rutidosis leptorhynchoides* seeds germinated 8-12 days after the first major autumn rains and continued to germinate through until early July.

Plant species richness

The richest terrestrial plant communities in Australia include the kwongan of south-western Australia with up to 103 vascular species in 0.1 ha and the herb-rich woodlands of western Victoria with up to 96 spp. in 0.1 ha, 93 species in 128 m^2, and 45 spp. m^{-2} (Lunt 1990d). The richest communities in the world have traditionally been considered to be the European chalk grasslands, with a maximum of 54 spp. m^{-2} (Lunt 1990d). One recently burnt grassland in the vicinity of Porto Alegre, southern Brazil, had maxima of 28 vascular spp. per 0.25 m^{-2}, 34 per 0.75 m^{-2} and approximately 450 spp. in 220 ha (Overbeck et al. 2007).

Vascular plant species richness in Australian temperate grasslands shows considerable variation across the range of spatial scales, but native richness is strongly related to the historical disturbance regime, particularly burning and grazing (Kirkpatrick *et al.* 1995, Dorrough *et al.* 2004). At the regional scale, Willis (1964) considered the Victorian Basalt Plains flora to be floristically 'deficient' in comparison with other regions of the State. However communities in this region can nevertheless be species rich at a small scales (Morgan 1998e). Sutton (1916-1917 p. 117) considered that the vegetation of typical Keilor Plains grasslands contained "some hundred or more species".

Patton (1935) calculated a species/area curve for basalt plains grassland and found an average of c. 8-9 species present in 1 m^2, rising to c. 14 spp. in 5 m^2, and to c. 17 spp. in 10 m^2 with a total of 45 spp. in all quadrats, and 73 species comprising the whole flora. A relatively high proportion of species occurred infrequently, or were only very sparsely present. Stuwe and Parsons (1977) found species richness of c. 12-18 m^{-2} in Victorian basalt plains grasslands. Kirkpatrick *et al.* (1995) considered it common for more than 40 native species to occur in an area of 100 m^2. Morgan (1998e) recorded 22 spp. in 0.25 m^{-2} and 27 spp. m^{-2} in some species-rich Victorian basalt plains remnants and total species data for two ungrazed roadside sites – 71 native and 22 exotic species in annually burnt site and 67 native and 19 exotic spp. in a bienially burnt site. Other data includes Groves (1965) study along the railway line at St Albans - 101 spp. including 64 natives; Evans St., Sunbury, c. 11-17 species m^{-2} (Morgan 1998d) and c. 103 species present in quadrats with 48 additional spp. recorded in 3.5 ha (Morgan and Rollason 1995); Derrimut Grassland Reserve, a 154 ha "species-poor" remnant with "a long history of domestic stock grazing and little or no recent burning" (Morgan 1998c) 102 native and 78 exotic species in the above-ground vegetation (Lunt 1990a) with 1 additional native species and 3 exotics found only in the soil seed bank (Lunt 1990b); five Victorian volcanic plains *T. triandra* grasslands with a range of historical fire frequencies (1 y, 3 y, >10y) and a total area of 32 ha surveyed in 1993-95 (Morgan 1998c) – 61 native and 30 exotic spp. in the vegetation, 32 native and 28 exotic in the soil seed bank of which 11 were not present in the vegetation; the same five sites plus an additonal one, all surveyed in August 1998 (Morgan 2004) – a total of 69 spp. from a single 150 m^2 quadrat at each site; New England tablelands an average of 19.9 native species in 30 m^2, with a maximum of 28 and minimum of 1 (McIntyre 1993); native pasture on the New England Tablelands (Chiswick) 124 species in 2.4 ha of which 26 were grasses, 11 Cyperaceae + Juncaceae and 87 other forbs, with a range of 4-26 spp. and means of 11-16 spp /0.25 m^2 in grazed areas and range of 1-9 and means of 3-4 spp./0.25 m^2 in grazed areas (Trémont 1994); 39 natural grasslands in the ACT - 191 spp., 56% forbs, including 10 native grass spp., with a range of 23-56 spp. in ten 1m^2 quadrats (Sharp 1997). On the Monaro Tablelands of New South Wales Dorrough *et al.* (2004) found mean plant species richness of 11.7, 12.6 and 15.7 species 0.25 m^{-2} in native pastures, on roadsides and in travelling stock routes respectively, with the richness of native species being 5.0, 7.8 and 8.6 and of exotic species 6.7, 4.8 and 7.1 respectively, with a total of 120 species in 100 m^2. Kirkpatrick *et al.* (1995) calculated a total of 771 vascular species in 77 families in the south-eastern lowland grasslands. In high-richness sites natives grasses are always the dominant species, whereas low-richness sites may be dominated by exotic or native Poaceae (New England tablelands, McIntyre 1993). The grasslands of the Victorian Volcanic Plains were generally floristically rich (DNRE 1997) but considerably less diverse than those of herb-rich grassy woodlands in the Grampians and Langi Ghiran areas of western Victoria studied by Lunt (1990d).

Areas of grasslands on sedimentary soils and soils derived from granites, which are generally less fertile, are less productive so grow much smaller grass tussocks and consequently tend to have greater floristic richness (Stuwe 1994).

Productivity

Little attempt appears to have been made to quantify the productivity of the temperate native grasslands of south-eastern Australia, although there has been considerable interest in the amount of above-ground biomass accumulated by dominant grasses, particularly *T. triandra*. In minimally disturbed (ungrazed and unburnt) communities the matrix species (dominant and subdominant grasses) grow large, accumulate abundant litter and suppress the intertitial forbs (Trémont and McIntyre 1994).

Groves (1965) undertook a seminal study of a *T. triandra* grassland at St Albans. He determined the above-ground biomass of *T. triandra* versus all other species and the root biomass for all species combined at 3-6 weekly intervals for 15 months from 1962 to 1964. The grassland had been burnt in the summer of 1961-62. *T. triandra* constituted the major component of above-ground biomass througout the period, with a mimimum of 62% and a maximum of 90%. The standing biomass one year after fire was about two thirds of that two years after the fire, but nevertheless fell to approximately the same level in summer in successive years. Standing biomass fell rapidly to very low levels in mid summer after a late spring- early summer peaks. Maximum levels exceeded 3000 kg ha^{-1}. Much dead biomass was apparently broken down or moved off site. Only a small fraction of root biomass penetrated below 15 cm. The below-ground biomass followed similar trends to that above ground in one summer and not the other, but consistently peaked in late spring and early summer. The maximum was c. 8000 kg ha^{-1}. In autumn, rapid growth resumed, many seedlings appeared and a carpet of moss developed. Standing biomass in April was etimated at 1025 kg ha^{-1}. During winter, growth was inhibited and many shoots of *T. triandra* died, but *Austrodanthonia* spp., *Dichelachne crinita* and the exotic annual grass *Rostraria cristata* (L.) Tzvelev grew vigourously. In spring rapid growth of *T. triandra* resumed and the native forbs *Eryngium ovinum*, *Plantago varia* and *Wahlenbergia stricta* grew. Growth ceased when soil moisture fell to the permanent wiliting point. *T. triandra* growth rate peaks from October to early December and growth continued into summer if there was adequate soil moisture, and there was a minor peak in autumn.

Morgan (1998e) calculated annual peak standing biomass for two *T. triandra* grasslands in the Victorian Volcanic Plains: 1300 kg ha^{-1} in December for a grassland at Derrinallum burnt annnually in February, and 2600 kg ha^{-1} for a grassland at Karrabeal, burnt biennially in summer, two years after burning. Annual dry matter production in improved pastures in the New England region of New South Wales varies from c. 8000 kg ha^{-1} in drought years to 16,000 kg ha^{-1} (Davidson 1982). Estimates for net above-ground primary productivity of Flooding Pampa grasslands include 5320 kg ha^{-1}, with green standing crops of 1550-2220 kg ha^{-1} (Soriano *et al.* 1992).

Dynamics

The dynamics of temperate Australian grasslands cannot be adequately explained within the classical botanical framework of succession, and there is no climax formation (Mott and Groves 1994). If the exotic components are disregarded, the composition varies little over time, but widely on a patch scale in otherwise uniform areas (Mott and Groves 1994). Morgan (1998e) investigated patch-scale (0.01 and 1 m^2) dynamics of exotic and native vascular species in Victorian volcanic plains grasslands and found a 50% increase in cumulative species richness over 4 years, involving high turnover rates and high spatial mobility of species, but little variation in mean species richness. Life-form characteristics were the main determinants of the patterns of plant movement: annuals and geophytes tended to have higher turnover and mobility while hemicryptophytes often had low turnover. The few species with large, persistent seed banks had high turnover, including exotic annual grasses. High turnover of geophytes was somewhat illusory, being explained by their frequent dormancy and failure to produce above-ground parts, but this ‘pseudo-turnover’ was displayed by c. 30% of species (Morgan 1998e). Such pseudo-turnover might be particularly significant with Orchidaceae, which may remain dormant for several years (Smith *et al.* 2009). About 40% of species had low mobility at the 1 m^2 scale (Morgan 1998e).

‘Dispersal limitation’ at a range of scales is a feature of many native grassland systems (MacDougall andTurkington 2007) and may in part result from loss of native animals that created safe sites for seedlings and dispersed seed, and low fecundity due to loss of native pollinators. Frequent fire has been suggested to be the most important cause of the mobility patterns in Victorian volcanic plains grasslands, but climatic variation may be important for some species (Morgan 1998e). Management history and ‘chance’ appear to be more important determinants of the status of a particular remnant than recurrent major disturbance (Mott and Groves 1994). The absence of a successional climax means that the dynamics of Australian temperate grasslands are best described by ‘state and transition’ models, with disturbance and management regimes determining the dynamics of the plant components. These are discussed in detail below.

Areas of bare ground at sites with low vascular plant richness are mostly due to exogenous disturbance, while at sites with high richness, they are more often the result of constrained production (McIntyre 1993) due to near-complete resource utilisation. Sharp (1997) created 1 m^2 areas of bare ground experimentally using glyphosate herbicide in Dry *T. triandra* and *Austrodanthonia* grasslands and studied colonisation of the gaps for 18 months. Native grass cover had not recovered to pre-treatment levels after 18 months, while exotic grass cover and richness initially increased, but after 18 months decreased to levels similar to those prior to treatment. Native and exotic forb richness and cover was increased. Sharp (1997) also experimentally removed litter in areas dominated by native grasses and tested combined treatments of gap formation by herbicides, litter removal/retention, and soil disturbance (scarification to 2 cm depth). When plant litter was retained, native forb richness and cover were higher than when litter was removed. The opposite response was found for exotic forbs. Soil scarification had no significant effects on recruitment of species.

The dominant native grass can reduce species richness in intertussock spaces (McIntyre 1993). This is a common feature of temperate grasslands around the world: in the absence of biomass reduction by fire or grazing, the highly productive dominant casepitose grasses accumulate dead leaves and litter and gradually exclude forbs, “irrespective of their habitus” (Overbeck and Pfadenhauer 2007). Intertussock spaces disappear in *T. triandra* grasslands not subject to regular biomass reduction because the *T. triandra* plants accumulate large canopies of dead leaves, which reduce and eventually eliminate bare ground and intertussock space (Stuwe and Parsons 1977, Morgan 1995b, Morgan 1997, Morgan 1998b, Henderson 1999). *T. triandra* is generally the only native plant with high cover and frequency and most native species have low cover and low frequency (Morgan and Rollason 1995). Germination of a high proportion of species requires exposure to light, but otherwise there are no specialised germination requirements in the majority of species (Robinson 2003). Regular opening of canopy gaps, e.g. by burning, is required for forb seedling recruitment (Morgan 1995b, Sharp 1997), but actual removal of vegetation, with associated soil disturbance is probably even more effective (Robinson 2003). The dominant tussock grasses may not only command most of the space and light but may also starve the intertussock species of moisture and nutrients (Keith 2004). *T. triandra* has been said not to compete directly for resources with the annual (exotic) grasses (Morgan 1994), but agricultural experience suggests that the exotic annuals deplete soil moisture prior to the main *T. triandra* growth period. Germination and establishment of *T. triandra* has also been reported to be unaffected by weeds (McDougall 1989, Morgan 1994 citing Hagon 1977) but there is likely to be a threshold above which it will be affected (Morgan 1994).

None of the native perennial intertussock species in existing native temperate grasslands are obligate seed regenerators, almost all being obligate resprouters, or resprouting and with limited seedling production, and mostly able to set, and actually setting, seed within 12 months of regeneration (Lunt 1990c, Morgan 1996, Lunt and Morgan 2002). Austral Toadflax *Thesium australe* R.Br. (Santalaceae) a peculiar semi-parasitic semi-shrub, once common in *T. triandra* grasslands, has a ruderal strategy, is short-lived (Keith 2004) and apparently dependent on annual seedling recruitment, but populations no longer exist at lowland grassland sites (Scarlett and Parsons 1993). Hosts of this species include *T. triandra* and a range of other native and introduced herbs and grasses (Keith 2004). At sites investigated by Morgan (1996) all perennial species but one had flowered 12 months after a late-spring fire. Only 19% of native perennials regenerated from seed after a fire at Derrimut (Lunt 1990c) and only one native species was present in the seed bank that was not found in the standing vegetation (Lunt 1990b). In a study of five western Victorian grasslands Morgan (1998c) found that only 12% of species, all annuals, formed large, persistent seed banks and that most native hemicryptophytes and perennials in general had a transient seed bank. *T. triandra* and perennial native forbs were present in the seed bank at "exceedingly low densities at all times" (Morgan 1998c p. 150).

Little is known about the persistence of native forbs in temperate Australian grasslands (Lunt 1996). Morgan (1995) found viable seeds of *Rutidosis leptorrhynchoides* in the seed bank only immediately after seed shed. All the seed of this species germinated within 4 months of shedding, immediately after autumns rains, and any seed that had not germinated by this time was either dead or had been "eaten by soil invertebrates" (op. cit. p. 5). Lunt (1996) found that no viable seeds of *Microseris scapigera* (G. Forst.) Sch. Bip. (Asteraceae) buried or placed in mesh bags under the canopy in a long unburnt *T. triandra* grassland in Canberra remained after 3 months and that virtually all germinated rapidly. Lunt (1995a) tested seeds of three native lilies and three other native daisies in the same way and found that >90% of the seeds of all but one species germinated or were unviable after 12 months, although greater longevity was recorded for some species if the seed was buried or on the surface. The daisy *Chrysocephalum apiculatum* (Labill.) Steetz. appeared to have the highest potential to develop a persistent seed bank, due to small seed size, inhibition of germination in darkness and an ability to remain viable when buried. The perennial native plant seed bank as a whole appears to usually be small and highly transient (Lunt and Morgan 2002), seedlings are generally uncommon (e.g. Morgan 1998d), most seed germinates or dies within 12 months, and only perennial forbs with small seeds (e.g. *Hypericum gramineum*, *Juncus* spp., *Wahlenbergia* spp.) have large, persistent seed banks (Lunt and Morgan 2002). The long-term native seed bank was considered to probably have "little functional importance" and "contribute little to seedling regeneration processes following disturbance" (Morgan 1998c). Scarlett (1994) reported a similar problem with plantings and direct seeding of native dicotyledonous grassland herbs: they set abundant seed, but had very low germination and seedling survival.

Species with transient seed banks are a common feature of world grasslands and "are normally able to exploit gaps in grassland canopies ... created by seasonally-predictable disturbances such as fire, drought and grazing": their seeds usually germinate whether or not suitable seedling establishment sites are available (Morgan 1995a p. 7).

In basalt plains grassland sites with a history of frequent fire the hemicryptophyte ('resprouter') rosetted forbs, including many of the common native forbs, had low turnover and mobility (Morgan 1997), as would be expected with a very low seed bank (Morgan 1998c). In total, 30% of species (notably geophytes) appeared to remain dormant underground in some years, despite a stable management regime (Morgan 1997). A high proportion of the seed bank in these grasslands consists of annuals which are largely exotic species (Morgan 1998c 1998d, Lunt and Morgan 2002). The annual monocots have a high turnover and high mobility (Morgan 1997). Native hemicryptophytes, chamaephytes and geophytes are largely absent from the seed bank (Morgan 1998c). Exotic species overwhelming dominate the soil seed bank in grazed grasslands in Victoria and Tasmania, with annual grasses, legumes and *R. rosea* being major components (Lunt 1995a). Dodd *et al.*(2007) found that native species comprised only 13% of the soil seed bank of six roadside grasslands along a 200 km urban-rural gradient west from Melbourne and that similarities between the species composition of the seed bank and the above ground flora was low and declined in more rural sites. Exotic annual graminoids dominated the seed banks (Dodd *et al.* 2007) with *Juncus capitatus*, *Isolepis* sp. and *Aira* spp. being the most abundant (Aaron Dodd pers. comm. October 2007).

Lack of recruitment of inter-tussock species is a widespread problem in native grasslands: inadequate seed availability appears to be the dominant cause, rather than weed competition or climatic stress (McDougall and Morgan 2005). Many species of native forbs may be physiologically unable to produce seeds with innate dormancy (Morgan 1998c). Instead the plants are long lived and rarely recruit from seed. According to Benson (1994) the major transformation of native grassland have resulted in widespread loss of long-lived, deep rooted perennials and their replacement with more ephemeral exotics.

The native grassland flora is also notable for the absence of myrmechorous (ant dispersed) species, in contrast to Australian forests, woodlands and heaths (Berg 1975). Very few of the 87 myrmecochorous genera mentioned by Berg (1975) are present in these grasslands and these may be viewed usually as 'trespassers' from grassy woodlands. In general however seed dispersal processes in these grasslands have not been studied.

Based on a study of a three Asteraceae in New England Tablelands grasslands, a rare native *Microseris* sp., a rare to common native *Cymbonotus lawsonianus* Gaudich. and an abundant exotic *Hypochoeris radicata* L., McIntyre (1995) argued that many native grassland forbs must have highly specific ecological requirements for regeneration that are rarely being met under current mangement regimes, and that many of these requirements might possibly be met by the types of exogenous disturbances often considered to be harmful management practices. For example, a suite of endangered grassland forbs appear to require soil disturbance, although the general result of soil disturbance is a decline of rare native species and enhanced cover of exotics (McIntyre 1995). This apparent paradox may be best resolved by determination of the type and nature of 'natural', endogenous grassland disturbances that have been lost, or now occur in few areas or at a different frequency (e.g. soil disturbance by marsupial foraging or burrowing), and by more detailed examination of processes and disturbances that occur in a range of marginal habitats in which rare and uncommon species persist or from which they have disappeared.

Morgan (1998) investigated germination responses of many of the forbs, none of which are promoted by darkness (i.e. seed burial) (Groves and Whalley 2002).

Robinson (2003) compared the survival of planted seedlings of *Podolepis* sp. 1 and *Bulbine semibarbata* in disturbed and undisturbed soil of a Victorian basalt plains grassland. Much greater survival of seedlings occurred on the disturbed soil. In the same grassland, Reynolds (2006) compared the establishment of seedlings of five native forb species (*Podolepis* sp. 1, *Ptilotus spathulatus*, *Velleia paradoxa*, *Rutidosis leptorhynchoides* and *Pycnosurus chrysanthes*) after surface sowing of seed and planting of seedlings on disturbed and undisturbed soil. Plots were treated with mowing, raking, repeated herbicide treatments over a period of a few months and fire to remove all above ground plant biomass prior to sowing. The disturbed soil was dug with a spade to a depth of at least 20-30 cm. Six months after sowing the proportion of seed that produced established seedlings on undisturbed soil did not exceed 2%, while in disturbed soil the proportion that established was 2-65%. Four species grown on disturbed soil flowered, but all seedlings on undisturbed soil remained very small. Mortality of seedlings after six months was greater on undisturbed soil (54% survival) than disturbed soil (80%) and significantly different for three of the four species for which there was adequate data. All species grew significantly taller and wider in disturbed soil. Soil digging created an abundance of suitable microsites for seed germination, whereas the smooth compacted surface of the undisturbed soil provided very few. Seedlings of exotic weeds originating in the soil seed bank had to be continuously removed from the disturbed plots during the period of the study but no data about them was provided. Reynolds concluded that the germination of both native forbs and exotic weeds would be promoted by such soil disturbance.

Soil disturbance affects the population dynamics of the native forbs in a range of ways that remain poorly understood. Soil disturbances increase seed incorporation into the soil, which advantages some species and not others. Lunt (1995a) found that buried seed had significantly greater survival than unburied seed for three of the species he tested. Some species exhibited major differences in the timing of germination between buried and surface seeds, while others did not.

Particular disturbances or disturbance regimes always favour a subset of native species and disadvantage some species. A changed disturbance regime is small remnants normally results in the disappearance of some species which are unable to recolonise because of the now highly fragmented geographical distribution of remnants (Kirkpatrick *et al.* 1995).

A vegetation assessment protocol that enables the classification of native grasslands on the basis of their botanical signficance has been devised for use in the Australian Capital Territory (Sharp 2006). A grassland is characterised as native if >50% cover consists of native species. The botanical significance rating (BSR) depends on the level of vascular plant species richness (very low, low, moderate, high, very high) and the presence of very common, relatively common, less common and uncommon native species, which in turn are very tolerant, moderately tolerant, sensitive or highly sensitive to anthropogenic disturbances. Grasslands with the highest BSR have several to many representatives from each of these native species groups including the most disturbance-sensitive taxa. The systems has been used for conservation planning in the ACT.

Non-vascular plants and fungi

Bryophyta (mosses), Hepatophyta (liverworts) and Anthocerophyta (hornworts), collectively known as bryophytes (Meagher and Fuhrer 2003) provide another component of biodiversity in south-eastern temperate grasslands. Bryophytes of Australian native grasslands are relatively poorly studied, e.g. Meagher and Fuhrer (2003) provided lists of genera for numerous habitats and vegetation formations, but not for native grasslands. The bryophytes along with lichens (symbiotic associations of algae or cyanobacteria with fungi) and algae, collectively known as cryptogams, are found on exposed rock surfaces but are more prevalent on the soil surface, forming what is known as the 'cryptogam crust' (Scarlett 1994), or where lichens are largely lacking, the 'bryophytic mat' Morgan 2004). This acts to restrict soil erosion and increase water infiltration (Lunt *et al.* 1998 p. 11). Many of the lichens fix atmospheric N (Lunt *et al.* 1998) and biological soil crusts also contribute significantly to C fixation (Morgan 2004). The lichen crust reportedly becomes apparent after the inter-tussock forbs die back (Kirkpatrick *et al.* 1995). Effects of the soil crust on shed seed and seedling germination differ between plant species (Morgan 2004). It can provide "a foothold for germinating seedlings" (Lunt *et al.* 1998 p. 11) but commonly restricts seedling establishment by limiting contact of the radicle with mineral soil (Mack 1989).

Cryptogam diversity in native grasslands has rarely been studied, but where it has, it has it has been found to be highly variable, e.g. there were at least 32 species at Evans St., Sunbury, but only 3 at Derrimut (Morgan and Rollason 1995) perhaps in part due to the 'overdominance' of *T. triandra* at the latter site (Lunt 1990a) and its long history of grazing. Soils crusts are poorly developed also at other previously grazed grasslands – Organ Pipes National Park and Laverton North Grassland Reserve (Scarlett 1994). Willis (1964) found a total of about 85 species in the Victorian basalt plains flora, markedly less than in non-grassland areas of the State. Scarlett (1994) found that railway reserve grasslands were dominated by mosses and liverworts, rather than lichens. Morgan (2004) surveyed six *T. triandra* grassland remnants on the Victorian volcanic plains and found a total of 19 mosses and 8 liverworts of which 9 were present only at single sites. The richest site has 10 mosses and 7 liverworts in 150 m^2, the poorest had 6 mosses and 3 liverworts in the same area. Again lichens were uncommon.

Like vascular plant diversity, community richness appears to be highly dependent on past management. Morgan (2004) found that sites burnt at 1-2 yr intervals had lower diversity in the bryophyte mat than those burnt at 4-20+ year intervals, apparently due to loss of mosses. The liverworts *Fossombronia intestinalis* Taylor and *Lethocolea pansa* (Taylor) G.A.M.Scott and K.Beckmann, and the moss *Rosulabryum billardieri* (Schwaegr.) Spence occurred at all sites and were considered to be adapted to fire at all frequencies. Morgan (2004) found a strongly significant positive correlation between the cover of *T. triandra* and the species richness of the bryophyte mat, but no correlation with vascular plant species richness.

Based on observations of ungrazed and grazed native grassland reserves and experimental studies by other workers Scarlett (1994 p. 127) determined that the cryptogam crust in *T. triandra* grasslands “delays the establishment of some alien weeds and minimises their cover/abundance when they are already established”. In south-eastern Australia, invasions of *Holcus lanatus*, *Briza maxima*, *Bromus hordeaceus* and *Vulpia* spp. are facilitated by crust damage. Soil crusts dominated by brypophytes have been found to delay or inhibit germination of some plants by affecting the penetration of light and its spectral characteristics, and through leachates, and the crusts also maintain a more humid environment at ground level. They increase the time a seed spends above ground, increasing its probability of predation, dessication or destruction by fire, although awned seeds, including those of *N. neesiana*, are less affected. They also could be expected to restrict root growth of any seedlings that do germinate (Scarlett 1994). Davies (1997) noted that seeds of native plants are generally better adapted to penetrating cryptogam crusts than those of many grassland weeds.

The commonest components of the soil crust in Victorian volcanic plains grasslands include the prostrate leafy and thallose liverworts *Riccia* spp., *F. intestinalis*, *F. pusilla* and *L. pansa*, the mosses *R. billardieri*, *Fissidens* spp., *Tortella calycina*, and the squamulose lichen *Cladia* sp. (Scarlett 1994, Morgan and Rollason 1995, Morgan 2004). Large mosses including *Bruetelia affinis*, *Triquetrella papilata* and *Campylopus clavatus* occur mainly around the bases of *T. triandra* tussocks and create denser cover, while *Polytrichum juniperinum* and various liverworts occur on stony rises. The basalt rocks are occupied by thallose and crustose lichens. Drier sites tend to have a crust dominated by crustose lichens and algae (Scarlett 1994). Thick moss mats are relatively rare and there is relatively little variation in composition of the crust over the 500-600 mm rainfall zone (Scarlett 1994). Non-vascular plants accounted for 25% of plant diversity at Evans St., Sunbury (Morgan and Rollason 1995), 28% at six sites surveyed by Morgan (2004) and 13.5% for the Victorian basalt plains flora as a whole (Willis 1964).

The non-lichenised fungi constitute another diverse element of the biota but little specific information related to Australian native grasslands appears to be on record. Fuhrer (1993) noted that some species are restricted to grasslands and recorded *Lycoperdon* spp. and *Xerula australis* (H. Dorfelt) R.H. Peterson from grasslands. Slime moulds (Protocista: Myxomycota) are similarly poorly known. Most fungi species are very small, a high proportion are undescribed and identification is difficult. Öster (2008) concluded from a study of semi-natural grasslands in Sweden that there was probably low congruence bewteen vascular plants and grassland fungi and that some grasslands with low plant richness can have high macrofungi richness. Many plant pathogenic fungi occur on grassland plants, notably on grasses, which are infected by a range of smuts, rusts and endophytic fungi.

Endophytic grass fungi

Grass endophytes, *Neotyphodim* spp., have not been found in 13 genera of Australian native grasses investigated, including *T. triandra*, *Microlaena stipoides*, *Austrodanthonia* spp., *Chloris* spp., *Poa* spp. and *Bothriochloa macra*, except for an unknown species in *Echinopogon ovatus* (G. Forst.) P. Beauv. and *Neotyphodium*-like hyphae in herbarium species of other *Echinopogon* species (Aldous *et al.* 1999).

A *Tilletiopsis* Derx. fungus, related to smut fungi, has been isolated from seeds of *Austrodanthonia pilosa* (R.Br.) H.P. Linder; an *Acrodontium* De Hoog. sp. from seeds of *Chloris ventricosa* R.Br., a species similar to *Neotyphodium* from seed of *Austrodanthonia racomosa* (R.Br.) H.P. Linder, and the seed-transmitted *Atkinonella hypoxylon* (Peck) Dell is common on a range of *Austrodanthonia* spp. (Aldous *et al.* 1999).

Soil microflora

The soil microflora of the temperate native grasslands of south-eastern Australia also appears to have been little investigated. Such floras consist mainly of bacteria and fungi that decompose organic matter and those that form symbiotic relationships with plants (Keane 1994). The vast majority of plants form sysmbioses with soil fungi via their roots, known as mycorrhizae. Many grasses and herbs form vesicular-arbuscular mycorrhizae with zygomycetes, that are characterised by “little bush-like growths inside the root cells and large, swollen vesicles within the roots”(Keane 1994 p. 132). The fungi have never been grown in pure culture and they benefit by gaining sugars from the plant while assisting plant P uptake. Orchids form more complicated symbioses with *Rhizoctonia* fungi. Legumes form associations with *Rhizobium* bacteria that are important N fixers. Some herbs and liverworts form associations with cyanobacteria that are capable of fixing atmospheric N (Keane 1994). The soil also contains parasitic microbes which can cause new plant disease problems when the soil is disturbed. Manipulation of the soil microflora is widely practiced in agriculture, but has been little investigated in Australian native vegetation, except in regard to orchids (Keane 1994). Exotic soil microbes may be important in south-eastern grasslands, but the best known species in Australia *Phytophthora cinnamomi* does not appear to cause problems.

Exotic plant components

The criterion of <70% exotic cover in spring or <50% cover at other times of the year in the definition of natural temperate grassland is intended to exclude areas such as pastures and urban wastelands that have only a minor native plant component (Carter *et al.* 2003). In practice it is difficult to apply, and highly dependent on the scale of assessment, since patchy areas of dense weed growth in remnant native grasslands are common, and cover under fire and grazing management regimes is highly variable. Perhaps what is meant, or what should be meant, is the proportion of vascular plant cover.

Exotic plants are now present almost universally in temperate Australian grasslands, and include a wide diversity of annual, biennial and perennial forbs, annual and perennial grasses, and occasionally some shrubs and trees (Trémont 1994, Kirkpatrick *et al.* 1995, Sharp 1997, Eddy *et al.* 1998, Groves and Whalley 2002, Carter *et al.* 2003, Dorrough *et al.* 2004). Carr *et al.* (1992) ranked fifteen broad vegetation formations in Victoria on the basis of the numbers of weed taxa and “very serious” weeds recorded in them. Lowland grassland and grassy woodland were ranked highest with 344 taxa of which 87 were considered very serious. Between one quarter and one third of the flora in each of the main grassland regions consists of exotics (Kirkpatrick *et al.* 1995). Weed invasion is a major problem for survival of the native flora. Dicotyledonous herbs are the most threatened group (Groves 2004). Weed diversity and dominance at grassland sites is often high. For example McIntyre (1993) found that 97% of samples in New England tablelands native grasslands in 1990-91contained exotic species. Trémont (1994) found that secondary grasslands in that area were composed of 27% exotics in areas ungrazed for 16 years and 32% in grazed areas, with exotics comprising 50% and 43% of the grasses in the two treatments respectively. In the Monaro region exotics accounted for an average of 35% of species, and sites on the Southern Tablelands generally had >20% exotic cover in spring (Sharp 1997). According to Kirkpatrick *et al.* (1995), the high invasibility of grasslands is probably related to their high soil fertility. McIntyre and Lavorel (1994a 1994b) reported declines in native species richness and increases in exotic richness on sites of increasing natural substrate fertility (granite < sediment < basalt) on the New England Tablelands and a similar trend for water enrichment.

Exotic invasion occurred simultaneously with the introduction of livestock and resulted from the carriage of seed in their coats or digestive tracts, or by movement of fodder, and the superior adaptations for survival that these plants possessed under the new grazing regimes (Kirkpatrick *et al.* 1995). Invasions may have been facilitated by the disappearance or dysfunction of the C_4 grass, the C_3 grasses, or the intertussock forbs (Groves and Whalley 2002) resulting from various forms of disturbance. Soil disturbance that raised the level of available nutrients *in situ* has had particularly insidious effects (Wijesuriya and Hocking 1999). Extraneous nutrient addition also commonly results in damage. Roadside grasslands in western Victoria were rapidly invaded by *Holcus lanatus* in 1983 after nutrient rich soil drifted from drought-affected agricultural land, a number of significant remnants being destroyed (Kirkpatrick *et al.* 1995). Competition from annual grasses may significantly impact on native forbs with similar cool season growth patterns (Morgan 1994) but invasion by perennial grasses including *N. neesiana* has resulted in much greater community change (Hocking 1998, Lunt and Morgan 2000).

In the New England grasslands low native diversity occurred in areas with greater frequency of soil disturbance and water enrichment, and was associated with thick litter cover and >5% bare ground (McIntyre 1993). Exotic species were rarely dominant, but *Hypochoeris* spp., *Plantago lanceolata* L., *Vulpia* spp., *Trifolium arvense* L., *Bromus* spp. and *Paspalum dilatatum* were dominants in a small number of 30 m^2 quadrats. The six sites with the lowest richness all had high soil disturbance and litter >5 cm deep, and were dominated by perennial exotic grasses. Severe soil disturbance in these grasslands eliminated a large number of native taxa, which were replaced largely by exotic species (McIntyre and Lavorel 1994a 1994b). The disturbance-intolerant species included many rare taxa which apparently were unable to recolonise disturbed ground or were uncompetitive in situations of high productivity (McIntyre and Lavorel 1994a). A group of disturbance-tolerant species were found over the range of disturbance states and included natives such as *Acaena* spp. and *Asperula conferta* Hook. f. and the exotics *Hypochaeris radicata* L. and *Centaurium erythraea* Rafn. A further group of "disturbance specialists" exploited areas that had been heavily grazed or where the soil had been disturbed, and were mainly exotics, including *Paspalum dilatatum* and *Plantago lanceolata* L., but included a few native herbs. Disturbance specialists tended to dominate the sward where disturbance was intense (McIntyre and Lavorel 1994a).

T. triandra grasslands of the Victorian volcanic plains in general have a large exotic vascular plant component, even those that have been minimally disturbed and are rich in native species (Morgan 1998c 1998d). For example 41% of the 102 species found in quadrats at Evans Street, Sunbury grassland in 1993-4 were exotics, 52% being annuals, and 77% of them having <1% cover (Morgan 1998d) or if a greater range of records of vascular plants at Evans St is considered, 151 spp. of which 33% were exotic, of which 45% were annuals (Morgan and Rollason 1995); 30 of 91 taxa in the standing vegetation and 28 of 60 taxa in the soil seed bank of five grasslands examined by Morgan (1998c) were exotic, and 24 of 41 species found in the soil seed bank at Derrimut were exotics (Lunt 1990b). Sharp (1997) found that 41% of species detected in surveys of 39 natural grasslands in the ACT were exotics.

Kirkpatrick *et al.* (1995) listed weeds considered locally common in lowland grassland communities and fifteen species found in more than half the communities: the annual grasses *Aira caryophyllea* L., *Briza minor*, *Bromus hordeaceus* and *Vulpia myuros* (L.) C.C. Gmel., the perennial grasses *Holcus lanatus* and *Lolium perenne*, the annual forbs *Trifolium dubium* Sibth., *T. subterraneum* and *T. glomeratum* L., and the perennial forbs *Centaurium erythraea* Rafn., *Cirsium vulgare* (Savi) Ten., *Hypochoeris radicata* and *Plantago lanceolata*. Most exotic vascular plants invasive in temperate grasslands are small annuals or geophytes (Kirkpatrick *et al.* 1995). Exotic Poaceae and Fabaceae usually dominate the soil seed bank in *T. triandra* grasslands (Morgan 1998c). *Aira* spp., *Briza minor* (both Poaceae), *Juncus bufonius* L. and *J. capitatus* Weigel were the most abundant seed bank species at five *T. triandra* remnants in western Victoria, accounting for 91% of all seedlings (Morgan 1998c). All are introduced species except *J. bufonius*, the status of which remains uncertain (Walsh and Stajsic 2007). In the ACT the main exotic dominant environmental weeds were considered by Berry and Mulvaney (1995 p. 19) to be *Phalaris aquatica*, wild oats (*Avena barbata* Pott ex Link, *A. fatua* and *Avena* spp.) and "other grasses and herbs". Mott and Groves (1994 p. 374) noted that *Eragrostis curvula* was "especially invasive in *Themeda* grasslands in southern Australia currently".

The exotic elements in *T. triandra* grasslands of the Victorian volcanic plains are of three types (Morgan and Rollason 1995, Morgan 1998d):

1. Generalist or tolerant species with non-specific habitat requirements, typically annuals, with large seed bank, low biomass, low cover and high frequency, not dependent on nutrient enrichment to become established or on soil distrubance for germination, probably favoured by frequent burning, and including various annual grasses (e.g. *Bromus hordeaceus* L., *Aira* spp.), *Romulea rosea* (L.) Eckl. (Iridaceae) and *Hypochoeris radicata* (Asteraceae);
2. Resource-limited species or disturbance specialists, typically perennials, with high biomass, associated with increased soil N and P and probably requiring disturbance for seedling establishment, e.g. *Agrostis capillaris* L. and *Lolium perenne* L. (both Poaceae) and various thistles (Asteraceae: Cardueae).
3. Intermediate species, with a range of life-forms and biomass, non-restrictive habitat and establishment requirements, a positive response to soil nutrients and possible limitation by fire e.g. *Holcus lanatus*, *Phalaris aquatica* (both Poaceae) and *N. neesiana*.

Opinions differ on the nature and intensity of disturbance required for weed invasion. Patton (1935 p. 175) considered intact grasslands on the Victorian basalt plains to be highly resistant: "So long as the natural vegetation covering, open though it be, is maintained, entrance to new-comers is denied." Lunt (1990a) found that areas of Derrimut Grassland ploughed during the 19th century were amongst the most diverse, with an average of 17 native and 13 exotic vascular plant species per 15 m^2, probably illustrating one of the dilemmas of native grassland management, that certain types of disturbance favour both weeds and the native flora (Trémont and McIntyre 1994). Some exotics allegedly invade without major prior disturbance, by virtue of their superior competive abilities (Carr 1993), but prior disturbance may often be difficult to detect, and effects of historical disturbance may resonate long into the future. Disturbance that destroys native species certainly facilitates invasion by weeds both in terms of species and population sizes, and their occupation reduces recolonisation by natives. Nutrient and water enrichment often favours the exotics (McIntyre 1993). Soil disturbance was found to be the most important factor determining variation in plant species composition in grasslands of the New England Tablelands, more important than altitude, topographic position, lithology or water enrichment, but the greatest floristic effects resulted from soil disturbance accompanied by grazing (McIntyre and Lavorel 1994a). Dorrough *et al.* (2004) found that the intensity of grazing explained significant increases in the exotic richness of Monaro Tablelands grasslands, but that exotic status itself did not significantly explain plant responses in matched areas with contrasting grazing history. Exotic plant diversity was high even at the lowest grazing frequency. In many areas the local species pool is more likely to contain exotics that are well adapted to wetter conditions than natives (Kirkpatrick *et al.* 1995). The annual grass *Bromus hordeaceus* can be abundant where fire has been absent for a long period but is quickly eliminated by burning (Kirkpatrick *et al.* 1995).

The consensus position of most grassland specialists appears to be well represented by McIntyre and Lavorel (1994a p. 381): "With little exogenous disturbance, the native grassland consists of a matrix of dominant perennial tussock grasses (e.g. *Poa*, *Themeda*) as well as smaller statured interstitial species that form the bulk of of species richness... including some exotic 'tolerant' species. With increasing disturbance, the tolerant species will persist and many 'intolerant' species will decline, to be partially replaced by disturbance specialists. At the highest levels of disturbance, the matrix of native perennial grasses is usually replaced by large statured exotic grasses or forbs ... species richness is very low and a only a few tolerant native species persist."

The presence of weeds in native grasslands may impact on native plants not only through direct competition, but also by ramifiying effects through the food chain. Foraging by cockatoos for the bulbs of *Romulea* has been recognised as a theat to the integrity of one northern Victorian grassland (Kirkpatrick *et al.* 1995).

Prevention of exotic weed invasion in grasslands has two main components, minimisation of disturbance to maintain an intact ground vegetation stratum, and hygiene measures to prevent entry of propagules (Davies 1997). Edges of grassland remnants tend to be the most highly invaded e.g. at Evans St. the road edges have significantly greater exotic plant richness and significantly lower native plant cover and richness than in core areas (Morgan and Rollason 1995, Morgan 1998d). Morgan (1998d) found no correlation between exotic plant richness and the amount of 'bare' (cryptogam encrusted) ground, a weak negative correlation with *T. triandra* cover and a stronger negative correlation with native plant richness.

Grasslands that are floristically rich with native species are considered of high quality and have high diversity of forbs, an open structure with a high proportion of intertussock space, few weed species and management regimes involving regular biomass reduction by grazing or burning (Henderson 1999). Floristically poor (low quality) grasslands have low forb diversity, a canopy of dominant grasses that is often closed, abundant weeds and often a management regime lacking regular biomass reduction (Henderson 1999).

Rare and endangered plants

"The most imminent threat to the biological diversity of grassland is the extinction of rare and threatened species and genotypes. These cannot be resurrected once lost, whereas the grassland communities could conceivably be re-established ..." (Kirkpatrick *et al.* 1995 p. 87).

A large number of rare and threatened plant species occur in native temperate grasslands of south-eastern Australia (Tables 6 and 7). Robinson (2005) stated that approximately 200 native forb species that occur in these grasslands are rare and endangered, many of which were formerly common and widespread. Scarlett *et al.* (1992) provided lists of depleted, rare, vulnerable, endangered and presumed extinct grassland plants in Victoria. Scarlett and Parsons (1993) compared the numbers of threatened vascular plants across major landscape types in Victoria, including a category consisting of grasslands, grassy woodlands and fertile lowland open forests (Table 6). The highest concentration of endangered species occurred in this 'grassy'category, whether assessed in the Victorian context or in terms of species populations throughout Australia. There was no doubt that undescribed taxa were under threat including species in *Senecio*, *Craspedia*, *Podolepis*, *Leptorhynchos* and *Microseris* (all Asteraceae), although some have subsequently been described. Herbs and low semi-shrubs comprised the majority of rare and threatened taxa. Kirkpatrick *et al.* (1995) listed 24 lowland temperate grassland taxa considered to be nationally rare or threatened, and calculated that 11% (79 species) of the total lowland grassland flora was rare or threatened. These data can now be considered to be poor indicators of current circumstances: "Even the most common species of lowland grassland forbs are now comparatively rare ..." (Robinson 2005).

Table 6. The number of extinct, endangered, vulnerable, rare and insufficiently known vascular plant taxa of Victorian grasslands, grassy woodlands and fertile lowland open forests in 1993. Source: Scarlett and Parsons (1993).

ConservationStatus	**Extinct**	**Endangered**	**Vulnerable**	**Rare**	**Insufficiently known**	**Total**
Australia-wide	3	16	19	5	5	48
Victoria	9	33	54	43	3	142

Table 7. Some extinct, endangered, vulnerable and rare vascular plant taxa of south-eastern Australian native temperate grasslands. See Scarlett and Parsons (1993) and Ross and Walsh (2003) for definitions of the categories. R = rare, U = unlisted, K = poorly known, X = extinct, E = endangered, V = vulnerable, - = not present, ? = status not determined

Species	**Common Name**	**Family**	**Aust**	**ACT**	**NSW**	**Vic**	**Tas**	**References**
Ammobium craspediodes	Yass Daisy	Asteraceae		U	V	-	-	Eddy *et al.* 1998
Amphibromus pithogastrus	Plump Swamp Wallaby-grass	Poaceae	K	?	?	E	-	Ross and Walsh 2003, Ashton and Morcom 2004, DSE 2009a
Calotis glandulosa	Mauve Burr-daisy	Asteraceae		U	V	-	-	Eddy *et al.* 1998
Carex tasmanica	Curly Sedge	Cyperaceae	V	-	-	V	V	Kirkpatrick *et al.* 1995, Morcom 1999, Ross and Walsh 2003
Colobanthus curtisiae	Colobanth	Caryophyllaceae	-	-	-	-	E	Kirkpatrick *et al.* 1995
Comesperma polygaloides	Small Milkwort	Polygalaceae	-	-	-	V		Ross and Walsh 2003, McIntyre *et al.* 2004
Cullen parvum	Small Psoralea	Fabaceae	E	-	X	E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Muir 2003, DSE 2009a
Discaria pubescens	Anchor Plant	Rhamnaceae	R			R	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, DSE 2009a
Diuris fragrantissima	Sunshine Diuris	Orchidaceae	E	-	-	E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Webster *et al.* 2004, Smith *et al.* 2009, DSE 2009a
Dodonaea procumbens	Creeping Hopbush	Sapindaceae	V	U	V	V		Eddy *et al.* 1998, Ross and Walsh 2003
Glycine latrobeana	Clover Glycine	Fabaceae	V			V	V	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, DSE 2009a
Lachnagrostis adamsonii	blown grass	Poaceae	V	-	-	V	V	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, DSE 2009a
Leucochrysum albicans subsp. *albicans* var. *tricolor*	Paper Daisy	Asteraceae	E	?	?	E	V?	Kirkpatrick *et al.* 1995, Ross and Walsh 2003
Maireana cheelii	Chariot Wheels	Chenopodiaceae	V			V	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, DSE 2009a
Microseris lanceolata	Yam Daisy	Asteraceae	-	-	-	-	-	Sharp and Shorthouse 1996: regionally uncommon in the ACT,
Pimelea spinescens subsp. *spinescens*	Spiny Rice-flower	Thymelaeaceae	V	-	-	V/E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Tumino 2004, DSE 2009a
Podolepis sp. 1	Basalt Podolepis	Asteraceae	-	-	-	E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Robinson 2005
Prasophyllum diversiflorum	Gorae Leek-orchid	Orchidaceae	E	-	-	E		Ross and Walsh 2003, Pritchard and Ingeme 2003, DSE 2009a
Prasophyllum fosteri	Shelford Leek-orchid	Orchidaceae	E	-	-	E		Ross and Walsh 2003, Coates 2003a, DSE 2009a
Prasophyllum petilum	leek orchid	Orchidaceae		E	E	-		Eddy *et al.* 1998
Prasophyllum suaveolens *P.*sp. aff. *suaveolens* (Western Basalt Plains)	Fragrant Leek-orchid	Orchidaceae	E	-	-	E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Coates 2003b, DSE 2009a
Psoralea tenax	Emu Foot	Fabaceae	-	-	-	-	-	Sharp and Shorthouse 1996: regionally uncommon in the ACT,
Pterostylis basaltica	Basalt Greenhood	Orchidaceae	E	-	-	E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Ingeme 2003, DSE 2009a
Pterostylis truncata	Brittle Greenhood	Orchidaceae	-			E		Ross and Walsh 2003, Bramwells 2003, DSE 2009a
Rutidosis leiolepis	Monaro Golden Daisy	Asteraceae		U	V	-		Eddy *et al.* 1998
Rutidosis leptorhynchoides	Button Wrinklewort	Asteraceae	E	E	E	E	-	Morgan 1995a 1995b, Kirkpatrick *et al.* 1995, Sharp and Shorthouse 1996, Eddy *et al.* 1998, Scarlett and Parsons 1993, Ross and Walsh 2003, Humphries and Webster 2003, DSE 2009a
Schoenus absconditus	Obscure Bog-rush	Cyperaceae	-	-	-	-	R	Kirkpatrick *et al.* 1995
Sclerolaena napiformis	Turnip Bassia	Chenopodiaceae	E			E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003
Senecio behrianus	-	Asteraceae	E	?	X?	E	-	Walsh 1999, Ross and Walsh 2003, DSE 2009a
Senecio macrocarpus	Large-headed Groundsel	Asteraceae	V	-	-	E	-	Scarlett and Parsons 1993, Kirkpatrick *et al.* 1995, Hills and Boekel 1996 2003, Walsh 1999, Ross and Walsh 2003, DSE 2009a
Senecio georgianus		Asteraceae	X	-	X	-	X	Kirkpatrick *et al.* 1995, Ross and Walsh 2003
Spyridium obcordatum	Dusty Miller	Rhamnaceae	-	-	-	-	V	Kirkpatrick *et al.* 1995
Swainsona adenophylla	Violet Swainson-pea	Fabaceae	-			E		Ross and Walsh 2003, Earl *et al.* 2003, DSE 2009a

Table 7 (continued).

Species	**Common Name**	**Family**	**Aust**	**ACT**	**NSW**	**Vic**	**Tas**	**References**
Swainsona monticola		Fabaceae	-	-	-	-	-	Sharp and Shorthouse 1996: regionally uncommon in the ACT,
Swainsona murrayana	Slender Darling-pea	Fabaceae	V			E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Earl *et al.* 2003, DSE 2009a
Swainsona plagiotropis	Red Swainson-pea	Fabaceae	V	V	V	E	-	Kirkpatrick *et al.* 1995, Ross and Walsh 2003, Earl *et al.* 2003, DSE 2009a
Swainsona recta	Small Purple Pea	Fabaceae	E	E	E	E	-	Kirkpatrick *et al.* 1995, Sharp and Shorthouse 1996, Eddy *et al.* 1998, Ross and Walsh 2003, DSE 2009a
Swainsona sericea	Silky Swainson-Pea	Fabaceae	-	-		V		Sharp and Shorthouse 1996: regionally uncommon in the ACT, Ross and Walsh 2003, Earl *et al.* 2003, DSE 2009a
Thelymitra gregaria	Basalt Sun-orchid	Orchidaceae	E	-	-	E	-	Ross and Walsh 2003, Coates 2003c, DSE 2009a
Thesium australe	Austral Toadflax	Santalaceae	V	U	V	V	V	Kirkpatrick *et al.* 1995, Eddy *et al.* 1998, Scarlett and Parsons 1993, Scarlett *et al.* 2003, Ross and Walsh 2003, DSE 2009a

Much less is known about the conservation status of plants at the intraspecific level. Groves and Whalley (2002) emphasised the need to conserve the widespread intraspecific variation in Australian grasses (polyploid complexes, ploidy levels, breeding systems). *T. triandra* for example, is widely variable, consisting of a polyploid complex, mainly of diploid and tetraploid populations in southern Australia (Hayman 1960) and different populations have varying flowering responses to photoperiod and temperature (Groves 1975).

Many of the rare and endangered plants have become scarce as a result of the same processes that have led to the loss and degradation of grassland communities. Continuous livestock grazing is considered to be a major cause of decline of such species as *Swainsona recta* A.T. Lee and *S. plagiotropis* F. Muell. (Fabaceae), *Rutidosis leptorhynchoides*, *Senecio macrocarpus* (Asteraceae) and *Thesium australe* R.Br. (Santalaceae), and, except for *S. plagiotropis* and *T. australe*, fire is probably, or should be, important in maitaining their habitat. Competition in dense *T. triandra* swards affects *S. recta*, *R. leptorhynchoides*, *S. macrocarpus* and *T. australe* (Scarlett and Parsons 1993). *Colobanthus curtisiae* J.G. West and *Stakhousia gunnii* Schltdl. disappear from grasslands when the perennial grass sward covers all the bare ground (Kirkpatrick 2007). *Rutidosis leptorhynchoides* survived in areas subject to frequent fires, but disappeared from two railway reserves in the Melbourne area when regular burning ceased in the 1980s (Kirkpatrick *et al.* 1995). Three sites where it existed, at Canberra, Queanbeyan and near Melbourne, were allowed to be developed on the condition that populations were transplanted, but the transplanting failed (Kirkpatrick *et al.* 1995). Morgan (1995b) considered it was restricted to remnant grasslands never subjected to grazing, ploughing and fertiliser application. *Senecio behrianus* Sond. and F. Muell. was formerly known from the Western District of Victoria and the Northern Plains and was apparently restricted to heavy clay, winter-wet soils (Walsh 1999). The one known site where it continued to exist appeared to have once been *Eucalyptus camaldulensis* woodland but was highly modified and difficult to botanically categorise (Scarlett and Parsons 1993).

Taxa endangered in the Riverina include two chenopods, *Maireana cheelii* (R.H. Anderson) Paul G. Wilson and *Sclerolaena napiformis* Paul G. Wilson, along with several from other families that are also found in the more mesic grasslands (Kirkpatrick *et al.* (1995).

Senecio georgianus DC “known ... probably from grassland” (Kirkpatrick *et al.* 1995 p 30) was recorded from Lake Omeo and the Macalister River in Victoria and from Western Australia, South Australia and Tasmania (Walsh 1999) but is now extinct (Walsh and Stajsic 2007). *Stemmacantha australis* (Gaudich.) Dittrich, the only Australian native thistle, known in Victoria from Lake Omeo and Murrindal, “probably” from grasslands, is now extinct in Victoria (Jeanes 1999b p. 677) and NSW, but survives in Queensland (Kirkpatrick *et al.* 1995).

Diuris fragrantissima, Sunshine Diuris or Fragrant Doubletail (Orchidaceae) is endemic to Victoria (Walsh and Stajsic 2007), in particular to an area with a 25 km radius now part of western urban Melbourne (Smith *et al.* 2009). It and was “once widespread on the Keilor Plains” (SGAP 1991 p. 206), and was so common at the time of European settlement that it was referred to as ‘Snow-in-the-Paddocks’ (Webster *et al.* 2004). It is now “exceedingly rare, restricted to remnant dry grassland on the basalt plains near Sunshine” (Entwisle 1994 p. 858) at two sites – a railway reserve at Tottenham and Laverton North Grassland where it has been planted (Webster *et al.* 2004, Smith *et al.* 2009). The site at Sunshine/Tottenham has few remaining plants, and the plantings at Laverton North have progressively declined and not resulted in a viable population (Smith *et al.* 2009). *N. neesiana* is a “very serious” direct threat to the small population at the Tottenham site, and the immediate surrounding area is extensively invaded (Webster *et al.* 2004).

The threatened Curly Sedge, *Carex tasmanica* Kuk grows in wetlands and at grassland edges, often in areas too wet to support tussock grassland (Morcom 2004). In Victoria it was known to exist at only nine sites, “in remnant grasslands” (Morcom 2004).

Leucochrysum albicans has no persistent seed bank, but disperses widely on the wind, and in part of its range is dependent on heavy sheep grazing to create patches of bare ground every few years in which seedlings can establish (Kirkpatrick 2007).

Many of the rare and endangered forbs produce large amounts of seed and are long-lived, and some reproduce vegetatively, but recruitment of new individuals is usually rare, for reasons that are poorly understood (Robinson 2005). Rare and threatened vascular plants of grasslands often survive in areas with ususual disturbance regimes, which also usually favour weeds and few other natives, so tend to be degraded, and to be assigned little conservation value (Kirkpatrick *et al.* 1995, Kirkpatrick 2007). These species usually have poor competitive abilities and are disturbance-dependent (Kirkpatrick 2007). Robinson (2003 2005) demonstrated that many species that recruit poorly in grassland remnants lack specialised germination requirements and can be propagated and grown relatively easily under nursery conditions, but that a range of Apiaceae, Fabaceae, Ranunculaceae and some Asteraceae do have specialised requirements such as cold stratification and after-ripening requirements that may rarely be met in the wild.

Factors that are probably important in limiting forb recruitment include the presence of weeds, particularly *Nassella* spp., herbivory by exotic invertebrates, grazing by livestock and rabbits, and the loss of small-scale soil disturbance formerly achieved by native vertebrates (Robinson 2003 2005). Reynolds (2006) demonstrated that soil digging is indeed an important factor, critical for recruitment of several species. Soil disturbance may have a significant role in increasing seed contact with the soil or actual seed burial, or may be more important in enabling penetration of the radical (Robinson 2005). Iincreased survival and flowering of *Diuris fragrantissima* established using soil digging might be due to enhanced functioning of its fungal symbiont due to improved aeration (Smith *et al.* 2009). The scale and intensity of the disturbance is of obvious importance in determining the effects on competitors, nutrient levels and other factors.

Ecological history

The pre-European disturbance regimes of temperate Australian grasslands are poorly understood (McIntyre and Lavorel 2007). Fire is universally recognised as an important factor, both pre-aboriginal and ‘managed’ aborignal burning (Kershaw *et al.* 1994, Hope 1994, Kershaw *et al.* 2000). Marsupial grazing must have had a large influence: Australian grasslands are presumed to have once been grazed by a now extinct marsupial megafauna, and known to have been occupied by numerous smaller herbivorous mammals, most of which are now extinct or have relictual distributions. Climatic variation has also been important in shifting the distribution, extent and composition of grasslands. All these major factors are compounded, their individual influences are difficult to determine from the limited palaeecological records (Hope 1994) and existing remnants may have little resemblance to their pre-European condition (Trémont and McIntyre 1994). The palaeontolgy of temperate Australian grasslands is discussed in the section on grasslands origins (above), while the pre-European influences of aboriginal grassland management, grazing and fire, and the post European disturbance and management factors are discussed in sections on these topics below.

Aboriginal management

In south-eastern Australia, apart from the coast, grassland was the main habitat occupied by aborigines (Kirkpatrick *et al.* 1995). The earliest undisputed evidence for aboriginal occupation of Australia remains at around 40,000 ypb in the Kimberley of Western Australia, close to the limit of resolution of radiocarbon dating, but evidence using other techniques indicates first occupation may have occurred c. 60 kybp (Kershaw *et al.* 2000). Coutts (1982) claimed that aboriginal people were present in Victoria at least as long ago as 40 kybp, but the oldest south-eastern mainland site known, at Willandra Lakes, is dated at c. 36 kybp (Kershaw *et al.* 2000). Most of Australia, including Tasmania was probably occupied by 35 (Hope 1994) or 32 kybp, all major environments were certainly occupied by 22 kybp, and occupational intensities increased after c. 5 kybp (Kershaw *et al.* 2000). Aborigines coexisted for many thousands of years with the extinct marsupial megafauna in the early prehistoric period (Coutts 1982, Kershaw *et al.* 2000).

Aboriginal people managed the land over many thousands of years (Zola and Got 1992) and would have witnessed the assembly of many Australian grasslands, notably on the Victorian Volcanic Plains, where the most recent terrain was formed several thousand years ago. The total aboriginal population of Victoria in 1788 has been estimated at 15,000 (Coutts 1982) but actual population is very uncertain. Mulvaney (1964) suggested a population density of one person per 13 km^2 in the western district of Victoria prior to European settlement, with a total population of 1,800. Mulvaney's estimate is probably much too low, since 800-1,000 western district aborigines were known to gather annually at Lake Bolac (Jones 1999b). The South East of South Australia supported an "unusually large population, perhaps numbering 2000" (Pretty *et al.* 1983 p. 116). The population in that region is estimated to have declined by half every five years, from the beginning of settlement in 1840 (Pretty *et al.* 1983). Numerous archaeological sites are recorded on the Victorian Basalt Plains including campsites, earthen mounds (probably long occupied campsites), burials, canals and weirs of basalt rocks used as fish traps, basalt block walls probably roofed with timber and used as huts, etc. (Coutts 1982). Indications are that some populations were more or less sedentary, rather than nomadic.

Digging and burning of the vegetation were probably the most important aboriginal activities in terms of grassland ecology, and areas of grassland appear to have been extended by aboriginal activities (Kirkpatrick *et al.* 1995). However in the mid to late Holocene some societies in more arid areas developed economies based on systematic harvesting and processing of grass seed (Kershaw *et al.* 2000, Gammage 2009). One species exploited was Barley Mitchell Grass, *Astrebla pectinata* (Lindl.) F. Muell., a common and very widespread species of the summer rainfall semi-arid and arid zones. It has "relatively large seeds that separate easily from the chaff" and "at one time provided an important part of the diet of the Aborigines" (Cribb and Cribb 1974 p. 101). Another grain, with distribution extending into more temperate winter rainfall areas of south-eastern Australia, was Native Millet or Windmill Grass, *Panicum decompositum* R.Br., a species "often associated with temporarily wet places such as creek beds and flood plains" (Jessop *et al.* 2006 p. 461). It was a major foodplant (Jessop et al. 2006), extensively cultivated (Gammage 2009), the seeds being ground into a paste and baked to form bread (Cribb and Cribb 1974). Another arid zone species harvested was Woollybutt, *Eragrostis eriopoda* Benth. (Jessop et al. 2006), which has abundant, readily husked, soft, easily-ground seed that is held on the plant for months (Low 1989). Other *Panicum* spp. were also used (Low 1989). Perhaps Hairy Panic, *Panicum effusum* R.Br., a common associate of *T. triandra* in temperate south-eastern grasslands, was used in a similar manner. *Eragrostis tef* (Zucc.) Trotter and *Panicum miliaceum* L. were amongst the grasses cultivated in pre-Islamic civilisations in Arabia (Pohl 1986). Current consensus appears to be that grasses were not important in the diets of aborigines living outside the dry interior, and Gammage (2009) has convincingly argued that they were little used in areas with a reliable supply of edible tubers. However the possibility that aboriginal management of cereal grasses influenced the structure and biodiversity of the temperate grasslands of south-eastern Australia should not be ignored.

Intensive digging took place in the temperate grasslands to harvest roots for food, particularly Murnong, *Microseris* spp., which was stockpiled and traded (Gott 1983), and Turrac (probably *Pelargonium rodneyanum*) (Lunt *et al.* 1998). Numerous other tuberous or bulbous grassland species were eaten (Gott 1999) including Vanilla and Chocolate Lilies *Arthropodium* spp. (Wigney 1994, Zola and Gott 1992), Bulbine Lily *Bulbine bulbosa* (R.Br.) Haw., Milkmaids *Burchardia umbellata* R.Br. and a range of other lilies and orchids (Zola and Gott 1992). Approximately one quarter of the vascular plant species recorded in the Victorian Basalt Plains were used by aboriginals, of which approximately 20% were used as food (Gott 1999). Over 100 plant species found in the grasslands and grassy woodlands of Tasmania are known to have been used by aborigines elsewhere in Australia (Kirkpatrick *et al.* 1995). Harvesting of roots resulted in improved aeration and water infiltration into the soil and nutrient incorporation from litter and ash, and would therefore have enabled better plant regeneration. Dug areas would have increased the availability of regeneration niches for many plants (Gott 1999). Recent studies have confirmed that this occurs with the orchid *Diuris fragrantissima*, where soil aeration, consisting of tilling to 20 cm depth, significantly increased the proportion of spring-planted plants that emerged and flowered (Smith *et al.* 2009). Aborigine thinned patches of the tuberous and bulbous food plants, deliberately replanted them and traded valued plant production between clans and tribes (Gott 1999).

Burning in the dry season in Victoria may have enhanced the abundance and distribution of some plants e.g. *Microseris* spp. (Gott 1983). According to Flannery (1994) fire was critical in releasing nutrients into the system to enable regeneration of plant foods, however this may have been of limited importance in grasslands because of the limited nutrient reserves in above ground vegetation during a significant proportion of the fire season. Burning was probably more critical to keep grass biomass low: the tuber feeding people burnt "to expose the tubers, to improve their taste, and to keep grass sparse and give tubers and herbs space" (Gammage 2009 p. 286). Burning was frequent on the Victorian Volcanic Plain prior to European occupation, being used by aborigines in hunting and to encourage new growth, and probably assisted in maintaining treelessness (Stuwe 1994, DNRE 1997). Fires were reported by early maritime travellers in Port Phillip region in all months from spring to autumn (Jones 1999b). Aborigines would have increased fire frequency above the background rate as a result of deliberate burning, accidental escapes from camp fires (Stuwe 1994) and possibily the use of fire as a weapon against invading non-indigenous people (Flannery 1994).

But little is known anywhere in the world about the motives, scale and ecological significance of aboriginal fire management (Murphy and Bowman 2007). The palynological records of grasses in lake and swamp cores indicate that south-eastern Australian grasslands existed long before aboriginal occupation and are not of anthopogenic origin (Jones 1999b, Kershaw 2000); rather, aboriginal activities modified existing grassy ecosystems and shifted their boundaries (Jones 1999b).

The European explorer Thomas Mitchell thought that burning was critical to aboriginal management of country: "fire, grass, kangaroos, and human inhabitants seem all dependent upon each other for existence" (Mitchell 1848, cited by Murphy and Bowman 2007). Fire use in hunting had two aspects: as a direct tool to flush the animals or drive them towards waiting hunters, and habitat manipulation, in which the young green growth attracted the animals, increased the carrying capacity and made the prey easier to locate and kill (Murphy and Bowman 2007). Numerous ecological studies show that kangaroos are attracted to burnt areas but there has been little investigation of the mechanisms that cause this response. In studies in northern Australian savannah and seasonal wetland Murphy and Bowman (2007) found that the abundance of *Macropus* spp. scats was much greater in burnt than unburnt moist areas, and in unburnt than burnt dry rocky areas, from 4 weeks to 1 year post-fire. Kangaroos moved into the burnt moist areas away from burnt, dry rocky habitats. The resprouting grass foliage contained higher N concentrations than senescent foliage and may have provided macropods with better quality nutrition. Aboriginal burning may indeed have created a self-reinforcing cycle by creating a mosaic of habitat patches, very different to that subsequently developed by Europeans.

Pastoral development had an immediate and devastating effect on the aboriginal population. Introduced livestock destroyed their prime feeding grounds and muddied and destroyed the waterholes and soaks (Zola and Gott 1992). Considerable numbers of aborigines were shot by European occupiers. Smallpox had already decimated the Victorian aboriginal population by 1835 and populations collapsed to an estimated 1,700 in 1871 and 850 in 1901 (Coutts 1982). The cessation of aboriginal fire regimes resulted in well-documented substantial change in vegetational structure, particularly involving increases in tree cover (Hope 1994).

European Management

European occupation of Australia brought a novel range of exogenous disturbances that resulted in rapid, abrupt changes to Australian grasslands (McIntyre and Lavorel 1994). Aside from the changes in land use that must have occurred as imported diseases decimated aboriginal populations, sheep and cattle grazing was the first major European impact and the shift to frequent livestock grazing is generally recognised as the major cause of vegetation change (Dorrough *et al.* 2004). Grasslands were preferentially occupied by squatters and their livestock very early in the colonial period. Pastoral settlement commenced in the 1820s in the Southern Tablelands of NSW and the ACT (Sharp 1997) and in the early 1830s on the Northern Tablelands (Johnson and Jarman 1975). In Victoria occupation commenced in the mid 1830s and there were 25,000 sheep in the colony before legal settlement commenced in 1836 (Mansergh *et al.* 2006a), over 41, 000 by May of the following year, along with 155 cattle and 75 horses (Jones 1999b). Sheep numbers reached 700,000 by 1841 and doubled by 1843 (Gott 1983), by which time most of the grasslands in Victoria outside of Gippsland had been occupied (Jones 1999b). There were over 6 million sheep in the 1850s, along with about 1 million cattle (Mansergh *et al.* 2006a). On the New England tablelands of NSW 66 stations occupied all of the best grazing land by 1840 and only a few more were added in rougher country by 1848 (Johnson and Jarman 1975). Thirty million sheep had been introduced to the grassy plains of Victoria and NSW by 1851 along with 1.7 million cattle and 32,000 horses (Lunt *et al.* 1998). European occupation, at least in Victoria, probably coincided with a major climate shift to drier and hotter conditions (Jones 1999b) which probably exacerbated the impact of livestock. However the impact on native grasslands up until the 1860s were relatively mild compared with what followed (Scarlett and Parsons 1993).

In Victoria the *Selection Acts* of the 1860s led to the alienation of large areas of Crown land and the advent of major cultivation, particularly cereal growing (Scarlett and Parsons 1993). In NSW the *Land Act* of 1861 allowed occupation of areas up to 259 ha before government surveys, and fencing began to be used instead of shepherding (Johnson and Jarman 1975). Land grazing under licence became legitimate in Victoria in the period to 1900. By 1891 livestock farming on large freehold properties was well established, particularly in the Western District (Powell and Duncan 1982). Landscape change was intensified by the extension and intensification of more efficient types of fencing (Powell and Duncan 1982). By 1910 pasture occupied c. 12 million ha in Victoria, of which <5% was sown (Mansergh *et al.* 2006a). Closer settlement schemes to establish small scale farming became a priority and by 1913 many large estates on the Western and Northern plains had been subdivided for this purpose (Powell and Duncan 1982). By 1916 Sutton (1916-1917 p.112) observed that the Keilor Plains grasslands to the north and west of Melbourne "had been put so throughly to pastoral and agricultural uses that hardly any part now remains in the virgin state." In the 1920s large areas were allocated to World War I servicemen in 'soldier settlement' schemes in most grassland areas of the State (Powell and Duncan 1982). After World War II soldier settlements were established by subdividing large grazing properties in the Western District and the intensified development that followed resulted in the clearance of the last remaining large areas of natural vegetation (Brown 1987). By the mid 1950s the proportion of sown pasture in Victoria had risen to about 25% and by 1980 to c. 70%. Over the whole century native pasture dropped through c. 8 million ha in 1950-51 to c. 2 million ha in 2000-01 (Mansergh *et al.* 2006a). Twentieth century changes in the proportions of major pasture classes reflect the conversion of native to 'improved' pasture and the conversion of pasture to cropping and other agricultural uses or *vice versa*. The most important grasses sown were *Lolium perenne, Dactylis glomerata* (Groves *et al.* 2003a) and *Phalaris aquatica* L. Grazing rapidly caused severe degradation and ecological breakdown of the native ecosystems (Mansergh *et al.* 2006a), "permanent" changes in floristic composition (Groves *et al.* 2003a) and led to the formation of vast areas which Matthews (1976) characterised as the "cultural steppe".

On other continents some large temperate grassland ecosystems subjected to continual intensive grazing by introduced bovid livestock have sufferred a similar fate to those in Australia. The process may be a general response of Mediterranean climate grasslands worldwide (Groves *et al.* 2003a). Introduced livestock have carried the seeds of exotic plants in their coats and digestive tracks wherever they have been transported, facilitating generalised weed invasion (Mack 1989).

Affected grasslands have been characterised by Mack (1989) as being dominated by caespitose (tussock-forming) grasses, and lacking in large, native, congregating, hard-hooved ungulate grazers since at least the Holocene (i.e.the last ice age). The decline of these systems is largely explained by the form and growth patterns of caespitose grasses, which develop by intravaginal tillering, the emerging tillers remaining erect inside the leaf sheaths. The bunching, erect form makes the plant more susceptible to ungulate grazers than the contrasting rhizomatous grasses, which have extravaginal tillering and axillary bud production. Ungulate grazers are able to reduce the reproductive potential of tussock grasses to a much larger extent than rhizomatous forms by grazing the emerging flower heads (Mack 1989). Another contributing factor was the perenniality of the dominant species, which "made annual re-establishment unnecessary" (Evans and Young 1972 p. 231). For example in the intermountain west of the USA the once dominant *Agropyron spicatum* (Pursh) Scribn. required above average rainfall to establish, so significant recruitment events were relatively uncommon.

In Australia the syndrome of decay had the following course. Continuous grazing by hard-hooved livestock preferentially removed the more palatable and sensitive intertussock herbs and the tall C_4 grass (*T. triandra*); fire exacerbated these losses; *T. triandra* was replaced by cool-season C_3 native grasses (such as *Austrodanthonia* spp.). Further grazing favoured short cool-season grasses and eliminated or greatly reduced the remaining palatable forb components, and loss of both these functional groups led to nutrient enrichment of the soil, particularly with N, which in turn allowed invasion by alien forbs and annual grasses (e.g. *Vulpia* spp.) of European origin, etc. (Moore 1973, Mack 1989, Moore 1993, Groves and Whalley 2002, Groves *et al.* 2003a). In temperate Australian grasslands, the main trends in plant composition have been from summer to winter-growing grasses, from perennials to annuals and from native to introduced species (Moore 1973, Stuwe and Parsons 1977, Mack 1989, Moore 1993, Groves and Whalley 2002).

Intense grazing of *T. triandra* during its reproductive phase when it is mobilising nutrients from leaves to storage organs may have been the critical factor in its extensive demise (Dunin 1999). Greater palatability compared with other native grasses, trampling damage to surface roots, reduced seed production and seedling establishment were probably additional important factors (Groves *et al.* 1973, Chan 1980). Alterations to drainage patterns and soil disturbance have also contributed to losses: Lunt (1990a) noted that *T. triandra* occurred at Derrimut Grassland only in well-drained areas that had not been ploughed, as well as areas subjected to no more than brief periods of heavy grazing. A similar mechanism to that reported by Grice (1993) for the proliferation of *Austrostipa* and *Aristida* spp. in the semi-arid woodlands of western New South Wales may be partly responsible: grazing did not cause greater mortality of the more desirable and long-lived grasses, rather, the plants avoided by sheep (*Austrostipa* and *Aristida* spp.) produced much more seed in grazed areas and so proliferated, while the more palatable native pasture grasses, were more fecund when ungrazed. *T. triandra* decline in inland New South Wales has been blamed on overstocking and low seed production (Whittet 1969).

Native pasture in turn was developed by addition of fertilisers, and the sowing of exotic grasses and herbaceous legumes (Moore 1973 1993). Naturalisation of *Trifolium* and *Medicago* species after accidental introduction and spread was important (Moore 1993 p. 345) probably from the time of first settlement onwards. Addition of nutrients as a feature of grassland 'improvement' for agricultural grazing became widespread after 1929 when the Australian Government introduced a superphosphate subsidy (Mansergh *et al.* 2006a). The advent of cheap superphosphate coincided with government promotion of introduced C_3 perennial grasses and legumes (*Trifolium* spp. particularly *T. subterraneum*, *Medicago* and *Lotus* spp.), varieties of which were bred by State Departments of Agriculture for use in 'pasture improvement' programs, which usually involved cultivation (Groves and Whalley 2002). Seed of *T. subterraneum* first became commercially available in the early 1920s and that of *T. fragiferum* L. in 1938, while cultivars of *T. repens* were first registered in the mid-1930s (Oram 1990). Use of *Trifolium* spp. and superphosphate increased rapidly in some areas in the mid 1930s (Browning 1954) and became commonplace during the 1940s and 1950s (Mansergh *et al.* 2006a). These changes raised the P and N status of the land to high, facilitating the invasion of new suites of weeds. The improved pastures, including a legume component, were able to support high intensity grazing, but required ongoing fertilisation and periodical resowing, and lifted productivity "in the short term" (Keith 2004 p. 105). Spread of the exotic grasses was the "desired outcome" sought by agronomists" (Cook and Dias 2006 p. 617) and some of these grasses escaped from the paddock and started to become major weeds of roadsides and eventually natural areas, including remnants of the natural grasslands - the weed potential of a species for a natural ecosystem being more or less equivalent to its hardiness, persistence and productivity values as a new pasture grass.

These changes led to the eventual disappearance of the native grasses, particularly *T. triandra*, in many areas, although some *Austrodanthonia* spp. can re-occupy high-nutrient, grazed sites (Groves and Whalley 2002). Groves *et al.* (1973, echoed by Chan 1980) thought that the mechanisms causing the loss of *T. triandra* remained to be properly identified, but listed a number of probable reasons including greater palatability to livestock than other native grasses, susceptibility of the adventitious roots to grazing damage at the soil surface, gradual exhaustion of underground reserves due to continuous shoot removal, low seed production and poor seed seedling establishment, and poor competitive abilities for light and nutrients. Chan (1980) demonstrated that repeated close (2 cm above ground) mowing at intervals of $\leq$3 months reduced yields and reproductive fitness of *T. triandra*, *Austrostipa bigeniculata* and *Austrodanthonia* spp., with the least affected of the native grasses examined being *Bothriochloa macra* because of its low habit and prostrate tillers. Similar results were obtained by Nie *et al.* (2009) on a range of native grasses cut at 3-5 week intervals to a height of 2, 5 or 10 cm. All species tested had reduced survivorship when cut to 2 cm height, but plant survival was least with the two C_4 grasses, *T. triandra* (c. 51%) and *B. macra* (c. 57%). Cutting to 5cm increased survivorship to c. 85% with *T. triandra* and >95% with *B. macra*. Cutting at 5 and 10 cm enabled *T. triandra* to increase its shoot biomass compared to the 2 cm cut far more than the other species. Furthermore, most of the species tested had little or no response to P fertilisation (Nie *et al.* 2009) so would be outcompeted by exotic pasture species when superphosphate was applied.

The ecological and evolutionary circumstances that led to the dominance of summer-growing *T. triandra* in south-eastern Australian temperate grasslands prior to European occupation have not been adequately explained (but see Bond *et al.* 2008). Ostensibly the species appears to be poorly adapted as a dominant in grasslands that have winter rainfall maxima, spring growing periods and dry summers. This peculiarity of "a system growing partially out of phase with the rainfall regime" may explain why sheep and rabbit grazing led to rapid decline of *T. triandra* in south-eastern Australia and complete disappearance in south-west Western Australia (Moore 1993 p. 351). *T. triandra* may have been at a disadvantage compared with spring-growing exotic grasses because its demands for water are highest during the driest time of the year (Groves 1965, Mack 1989). However swards of *T. triandra* are able to more effectively trap rainfall and reduce runoff than swards of C_3 grasses, so soil moisture from spring rainfall appears to be effectively preserved for later use (Dunin and Reyenga 1978, Dunin 1999, Singh *et al.* 2003). Grazing may have resulted to general dessication of the system: reduced rainfall infiltration due to soil compaction, general opening of the sward and destruction of deep rooted perennials with access to subsurface soil moisture.

Currently most of the pasture legumes and some of the deliberately introduced grasses have poor persistence under livestock grazing, due in part to the prevailing high variability and extremes of climate, difficulty in managing grazing intensity, and to their near-monoculture nature (pastures with one grass + one legume, or just a single legume species, with volunteer broadleaf species) (e.g. Madin 1993) which makes them more prone to pest and disease attack. Continued increased nitrification by legumes has enabled invasion by nitrophilous species such as thistles, while continued use of superphosphate has resulted in widespread soil acidification (Moore 1993). These 'improved' pastures are unstable, requiring ongoing inputs or renovation (McIntyre and Lavorel 2007).

McIntyre and Lavorel (2007) presented a unifying conceptual model of the states and the transition processes for the grasslands of south eastern Australia that exemplifies historical chain of developments (Fig. 5). Transitions from one state to another occur as a result of specific managment activity (or the lack of it). Invaded grasslands with moderate or high exotic components have been permanently altered (Mack 1989) and appear to represent new metastable states that do not revert to their former status (Sharp 1997). Native pasture may revert back to native grassland, but its properties and composition will have been more or less altered. McIntyre and Lavorel (2007) introduced the concept of "enriched grassland", to include those areas no longer cultivated or managed for grazing, but which remain nutrient enriched. These are largely dominated by robust exotic perennial pasture grasses including *Paspalum dilatatum*, *Dactylis glomerata* and *Phalaris aquatica*, along with exotic rosette-forming herbs such as *Plantago lanceolata* and *Hypochoeris radicata*. Much of the enriched grassland is currently in shelterbelts and other areas of recent tree and shrub planting (McIntyre and Lavorel 2007) although many former pastures on the edges of urban areas are in this state, and some disused pastures dominated by *Nassella* spp. can be included in this category. Little is known about the floristics, functioning and successional dynamics of enriched grasslands but they appears to be "an alternative stable state [requiring] a very high level of management to shift" (McIntyre and Lavorel 2007p. 15). Management inputs required include nutrient depletion, weed control (including the dominant grasses) and reintroduction of native species, particularly forbs. A similar set of problems is faced in extensification of former pastures to species rich grassland in Europe (Eschen *et al*. 2007).

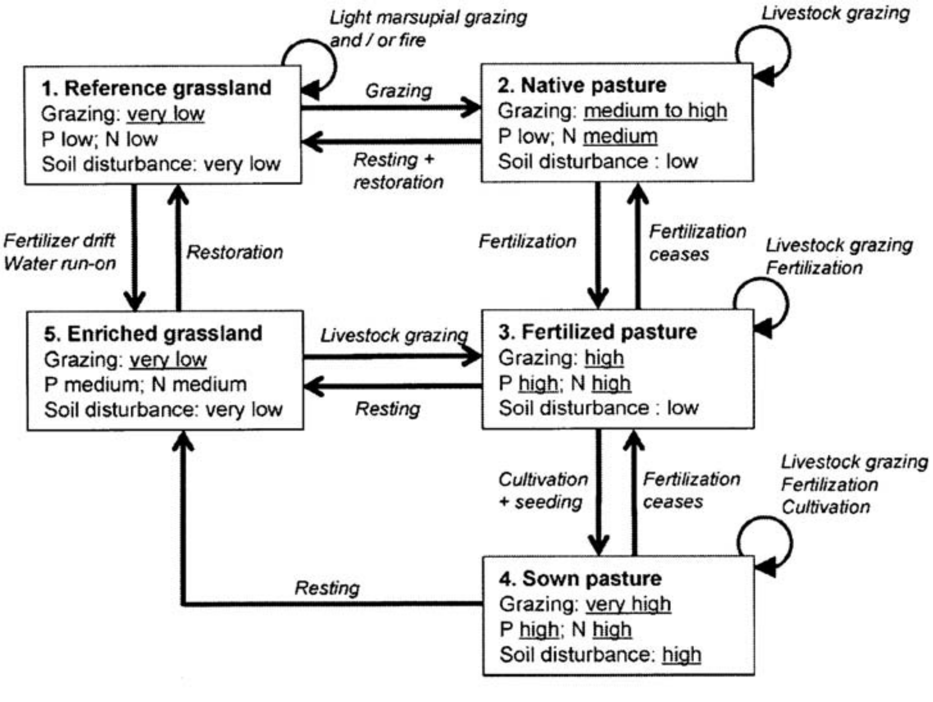

Figure 5. State and transition model for temperate grassy woodlands of south-eastern Australia. Each state is characterised by a level of livestock grazing, soil disturbance and soil fertility, straight arrows indicate mangagement factors associated with transitions between state and ciruclar arrows indicate management associated with maintenance of the state. Source: McIntyre and Lavorel 2007, p. 14.

Fertilised and sown pastures are considered to be the most unstable states because of their ongoing requirements for inputs (McIntyre and Lavorel 2007). Removal of inputs results in transition to enriched grassland or to a native pasture. Transition from reference grassland to enriched grassland generally occurs accidentally through nutrient enrichment from fertiliser drift or water movement. Changes in composition and function of areas that have 'regressed' to native pasture are probable, but currently unknown.

There are pronounced differences in scientific understanding of the states and processes. This reflects the historical agronomic approach to the study of agricultural land, and the use of floristic ecological techniques in natural grasslands. The overall floristics of sown pastures and of enriched grassland are very poorly known, while there is little data for native forbs in fertilised pasture. The least understood transitions are those that may be classed as restoration: from developed pastures through enriched grassland back to native grassland (McIntyre and Lavorel 2007).

McIntyre and Lavorel (2007) tabulated known and hypothesised leaf, broad morphology and regeneration traits of the grasses associated with each of the vegetation states. The traits considered were for leaves: specific leaf area, N content, dry matter content, toughness and life-span; for morphology: size, form, annual/perennial; and for regneration: seed size (large, medium or small), flowering period (early-late) and presence or absence of vegetative regeneration. European experience has demonstrated the utility of such simple biological modelling in predicting and managing transitions between states. The traits are poorly known for the Australian grasses, but if found to be universally applicable they should enable prediction of the effects of land use change on ecosystem services.

ACT Government (2005) provided a useful tabulation of the degree of disturbance corresponding with various levels of botanical significance in temperate grasslands of the ACT. Very low disturbance levels correspond with the highest botanical significance level. The ground layer includes the most sensitive species including orchids (*Diuris* spp. *Caladenia* spp., *Thelymitra* spp.) and lilies. Under low levels of disturbance the most sensitive species disappear but forbs such as *Dichopogon* spp., *Bulbine bulbosa*, *Pimelea* spp. and *Wurmbea diocea* survive, along with *T. triandra*. At moderate disturbance levels, sensitive species are rarely present, and the native herbs are generally disturbance tolerant, including *Chrysocephalum apiculatum*, *Convolvulus erubescens*, *Plantago varia* and *Asperula conferta*. High disturbance levels may contain a range of native grasses but *T. trianda* and most native forbs disappear. Very high disturbance sites are dominated by perennial exotic species or a low cover and diversity of native species, mostly grasses. These categories have reasonable correspondence with the states in the McIntyre and Lavorel model. Vey low and low disturbance = reference grassland. Moderate disturbance = native pasture. High disturbance = possibly improved native pasture. Very high disturbance = enriched grassland.

Most of the native grasslands of south-eastern Australia have been irreparably altered by pastoralism and agricultural intensification, but large areas have been destroyed by other developments including urbanisation (Sharp 1997). Much of the remaining native grassland and native pasture is currently managed by grazing of livestock. The ecological effects of grazing will next be examined in more detail.

Mammal grazing

“The countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the gunaco, deer, and ostrich.” Charles Darwin, *The Voyage of the ‘Beagle’*, 19 September 1833, on the Argentine pampas in the Buenos Aires region.

The grazing of domestic livestock has been more important than any other exogenous disturbance in altering the composition and structure of Australian temperate grasslands (Trémont and McIntyre 1994). “Grazing has a detrimental impact on communities with little history of grazing, but is necessary to maintain communities with a long history of grazing” (van Andel and van den Bergh 1987 p. 11). Sheep and cattle grazing initially caused increases in plant diversity in south-eastern Australia, resulting from the decline of the dominant native grasses, and invasion by exotics and native species from adjacent drier communities (Moore 1993). But ultimately under the nearly geographically uniform regimes of continuous grazing at set stocking rates, vascular plant diversity declined across large areas (Moore 1993). The irregular occurrence of severe drought, combined with plagues of introduced grazers, particularly rabbits, led to to episodes of intense overgrazing which have severely altered the natural grasslands. Overgrazed areas largely became “synthetic communities” (Trémont 1994 p. 511), lacking most of the orginal native plants and with a high proportion of exotic species.

The long term detrimental effects of overgrazing by livestock on south-eastern Australian temperate grasslands need to be kept in perspective. Grazing reduces the competitive effects of dominant species and creates open ground suitable for plant colonisation, so in general results in increased diversity of plant species and functional groups, with annuals particularly favoured (Trémont 1994, Trémont and McIntyre 1994, Lunt 1995c, Overbeck *et al.* 2007). Grazing at low intensities has maintained vascular plant diversity over large areas of so-called native pasture. Trémont (1994) compared native pastures intermittently grazed by sheep from the time of European tree clearing in the mid 1800s to 1976, and then either left ungrazed for 16 years or grazed at a stocking rate of 6.7 sheep ha^{-1} over the same period. Both areas were dominated by native grasses and most species present were native perennial forbs. The grazed treatment had a more open canopy, more bare ground, much greater species richness including small forbs and grasses and more common exotic annuals, whereas the ungrazed treatment had dense grass and litter cover, was species poor, but had a higher proportion of native perennials and more vegetatively reproducing forbs species. Dorrough *et al.* (2004) compared areas that were frequently grazed (native pastures), infrequently grazed (travelling stock reserves) and minimally grazed (roadsides) on the Monaro Plains and found that infrequently grazed areas had the highest native and exotic richness

The maintenance of high plant diversity in many grasslands is dependent on continued grazing, but negative biodiversity impacts, particularly on native species, may occur if grasslands have a limited evolutionary history of grazing (Hobbs and Heunneke 1992). Any change in the grazing regime may constitute a disturbance, and the impact of the changes on diversity and invasive species depends on their nature in relation to the historical regime (Hobbs and Heunneke 1992). As cogently observed by Trémont and McIntyre (1994 p. 646), “the absence of grazing stock from grassy communities is as important, in terms of community structure, diversity and composition, as its presence”.

Large grazing mammals coevolved with grasslands in the Americas (Webb 1977 1978), Africa and Eurasia and probably Australia (Jones 1999b). According to Bouchenak-Khelladi *et al.* (2009 p. 2398) a “major and rapid radiation of vertebrate herbivores ... occurred between 20 and 10 million years ago ... along with a near simultaneous rise to ecological dominance of grasses ... suggesting that grasses coevolved tightly with vertebrate herbivores”. Occupation of C_4-dominated grasslands by ungulates is inferred to have commenced c. 26 mybp, with occupation by Bovideae and Cervideae occurring in the early to late Miocene (23-5 mybp). Significant increases in silica density in C4 lineages, believed to be anti-herbivore defences that decrease palatability, digestibility and nutritional value, coincided with increases in ungulates with hypsodont characters, i.e. high-crowned, longer lasting teeth (Bouchenak-Khelladi *et al.* 2009).

During the late Tertiary and the Pleistocene epoch of the Quaternary in Australia a wide range of herbivorous birds and mammals developed in association with the wide occurrence of grassland. These included the 2-3 tonne *Diprotodon optatum*, giant macropods *Sthenurus*, *Procoptodon* and *Protemnodon*, the small grazing diprotodon *Palorchestes azael* and open country flightless birds (Frith 1973, Hope 1994, Johnson 2009). But in all continents except Africa the open country megafauna largely became extinct during the late Pleistocene, and the grazing regimes were therefore completely changed, with major ecological repercussions (Johnson 2009). The Australian herbivorous mammalian fauna was more severely affected than the Americas and Africa, losing almost all species over 100 kg in weight (Johnson 2009). Some 20 of the 50 Australian species that disappeared were grazers, with *Macropus* spp. being the largest survivors (Jones 1999b). Loss of the megafauna due to aboriginal overkill, as argued by Flannery (1994) remains contentious, but the major role of hunting in the extinctions throughout the world now appears to be widely accepted (Johnson 2009). The extinctions appear to have occurred over a long period from 50-30 kybp for the larger species, through to c. 10 kybp for the smaller (Hope 1994). Kershaw *et al.* (2000) argued that people coexisted with the megafauna for many thousands of years, but conceded (pp. 502-503) that recent redating of significant fossil megafauna sites largely reduced the overlap, making it unlikely that climate or habitat change were to blame. Loss of the megafaunal grazers would have resulted in major change in the vegetation (Flannery 1994), particularly by reducing tree and shrub herbivory, as in African savannas (Hope 1994). Knowledge of megaherbivores indicate that they effectively acted as ecological engineers. Their extinction has likely led to the replacement of large areas of open vegetation with closed, woody formations, a decline in the heterogeneity of vegetation across a range of scales, increased fire, primarily due to increased fuel loads and possibly resulting in new areas of uniform grassland, and the decline of coevolved plants, including the species they dispersed or which had evolved defences against them (Johnson 2009).

Grazing of sheep and cattle is now the major form of management in a large range of native grasslands, notably in the Australian Capital Territory (ACT Government 2005) and in many privately owned native pastures (particularly in southern NSW), and is a substitute for burning to reduce the biomass of dominant grasses (Stuwe 1994). Moderate or more intense grazing pressure can be more effective than fire in maintaining bare ground and the low biomass of dominant grasses required to maintain high diversity of indigenous annuals and prostrate species, but disadvantages the taller, upright herbs (Kirkpatrick *et al.* 1995). Native pastures near Armidale NSW ungrazed for 16 years had a species richness of only 20 species per 30 m^2 because of large grass tussocks, dense grass litter and little bare ground, while areas grazed continuously by sheep at moderate to low stocking rates were much shorter, with small tussocks, little litter and abundant small bare areas, and had a diversity of 36 species (Trémont and McIntyre 1994). Based on experimental results from disturbance treatments Sharp (1997) recommended retention of livestock grazing as a management regime in the ACT, particularly at sites with high diversity of small intertussock forbs. Thus it appears that sites that have been managed by livestock grazing for long periods will degrade if grazing is removed, but can be managed without significant biodiversity loss by continuing the established grazing regime.

The effects of introduced livestock grazing on native grasslands are complex, being dependent, *inter alia*, on the grazer species, the intensity and duration of the grazing pressure, and interactions with other environmental and management factors (Kirkpatrick *et al.* 1995, Lunt 1995c, McIntyre *et al.* 1995, Aguiar 2005). Some of the most basic components of grazing impact in Australia have been poorly understood and await adequate investigation (Johnston *et al.* 1999). For instance conceptions of what plants are important fodder have significantly changed historically. White (in the foreword in Leigh and Mulham 1965, p. v), commenting on the findings of pastoral research in the NSW Riverina, wrote that the pastoral research group had investigated “the question of which species are important at various seasons of the year. Often thirty or more species are available for selection and the extent to which the sheep exercises this opportunity is quite surprising. In many instances, in spite of appearances, inconspicuous plants or rather unattractive shrubs are more important to sheep than was formerly believed”. Lack of understanding of appropriate grazing regimes for natural grassland management continued into the period when grassland preservation became a *cause célèbre*: “Currently it is not known if it is preferable to maintain a continuous, light grazing regime or to graze intermittently, either lightly or heavily ... avoiding peak flowering and seeding times for native plants ... It may be that particular sites require different regimes, on the basis of the different species mix present, type of exotic infestation, drainage or other factors” (Sharp and Shorthouse 1996).

One effect that was believed to result in the deterioration of native grassland as a productive pasture was depletion of soil P through the harvest of livestock and from continual removal of wool (Wadham and Wood 1950). However Groves *et al.* (2003a) considered nutrient *addition* from continuous grazing to be a major factor in historical changes in grassland species composition, initially due to increased nutrient mobilisation through soil disturbance and death of native plants, and increased returns from faeces and urine, later through the addition of fertiliser and the sowing of legumes. Grazing adds highly labile mineral N direct to the soil, leads to higher average plant tissue N concentrations, decreased root: shoot ratios and sometimes less efficient N-uptake (Wedin 1999). Deposition of urine and faeces also alters the cycling rates of other nutrients. Nutrient enrichment and soil compaction associated with livestock camps in native grasslands favours weeds (Kirkpatrick *et al.* 1995).

Mammalian herbivore grazing impacts on patterns of recruitment, production and mortality of grazed and ungrazed species, on plant resource use and on resource availability. The most direct effect is removal of and damage to the above-ground parts that are consumed or trampled (Kirkpatrick *et al.* 1995), but the effects on plants that are not eaten may be among the largest impacts. Interactions between defoliation and release from competition can result in complex changes in structure and composition (McIntyre *et al.* 1995). Grazing alters the composition of the community by differentially altering the population density, genetic composition and structure of the component plants (Aguiar 2005) and by creating bare patches suitable for colonisation (McIntyre *et al.* 1995). It may also affect the structural diversity at the community level, although this possibility has been widely ignored (Aguiar 2005). Status as a grassland may be dependent on grazers that differentially destroy juvenile trees and shrubs, preventing reversion to woodland or shrubland (Hobbs and Heunneke 1992). The accessibility of perennating buds to the grazing animals is an important determinant of survival, so suvival of hemicryptophytes (with buds close to ground level) tend to decline only when grazing is intense (McIntyre *et al.* 1995). One immediate structural effect is that green leaf material becomes more concentrated close to the soil surface (Soriano *et al.* 1992). Plants that avoid grazing because of their small size or height tend to benefit more from relaxed competition under grazing pressure (McIntyre *et al.* 1995). In pampas grasslands, livestock grazing markedly reduces the average distance between plants by dividing large tussocks into multiple smaller plants (Soriano *et al.* 1992). Grazing may affect larger-scale patterns in vegetation including the 'dual-phase mosaic' or 'banded vegetation' of semi-arid rangelands, which consist of patches or bands of high cover vegetation in a matrix of low cover with different dominant plants; and since the matrix controls the hydrology and water availability in the patches, any disruption to it can impact the whole system (Aguiar 2005). At the small scale, grazing tends to reduce the biomass of dominant grasses, enabling higher vascular plant diversity. It commonly enables continued existence of the range of native grassland species, but allows the entry of a pool of exotics (e.g. Soriano *et al.* 1992 p. 392). Grazing in flooding pampas grasslands has increased plant diversity at the stand scale in this way, but has decreased it at the landscape scale because the exotics are mainly generalists with wide environmental tolerances (Perelman *et al.* 2001).

Grazing can exert strong selective pressure by altering the population structure of grazed and ungrazed species. Populations that are reduced in size can lose significant genetic diversity through genetic drift and inbreeding depression, while palatable species may evolve traits that provide grazing resistance or enable grazing avoidance (Aguiar 2005). Development of pastoral agriculture in the South American pampas has led to an increase of species that produce toxic secondary metabolites such as alkaloids and terpenoids (Aguiar 2005), and similar concerns have long been a focus of pastoral weed research in Australia.

Grazing directly affects litter degradation rates, and, by altering the floristic and growth form composition of the vegetation by removal of palatable and less grazing-tolerant species, alters litter makeup, decay rates and nutrient turnover (Villarreal *et al.* 2008). Reduction of litter by grazing reduces fuel loads and the probability of wild fire (Aguiar 2005).

Trampling can create openings for seedling establishment, reduce the dominance of tall growing species or directly reduce fragile species (Hobbs and Heunneke 1992). Direct evidence of trampling damage has been noted for example by Archer (1984) who recorded cattle and feral horse damage to colonies of *Thesium australe* (although not in temperate grassland).

Grazing animals also disperse seeds of native plants and exotic weeds, in their dung and externally (Hobbs and Heunneke 1992), discussed in more detail below. Other less direct effects include soil disturbance and compaction, destruction of the cryptogam crust, redistribution of nutrients via urine and dung, and the creation of bare ground (Mack 1989, Kirkpatrick *et al.* 1995. Sharp 1997). All of these changes can facilitate exotic grass invasion. The effects can be highly concentrated by congregation of herding livestock, resulting in wide variability in the spatial arrangement of damaged patches (Hobbs and Heunneke 1992). Studies in arid Australia have shown that sometimes >50% of the grazing in a paddock occurs in <25% of the area (Mott and Groves 1994). The location of watering points and fencelines, prevailing winds and stock preferences for particular plants are important factors influencing the pattern of grazing (Mott and Groves 1994).

The range of impacts alone or in combination can result in trophic cascades affecting native animals, and can lead to permanent changes in the physical characteristics of the land. Major degradation of pastures occurs when >30% of annual production is removed by grazing animals (Mott and Groves 1994). Drought periods are common in many Australia grassland areas and throughout the historical record, stocking rates have commonly not been altered to correspond with the accompanying reduction in forage production (Mott and Groves 1994). Continued grazing at accustomed levels during periods of climatic stress and alterations in other disturbance regimes can result in transformative shifts in grassland state (Aguiar 2005).

Grazing reduces the insect biodiversity of grasslands by simplifying the structural complexity of the plant components, with different major taxonomic groups affected in different ways (Tscharntke and Greiler 1995). Invertebrates can suffer particularly negative impacts from trampling (Hobbs and Heunneke 1992). Greenslade (1994) found indications that grazing has a strong impact on the composition of the Collembola fauna of ACT grasslands, one of the important detritivore groups, reflecting a general trophic cascade through the system.

Sheep and cattle

Audas (1950 p. 472) considered many Australian native grasses to be "excellent pasture or fodder plants ... equal, and in some cases superior to, the cultivated exotic kinds", including *T. triandra*, *Austrodanthonia penicillata*, *Microlaena stipoides*, eight species of *Adropogon*, and fifteen species of *Panicum* (Mitchell Grass and Umbrella Grass) ("splendid fodder" *op. cit.* p. 472). He noted the "rich, succulent and varied character" of indigenous pasture during spring and summer but the paucity of green foliage in winter. However quality is mainly determined by environmental conditions, and all species, native or exotic, have periods in which their forage quality is low (Johnston *et al.* 1999). The lack of cool season feed provided by native grasses contributed to a strong focus on the introduction, breedings and widespread planting of exotic C_3 grasses for pastoral use in south eastern Australia. A widespread perception developed from the late 1950s, based on unreplicated and otherwise biased studies, that native species were of little pastoral value (Johnston *et al.* 1999).

Long term continuous grazing by introduced bovid livestock, primarily by sheep *Ovis aries* and cattle *Bos taurus*, has resulted in major changes in the vascular plant species composition of grasslands throughout Australia (Moore 1993, Trémont 1994, Kirkpatrick *et al.* 1995, Groves and Whalley 2002). The most immediate effect of continual grazing, particularly by sheep, was to suppress or eliminate the most palatable and most easily damaged plants, which were eaten, trampled or failed to regenerate. Intertussock herbs were the first to disappear (Stuwe and Parsons 1977, Groves and Whalley 2002, Groves *et al.* 2003a). Murnong, *Microseris* spp., a staple food of aborigines, and once very abundant on the open plains, was greatly diminished or eliminated in some areas by 1846 due to depradation by sheep, which learnt to root up the whole plant, or continually defoliated it (Gott 1983). This species was also highly palatable to rabbits (Lunt 1996). Of 59 Victorian grassland sites sampled by Stuwe and Parsons (1977) *Microseris* was present at only one, an ungrazed railway grassland. Other Asteraceae including *Senecio macrocarpus* Belcher and *Rutidosis leptorrhynchoides* were unable to tolerate heavy grazing and are now severely depleted (Morgan 1995a, Humphries and Webster 2003, Hills and Boekel 1996). The grossly contracted range of *R. leptorrhynchoides* known in the mid 1990s consisted entirely of areas protected from domestic livestock (Morgan 1995a). Native legumes were probably also heavily affected: e.g. grazing and trampling by cattle is considered an important current threat to *Psoralea parva* (Muir 2003). By the 1990s, all remnants of Victorian basalt plains grassland with high vascular plant richness had been protected from livestock grazing for decades (Morgan 1998c). The fragile cryptogam crust also sufferred major early impact.

The grass component was more resilient than the forbs because grasses are less palatable, grass leaves continue to elongate from the base, dormant buds that develop lateral shoots are rapidly induced after destruction of apical meristems, and much of the meristematic tissue is located in the crown and is protected from grazing damage (Tscharntke and Greiler 1995). In general, rhizomatous and prostrate grasses are the least affected by bovid livestock (Mack 1989) or are favoured, so that grazed grasslands tend to become two-layered – a short layer of grazed species and a discontinuous taller stratum often dominated by caespitose Poaceae and other unpalatable species (Overbeck *et al.* 2007). In south-eastern Australian native pastures the 'layering' in the more heavily grazed grasslands tends to have a temporal rather than spatial dimension, with small short lived annual grasses such as *Vulpia* forming a large component of the living biomass in spring.

Most of the historical grazing regimes in Australian temperate grasslands have resulted in major alteration to the grass components. Throughout the world, selective herbivory of palatable grasses by domestic livestock is a major cause of species replacement (Mack 1989, Moretto and Distel 1998). *T. triandra* is regarded as a "good forage" in native pastures, although "mature plants are neglected" (Chan 1980 p. 22), and Audas (1950) warned of the danger of *T. triandra* being "eaten out" if grazed in spring and summer. However *T. triandra* has a high C:N ratio, which makes it less palatable than many other grasses (Moretto and Distel 2002). It is lost along with other native perennial grasses when there is continuous heavy grazing by sheep (Stuwe and Parsons 1977, Chan 1980) and it is more susceptible to elimination when grazing follows fire (Groves and Whalley 2002). Heavy grazing by sheep or cattle causes more damage to *T. triandra* than that by macropods or horses (Kirkpatrick *et al.* 1995). In the Australian Alps, cattle "prefer inter-tussock herbs (such as *Craspedia* spp., *Celmisi*a spp. and *Leptorynchos squamatus* subsp. *alpinus*) but make up bulk in their diet with tussock grasses (*Poa* spp.)", so they spend more time in grassland communities than other vegetation formations (McDougall and Walsh 2007 p.6). Discontinuous bovid grazing however enables a high proportion of native species to survive (Kirkpatrick *et al.* 1995). Losses of native grasses can continue even after pastures become highly degraded by invasion of exotic perennial grasses: data of Badgery *et al.* (2002) indicated declines of (un-named) perennial C_4 grasses under sheep grazing at 4.5 DSE ha^{-1} in areas with up to 50% coverage of *Nassella trichotoma*, along with declines of about 30% with grazing plus fertiliser (120 kg N and30 kg P ha^{-1} y^{-1}). Stafford (1991) found that remnant *T. triandra* in the East Torrens region of South Australia was generally found at sites with a long history of stock exclusion. However *T. triandra*, *Poa* and *Austrodanthonia* may survive long after the intertussock herbs have been eliminated (Groves *et al.* 2003a).

T. triandra is eventually replaced by exotic winter-growing species adapted to trampling and close grazing (Moore 1973, Gott 1983, Moore 1993, Kirkpatrick *et al.* 1995). At Derrimut, Victoria, *N. neesiana* presence and density is strongly negatively correlated with that of the dominant grass (*T. triandra*) and is probably a long-term result of previous heavy grazing and ploughing (Lunt and Morgan 2000). Grazing exclusion can lead to the dominance of tall caespitose grasses in the pampas (Overbeck *et al.* 2007). Long term grazing results in forb loss also in areas that are both burnt and grazed (Lunt 1990b 1997, Morgan 1997). Intermittent grazing has less severe effects on species composition and may alter or reverse the changes in the general degradation syndrome (Groves *et al.* 2003a). Hadden (1997) suggested that suitably modest regimes were 2DSE ha^{-1} during summer and autumn in Western Plains Grasslands, and 1DSE ha^{-1} during winter and summer and possibly parts of autumn in the drier Northern Plains.

Loss of intertussock plant species diversity also occurs in *T. triandra* grasslands that are protected from ungulate and rabbit grazing, and not frequently burnt. In the Western Basalt Plains, Hadden (1998) and Hadden and Westbrooke (1999) found a significant decline in herb species in plots protected from sheep and rabbit grazing in native pasture but an increase in cryptogam cover. Decline of herbs was due to *T. triandra* canopy thickening and closure over 2 years. Increase in cryptogams was attributed to absence of soil trampling. Native grass cover of ungrazed areas reached c. 80%, compared to 35% in grazed areas, while total plant biomass reached 3,575 kg ha^{-1} compared to 718 kg ha^{-1} in grazed areas. Trémont (1994) found that grazed grasslands in northern NSW contained greater native plant richness than ungrazed grasslands, probably as a result of suppression of dominant grasses (Sharp 1997). Hadden (1998) found no significant changes in botanical composition between grazed and ungrazed plots in a Victorian Northern Plains grassland when grazing was excluded.

Bovid grazing continues to threaten grassland remnants, notably along roadsides used for droving and grazing in drought conditions, e.g. to *Comesperma polygaloides* (McIntyre *et al.* 2004).

Gap creation intensifies with increased grazing pressure and pasture gaps are subject to less root and shoot competition and thus favour the survival of grass seedlings (Moretto and Distel 1998). In native grassland in Argentina Moretto and Distel (1998) found that gaps in the vegetation dominated by *Nassella clarazii* (Ball) Barkworth, characterised by low competitive pressure, enabled seedling establishment of the unpalatable stipoid grasses *Jarava ichu* Ruiz and Pav and *Nassella tenuissima*. However they did not compare regeneration of the palatable species, *N. clarazii*, so failed to test their stated hypothesis, that such gaps favour the unpalatable species. Creation of such gaps by overgrazing of the palatable species was nevertheless suggested as the mechanism enabling establishment of the undesirable grasses.

Bovid livestock are hard-hooved and weigh from 40 kg (*Capra hircus*) to nearly 1 tonne (*Bos taurus*) (Groves 1989) Their activity thus causes soil compaction, exacerbated with proximity to watering points, which they must visit regularly (Moore 1993). Physical effects include increases in bulk density and bearing capacity and decreases in hydraulic conductivity (a measure of infiltration) that are directly related to stocking rate (Willatt and Pullar 1983). Hoof pressures of >160 kPa for cattle and 64-100 kPa for sheep have been calculated for animals standing flat on four feet, and higher pressures result when animals are moving. Comparable pressures from tractors are 30-150 kPa (Willatt and Pullar 1983). Biological effects of compaction include significant decreases of arthropods and reduction of earthworm body weight and numbers (Brown 1987). In the early days of ungulate grazing, the basalt soils at Sunbury, Victoria, were changed from loose to hard by continuous trampling (Gott 1983). Thus *Microseris* spp., which preferentially germinates in loose soil (Gott 1983), was affected. Soil compaction makes harder soils, and many studies have demonstrated that root growth is negatively affected as penetration resistance increases (Willatt and Pullar 1983).

Disturbance of the soil and damage to the cryptogam crust favours exotic species over native (Stuwe 1994). With high levels of grazing the crust is often completely eliminated except where protected from trampling (e.g. along fence lines), but with sheep grazing at or below about 2.2. sheep ha^{-1} the soil crust is discontinuous and still noticeable (Scarlett 1994).

Bovids crop their food between the incisor-canine row and a hard pre-maxillary pad, with sheep cropping directly, close to the ground through a cleft in the upper lip, or after the fodder has been pulled into the mouth by the tongue (Groves 1989). They graze with a tearing motion, as opposed to the shearing, scissor-like motion of the incisors of marsupials and thus tend to pull whole plants from the ground, so have a more detrimental impact on perennial grassland species like *Psoralea parva* than macropods (Muir 2003). Sheep graze more closely to the ground than cattle and are more selective so can be more damaging to natural grassland (Moore 1993). They can prevent regeneration of chenopod dominants in drier *Atriplex-Maireana* grasslands (Moore 1993). Carr and Turner (1959) found that on the Bogong High Plains of Victoria *Poa* inflorescences were highly palatable to cattle but the mature leaves were not. Cattle feeding on snowgrasses generally pulled parts of tussocks out of the ground, causing damage to swards. Archer (1984 p. 85) found that cattle and horses not only ate the endangered *Thesium australe* "but tended in the process to uproot them or break them off at ground level".

The impact of feral sheep on vegetation and landscape in the absence of other livestock has been well documented for the Mexican island of Socorro by Walter and Levin (2008). Sheep were introduced in 1869 and have been the key cause of ecosystem degradation. Sheep trampled and pulverised the soil to dust, ate even tiny seedlings in overgrazed areas and transformed the native forest and woodland into open habitats with a mix of native and exotic vegetation. The half of the island without sheep was found to contain only one exotic vascular plant species, compared to 44 spp. in the sheep impacted half which contained many hectares of denuded ground and was susceptible to severe erosion. Sheep grazing favoured some poisonous unpalatable plants, enabled the rapid spread of some exotic grasses and was a causative factor in the decline and replacement of endemic birds.

Slashing, with removal of slashed material, and fire can be interpreted as grazing surrogates in so far as they result in removal of herbage. Slashing of *T. triandra* grassland once in April or twice in successive Aprils made no significant difference to intertussock gap distance at Derrimut compared with similar burning treatments (Henderson 1999). Stuwe and Parsons (1977) found that the only plant species more common in grazed sites than frequently burnt (railway) sites or roadsides were exotics: two spp. of *Briza* and *Centaurium* spp.

Insect faunas are generally impoverished under increasing intensties of livestock grazing (Samways 2005). Grazing alters invertebrate habitat by affecting plant components, vegetation structure, microclimates, litter and soil properties (Yen 1999). On the New England tablelands fertilised, improved pastures grazed by sheep have been found to have a higher proportion of exotic invertebrates than native pastures (Yen 1999 see his reference). Hadden and Westbrooke (1999) examined the effects of removal of sheep and rabbit grazing on the Formicidae, Coleoptera and Araneae fauna of long-grazed native *T. triandra* pasture near Ballarat, Victoria. 6 m x 6 m plots were fenced out of the pasture, grazed by sheep at 3 DSE/ha, for 2 years. Of the 7 most abundant ant species, the abundance of 2 species significantly declined, as did the abundance of the hot-climate functional group, a result attributed to increased plant cover. Of the most abundant Coleoptera, significant increases were found with 2 spp. and significant decreases with 3 spp., due to a complex of effects. The nominal "decomposer" functional group (comprising only Anthicidae) decreased. The two most abundant species of Araneae significantly declined in ungrazed plots. Changes in the proportions of spiders were related to structural change in the vegetation. As part of the same study Hadden (1997) found no significant differences in the richness or abundance of the same taxa individually or when grouped between ungrazed and grazed plots on the Northern and Western Plains over the whole two year period. Removal of grazing appeared to offer no short term improvements in the biodiversity of these groups. The fauna appeared to be well adapted to the grazing regime.

Rabbits and hares

The effects of overstocking with sheep and cattle are difficult to distinguish from those caused by large populations of European Rabbits, *Oryctolagus cuniculus* Lilljeborg, in Australia (Rolls 1984) and it is impossible to retrospectively separate their effects for the purposes of determining ecological history (Frith 1973). European Hares *Lepus europaeus* Pallas, have had a lesser impact and their effects are also confounded with those of livestock. Although hares are approximately twice the weight of rabbits, the two species are trophic competitors: both are herbage-feeding lagomorphs which include woody twigs in their diet under extreme conditions during summer. Both have digestive systems with caecal fermentation of digesta, both re-ingest soft faeces (caecotrophs) and daytime hard faeces and both are poor digesters of cellulose (Stott 2007).

Large populations of rabbits first became widely established in Australia on the Victorian basalt plains near Winchelsea in 1859 and by 1890 had occupied all suitable habitat in Victoria (Menkhorst 1995d). The first reports of pastures being "eaten out" were made in 1868 (Rolls 1984 p. 30). The impact on native grasslands was ecologically disastrous e.g. factories at Colac and Camperdown canned half a million rabbits from the stony rises in 1881 (Rolls 1984 p. 53) and a factory was opened in Hamilton in 1892 which processed 720,000 animals in 1894 and a million in the first eight months of 1895 (Brown 1987). Rabbits had spread widely on the Central Coast of NSW by 1883 and were present on the New England tablelands in 1862 after release in 1854, but did not become abundant there until the early 20th century (Rolls 1984), with significant impacts in the Armidale region from c. 1909 (Johnson and Jarman 1975) and plague proportions in the Glen Innes district by 1920 (Cameron 1975). Areas of the NSW western plains and Riverina were occupied in 1879 and suitable areas in the rest of the State were slowly occupied by 1925, at a rate of about 15 km per year (Rolls 1984). Rabbits occupied the burrows of wombats in wetter areas, bilbies in the inland (Rolls 1984) and burrowing bettongs *Bettongia lesueur* (Quoy and Gaimard) (Noble 1993, Noble *et al.* 2007).

Rabbits extensively graze grasslands, reducing total herbage yield markedly, altering floristic composition and facilitating weed invasion (Long 2003, Bloomfield and McPhee 2006). Cameron (1975 p. 22) considered it "clear" that they "eradicated a number of the species of better natural grasses" in the Glen Innes district of NSW. Depradation of rabbit populations following the first myxomatosis epidemics resulted in the appearance of grassland on previously bare and stony lands (Frith 1973).

Rabbits are selective feeders, with a high rate of feed intake, rapid gut passage, selection excretion of fibre and selective retention of non-fibre constituents for microbial fermentation in the hind gut (Stott 2007). Rabbits graze very close to the ground (Long 2003) and preferentially eat new seedlings during autumn and winter, in spring increasingly consume grass flower heads and leaves of broadleaf species and later the inflorescences of other dicots, and in summer the green feed of summer-growing native grasses, which may be eaten 'as fast as they grow', along with inflorescences and roots of *Trifolium* spp. (Menkhorst

1995d p. 280). Rabbit grazing preferences reportedly result in increases of less palatable grasses and weeds (Frith 1973). In the Riverina the combined effects of rabbit and sheep grazing “practically eliminated” *T. triandra* (Lunt *et al.* 1998). Annual grasses, such as *Hordeum* spp. often proliferate where rabbit damage has been severe (Bloomfield and McPhee 2006).

Rabbit grazing is a recognised threat to a range of endangered vascular plants in temperate grasslands. These include *Senecio macrocarpus* (Hills and Boekel 1996 2003) and *Comesperma polygaloides* (McIntyre *et al.* 2004). Grazing by rabbits or European hares *Lepus capensis* L. is a threat to remnant populations of *Swainsona* spp. in the Wimmera and Northern Plains of Victoria (Earl *et al.* 2003). *Thesium australe*, once common in grasslands, is also threatened by rabbits (Archer 1984).

Rabbit grazing, like that of bovid livestock, can also be beneficial by reducing cover of grasses. Lunt (1990d) thought it may have contributed to the high richness of vascular plants in herb-rich woodlands he surveyed in western Victoria.

Rabbits and the rabbit industry had a severe impact on grassland animals. Large number of bandicoots were killed in rabbit traps, by poisoning, and the fumigation and ripping of burrows and the spread of rabbits probably assisted the proliferation of foxes, which after the introduction of myxomatasis in the early 1950s, had to switch their prey preferences to include a larger proportion of native animals (Brown 1987). Paradoxically, for a time, the availability of rabbit burrows for shelter may have aided the survival of the Eastern Barred Bandicoot *Perameles gunnii* Gray after destruction of tussock grass cover (Brown 1987).

Rabbits “not only till the soil they fertilize it as well” (Bloomfield and McPhee 2006 p. 150): rabbits displace large quantitites of soil by digging, create bare areas around their warrens and deposit large quantitites of dung at discrete latrine sites, which become nutrient enriched. These areas seasonally support dense patches of weeds and can function as establishment foci for new weeds (Hobbs 1989, Bloomfield and McPhee 2006).

Rabbit plagues accompanied by livestock grazing have severely affected grasslands in the Victorian Wimmera and Murray Mallee (DNRE 1997) and overgrazing by rabbits is still a problem in native grasslands west of Melbourne (Brereton and Backhouse 2003) and elsewhere.

Hares select higher quality food than rabbits, consume much more food per unit body weight and produce much more faecal material, but have relatively smaller stomachs and caeca and retain a significantly smaller proportion of poorly digestible material (Stott 2007). They forage much further from cover than rabbits (Stott 2007). European hares were introduced into Victoria in the 1870s and spread through much of south-eastern Australia “particularly in the better-grassed areas” (Frith 1973 p. 81). In the Glen Innes area of the Northern Tablelands the first sightings occured in 1889, numbers increased steadily through the 1890s with a bounty first offerred for scalps in 1893, but populations declined and ceased to be problematic by 1920 (Cameron 1975). A bounty was offerred in the Armidale district by 1902 and scalp returns peaked in the middle of that decade, decling to c. 30,000 by 1914 when the bounty was removed due to budgetary problems (Johnson and Jarman 1975). The grazing habits of hares in Australia have not been studied (Frith 1973, McDougall and Walsh 2007).

Marsupials

South-eastern Australian grasslands were once occupied by a diverse array of marsupial herbivores (see section below on the mammalian fauna of grasslands) of which nearly all are now absent. Little is known about the intensity or nature of marsupial grazing (Ellis 1975, Morgan 1994). Moore (1993 p. 351) stated that southern Australian *T. triandra* grasslands “evolved under light and intermittent grazing by native marsupials”, but this statement conceals a pronounced level of ignorance and is probably a misleading generalisation. Marsupials would have consumed significant quantities of plant material and maintained a much more rapid and patchy cycling of nutrients than occurs today in ungrazed grasslands (Flannery 1994). Kangaroos would have been very numerous, particularly in areas with adjacent tree cover (Willis 1964, quoting George Russell, an early settler). Early historical records in Tasmania describe ‘marsupial lawns’ created by heavy marsupial grazing, and such closely grazed areas exist today in areas where large numbers of *Macropus* spp., *Thylogale billardierii* (Desmarest) and *Vombatus ursinus* (Shaw) occur, as well as in areas grazed both by sheep and marsupials (Kirkpatrick 2007).

Little information appears to be available about the ecological functioning of marsupial grazers in native grasslands and their impact on exotic grasses. Ellis (1975) mentioned studies in north-eastern NSW that found that nine sympatric species grazed both native and introduced plants and maintained niche segregation by differences in habitat utilisation. Cameron (1975 p. 20) reported that kangaroos in the Glen Innes area of the Northern Tablelands “seemed to prefer the green shoots on the kangaroo grass in the late spring and summer”, but there were “signs that [they like] the imported grasses and ... numbers will increase” (p. 24). Robertson (1985) investigated the interactions between the most important and widespread of the extant marsupial herbivores, the Eastern Grey Kangaroos *Macropus giganteus* in open grassy woodlands at Gellibrand Hill, Victoria. The diet of *M. giganteus* was found to consist almost entirely of monocots, mainly grasses. Green shoots and new growth were selectively eaten and the species selected tended to be those with the highest nutritional value at a particular time. From late spring to autumn *T. triandra* was by far the most important dietary constituent, but other warm season grasses were also eaten. Cool season grasses were the main forage during other periods, with *Austrodanthonia* spp., *Microlaena stipoides* and a range of exotic species being the most important. Grass inflorescences were readily consumed, particularly those of the exotics *Lolium rigidum* and *Briza maxima* L., but species with long awned and sharp seeds such as *Austrostipa* spp. and *T. triandra* were usually avoided. *Poa sieberiana* Spreng. and *Austrodanthonia* spp. , both large grasses with relatively fine leaves, were largely avoided once they developed large amounts of attached dead litter, but *T. trianda* plants with high standing litter were not. Burning provided more palatable and accessible fodder. McIntyre (1995) noted that grassland sites in National Parks on the Northern Tablelands of NSW were rich in native vascular plant species, *because* they had marsupial grazing, an effect resulting from release from competition with the dominant grasses (Morgan 1994). Lunt (1990d) thought kangaroo grazing may have contributed to the herb richness of woodland vegetation in the Grampians and Langi Ghiran in a similar way. Murphy and Bowman (2007) referred to a study in semi-arid western NSW which found that 16 months post-fire, areas burnt but ungrazed by kangaroos had four times the abundance of *Austrostipa variabilis* (Hughes) S.W.L. Jacobs and J. Everett than areas that were kangaroo-grazed, suggesting a feedback loop between fire, kangaroos and the dominant grass.

The toes of macropods are padded and soft in comparison with the feet of bovid livestock, and extant large macropods have masses much less than cattle (large male *Macropus giganteus* 80 kg: Hume *et al.* 1989) and more comparable with sheep. They are therefore less likely to disturb the soil and damage the cryptogam crust. The digestive system and digestive physiology of the large macropods have many similarities to those of ruminants (Frith 1973), but they are much better able to process high fibre grass than ruminants, whose intake increasingly declines as the proportion of cell wall constituents in the feed increases (Hume *et al.* 1989). Large grazing *Macropus* spp. "appear to be ideally adapted to maintaining their feed intake as grasses mature during dry periods and increase in fibre content" (Hume *et al.* 1989, p. 684) and some species can efficiently use low-quality forage (Frith 1973, Ellis 1975). Macropod diets consist mainly of leaves of monocots and dicots, grasses being the most important food of the larger species (Ellis 1975, Hume *et al.* 1989, Morgan 1994, Bennett 1995), with readily digestible green leaves being prefered. The diet of *M. fuliginosus* (Desmarest) includes "many other plants, particularly forbs" and dietary shifts during periods when grasses decline commonly occur (Bennett 1995 p. 138).

Kangaroos eat many plants which livestock usually avoid. They are able to be more selective feeders than the blunt-muzzled bovids because they possess narrow muzzles, bearing narrow incisor arrays (Groves 1989). Under good conditions macropods can coexist with livestock, particularly cattle and horses, because they select a very different set of food items (Frith 1973, Hume *et al.* 1989). However where weedy dicots are a problem, their preference for grasses may exacerbate invasion (Morgan 1994). Other macropods, including the Spectacled Hare-wallaby *Lagorchestes conspicillatus* and the Bridle Nail-tailed Wallaby *Onychogalea fraenata* have decreased greatly as a result of overgrazing of livestock on *Astreleba* grassland and chenopod shrubland (Ellis 1975).

Many macropod species, including *Macropus* spp., cause minor soil disturbance at resting sites, often in the shade, or at basking sites (Hume *et al.* 1989).

Overgrazing by kangaroos is also a threat to grasslands. The population of *Senecio macrocarpus* at Yan Yean, Victoria, is thought to have dramatically declined rapidly between 1987 and 1992 due to high kangaroo density (Hills and Boekel 1996 2003).

No information appears to be available on interactions between *N. neesiana* and macropods. Existing knowledge of their ecology suggests they may be better able to suppress it than domestic livestock, and theoretical considerations based on recent analyses of biotic resistance (Parker and Hay 2005) suggest that they might prefer it to native grasses. *Macropus* spp. are probably poor vectors of seed in comparison to sheep, since they have short pelage and more flexible mode of foraging, making them less likely to contact seeding culms, and have coexisted with the similarly hazardous seeds of *Austrostipa* spp. in evolutionary time.

The role and effects of fire

"In grassy plains unoccupied by the larger ruminating quadrupeds, it seems necessary to remove the superfluous vegetation by fire, so as to render the new years growth serviceable". Charles Darwin, *The Voyage of the 'Beagle'*, 15 September 1833, on the Argentine pampas between Bahía Blanca and Buenos Aires.

Fire is a regular feature of temperate grasslands throughout the world. In Australia fire became an important environmental factor in the late Miocene (c. 10 mybp), coincident with the decline of rainforest (Martin 1994). It has been a constant and generally increasing feature through the Quaternary period (c. 1 mybp +) but "it has not proved possible as yet to quantify vegetation/fire relationships" (Kershaw *et al.* 2000 p. 482).

Fire is a critical process in maintaining open patches and the maintenance of high productivity in fire-dependent grasslands (Hobbs and Heunneke 1992). Fire reduces the cover of all herbaceous grassland plants to close to zero, with generally only 'fire-resistor' perennial caespitose grasses retaining some standing live biomass, slightly above the soil surface, after burning (Overbeck and Pfadenhauer 2007). Post fire, the contribution to total plant cover from caespitose grasses gradually increases (Overbeck and Pfadenhauer 2007) and after several years can approach 100%, under suitable climatic conditions, leading to the loss of a high proportion of other vascular plants. Thus plant diversity is "directly linked to the fire cycle" (Overbeck and Pfadenhauer 2007 p. 36). Biomass accumulation has been well documented in Australian *T. triandra* grasslands, where Lunt and Morgan (1998a) recorded doubling of *T. triandra* density in the first year post-fire, doubling again in the second year to c. 5 tonnes ha^{-1} with c. 50% the biomass dead, and doubling again >6 years post-fire, by which time biomass levels of 8 t ha^{-1} had been reached of which over 5 t ha^{-1} consisted of dead material.

The mechanisms by which fire alters the composition and functioning of communites include the removal of the litter layer, creation of bare ground for seedling establishment, removal of shade and transpiration and thus alteration of microclimate, addition, depletion and creation of nutrients and the formation of ash beds. Fires in grasslands usually result in brief increases in soil fertility (Hobbs and Heunneke 1992), with temporary increases in N, K, Ca, Mg and pH in the uppermost layer, but can reduce fertility in the long term, depending on frequency, severity and season of burning (Overbeck et al. 2007). Nutrient addition from fire could result in increased invasion (Hobbs 1989). Fire results in liberation of plant-stored N to the atmosphere and alterations to the fire cycle resulting from grass invasion may thus impact on N fluxes in a grassland (Rossiter *et al.* 2003).

Particular plant species may be promoted or disadvantaged depending upon the frequency, seasonal timing and intensity of fires, the condition of the vegetation, and the biology of the native and exotic plants in the community (Hobbs and Heunneke 1992, Adair 1995, MacDougall and Turkington 2007). Fire probably commonly has differential effects on different life stages of particular species (Overbeck and Pfadenhauer 2007) so deliberate grassland management using fire must consider not just the seasonal phenologies of the native species (MacDougall andTurkington 2007) but the demographic structure of the species populations (Hobbs and Heunneke 1992).

The effects of fire on the flora of native grasslands is dependent on its thoroughness (patchiness), which is related to fire intensity but dependent on landscape features and local site characteristics such as presence of rocks and steep slopes, and on the season of burning (Stuwe 1994, Overbeck and Pfadenhauer 2007). Fires during different seasons favour different sets of plants. For instance annual species can be lost if fire occurs after full germination of their seed bank but before flowering (Kirkpatrick *et al.* 1995). The patchiness of fires determines the amount of diversity at the community level in grasslands (Lunt and Morgan 2002).

Soil temperatures below 45-55ºC cause little damage to vascular grassland plants and higher temperatures resulting from fire are generally restricted to the top centimetre of soil (Overbeck and Pfadenhauer 2007).

Fire-suppression can have serious negative consequences for biodiversity in fire-adapted grasslands and may result in their transformation into shrub or tree dominated systems (Hobbs and Heunneke 1992). The extent to which native grasslands in south-eastern Australia were subject to fire prior to European settlement remains controversial, as does the role of fire, as opposed to climatic factors, in the maintenance of grasslands through ecological time (Jones 1999b). Flannery (1994), amongst others, marshalled substantial evidence that grassy woodlands and grasslands were the dominant vegetation types on the mainland before 1750, or at least much more widespread than contemporary vegetation suggests, and that the land was regularly burnt by aborigines. According to Kirkpatrick *et al.* (1995 p. 25) "all evidence suggests that fire was highly frequent, if not annual" before European occupation. Moore (1993 p. 351) stated that southern Australian "*Themeda* grasslands evolved under ... periodic burning", a clear exaggeration of the extent of scientific understanding.

Benson and Redpath (1997) examined these views of pre-European fire regimes and found no evidence of large scale annual aboriginal burning in south eastern Australia as a whole. They identified misinterpretation and unwarranted extrapolation from the records of early explorers and settlers as the basis for the view that 'fire-stick farming' was widespread in south-eastern Australia. However they appear to be overenthusiastic debunkers: no serious researchers make claims that grassy ecosystems were present in many of the areas they discuss.

Jones (1999b) argued that the persistence of grassland requires fire at a certain frequency, that can burn without impediment across the landscape. Pollen in a core from Lake George on the southern tablelands of New South Wales indicates that communities with significant grass components were present during periods of glaciation. According to Jones (1999b) a major change to the dominance of Poaceae and *Eucalyptus* occurred during the late Pleistocene (uncertainly dated to c. 130 kybp), but Kershaw *et al.* (2000 p. 501) argued that eucalypt and grass dominated vegetation "with fire as a well-established environmental component" existed for most of the Quaternary before this time, possibly largely due to regional warming. Pollen of Poaceae is present throughout a swamp core from Lake Terang in western Victorian covering a period to c. 120 kybp, but increases towards the Holocene (Jones 1999b). Records from charcoal deposits are complex, but they currently provide no general, strong indication of an increase in fire during the periods (30-50 kybp) of first human occupation and the extinction of the megafauna (Johnson 2009). It appears likely therefore that any general increase in vegetation biomass expected with the loss of the megafauna was mainly of shrubland that was not susceptible to wide scale burning under the prevailing cool, wet conditions (Johnson 2009). However, grassy steppe vegetation that occurred in areas now in Bass Strait 25 kybp "shows abundance evidence for fire" and carbon particles reach high levels at Lake George at the start of the Holocene (Hope 1994).

According to Stuwe (1994), natural fires, ignited by lightning were of frequent occurence in the natural temperate grasslands of continental south-eastern Australia. Enough fuel accumulates in most grasslands to allow an annual fire (Kirkpatrick *et al.* 1995). Kirkpatrick (2007) argued that lightning has been relatively rare in Tasmania during the last few thousand years but that it currently caused fires and must have caused the charcoal deposits present in Tasmanian soils before aboriginal occupation. Flannery (1994) argued that there are more than enough natural ignition events in most areas to burn the standing crop of fuel before it can decompose, and that deliberately lit fires would therefore have increased fire frequency but decreased fire intensity. The extent and temporal variation of natural fires are "largely unknown" though evidence suggests that soil and climate rather than fire determined treelessness, and lack of recent evidence of tree invasion of grasslands not managed by fire supports this conclusion (Lunt and Morgan 2002).

Very little is known about the frequency and seasons of aboriginal burning in south-eastern Australian grasslands (Morgan 1994). Aboriginal activities increased the fire frequency (Stuwe 1994), but opinions differ about the magnitude of the increase and the effects. Benson and Repath (1997) considered that "the extent, frequency and season of their use of fire is largely unkown". In "the more developed areas" of Tasmania wide aboriginal use of fire appears to have occurred in the last 10,000 years (Kirkpatrick 2007). Gott (1999) argued that burning of the temperate grasslands was deliberately controlled and timed to provide the most beneficial effects in terms of food production. Lunt *et al.* (1998) concluded that early historical records indicate that indigenous grasslands were frequently burnt. Any plants not adapted to frequent fires must therefore have been eliminated or confined to fire-free refugia long ago (Stuwe 1994).

Grasslands taken up for livestock grazing were not managed with fire. In contrast, non-agricultural grassland remnants were frequently burnt in rail reserves (1860s?-1970s, often annually in late spring) and on roadsides (Western Victoria at least 1940s-1970s), as a cost-effective form of management (particularly to protect against wildfires) and those areas had the highest vascular plant diversity of all grassland remnants (Morgan 1997, Lunt and Morgan 2002), although some species were "presumably... eliminated" by the historical management activities (Morgan 1997). Sutton (1916-1917 p. 117) observed that in the Keilor Plains the "fires of spring ... never quite die down". Recent fire regimes involve deliberate small scale management fires and occasional wildfires. Many linear remnants (roadside and rail easements) have been regularly burnt in early summer while conservation reserves have been subject to irregular (often "erratic") early autumn burning (Lunt and Morgan 2002 p.180).

The fire intensity (energy release per unit area) in temperate south-eastern Australian grasslands is generally low (in comparison to tropical grassland fires), because of the small quantitites of fuel and the slow rate of spread of managed fires (Lunt and Morgan 2002). In *T. triandra* grasslands above-ground plant biomass is in the range of 7-11 tonnes ha^{-1} in infrequently burnt grasslands (7-11 years since fire) to c. 1-4.8 tonnes ha^{-1} in grasslands burnt 1-2 years previously (Lunt and Morgan 2002). *T. triandra* stands rarely produce enough litter in the first year after a fire to enable another burn (McDougall 1989). In *Poa* and *T. triandra* grasslands the dominant grass often accounts for >90% of the biomass (Groves 1965, Lunt and Morgan 2002).

Nutrients in ash are more readily lost in runoff or by wind erosion after fire (Flannery 1994). Fire also directly releases nutrients to the atmosphere, particularly N, and the levels of available soil N are often affected by repeated burning (MacDougall and Turkington 2007). An estimated 24 kg ha^{-1} of NO_2 was lost when tropical grassland at Katherine, Northern Territory was burnt (Flannery 1994). MacDougall and Turkington (2007) however found no such effect of N loss in savannahs in British Columbia, consistent with other recent studies, and thought that a combination of fire effects on litter, soil temperature, soil microbes, etc. could have suppressed N mineralisation. Moore (1993 p 352) stated that fires in *T. triandra* grassland ungrazed by livestock result in a "short-term flush" of N mineralisation in the soil, and suggested that *T. triandra* is uniquely able to take advantage of this resource.

The critical factor for survival and resprouting of vascular plants of frequently burned grasslands is the degree to which buds are protected from fire damage (Overbeck and Pfadenhauer 2007). In general in temperate south-eastern Australian grasslands fire promotes vigorous resprouting by native perennials, but generally very little perennial seedling recruitment: fire enhances the vigour and flowering of many perennial herbs but results in little change in plant species composition (Lunt and Morgan 2002). However buring can lead to major increase in the abundance of annual exotic species on long-unburnt sites (Lunt 1990c). *T. triandra* grassland fires are relatively cool, and when occurring in summer and early autumn have little negative effect on the flora, which survives with maximal underground carbohydrate storage, buried buds and buried seed, although seeds on the soil surface are destroyed (Lunt and Morgan 2002). The majority of intact *T. triandra* grasslands on the Victorian volcanic plains are burnt at intervals of 1-5 years (Morgan 1998d) a frequency recommended by McDougall (1989). Healthy *T. triandra* swards are usually maintained with fires at this frequency and no grazing (Lunt and Morgan 2000). The time of burning (late summer or autumn) is probably not critical for the health of *T. triandra* populations, but fire greatly reduces the amount of *T. triandra* seed produced in the following autumn (McDougall 1989). Reduced fecundity in the short term is compensated for by increased plant surival and vigour. Morgan (1997) predicted that reducing the fire frequency from 1-2 years to 5 or more years would substantially alter the dynamics of the population if seedling recruitment was reduced and established plants were incapable of adjusting.

Most of our knowledge relates to the grasslands in which *T. triandra* is dominant and highly productive, systems that naturally promote fire. Much less is known about fire effects in grasslands not dominated by *T. triandra*. *Poa* spp. "appear to be able to maintain their dominance without disturbance by burning or other forms of biomass removal" while *Austrodanthonia* and *Austrostipa* grasslands accumulate little biomass and are not thought to need regular biomass reduction to maintain plant diversity (Lunt and Morgan 2002 p. 183). Little seems to be known about fire effects in the Riverine Plains grasslands.

Themeda triandra biomass accumulation and senescence dieback

The dependence of *T. triandra* grasslands on fire is almost universally recognised, despite the very limited understanding of their evolutionary origin and palaeoecology, particularly in relation to ancient grazing regimes. They appear to be similar to temperate fire-adapted grasslands with C_4 dominants worldwide, where the C_4 species promote their own dominance by building high levels of biomass and thus promoting fire. *T. triandra* stands that are not burnt, or otherwise biomass-reduced, gradually develop massive quantities of dead leaves and litter, and failure to remove this biomass can cause tiller and plant senescence, attributed to "self-shading" (Lunt and Morgan 2000). Major *T. triandra* mortality occurred at Derrimut and Laverton North grasslands when fire frequency exceeded 5 y, and when fire was finally used, plant and tiller densities were much lower than in regularly burnt grassland (Morgan and Lunt 1999, Lunt and Morgan 1999a 1999c). Mass dieback of *T. triandra* resulting from the absence of fire or other biomass reduction has been described as "grassland collapse" (C. Hocking pers. comm.).

According to Lunt and Morgan (1998a p.70) "the grassland becomes increasingly choked up with dead grass material, above which the tussocks form a thin mantle of new, green growth", and eventually living tillers can "no longer poke up through the dead grass to reach the sunlight, causing the tussocks to die". Supposedly, there is "insufficient light penetrating through the canopy of old foliage to the young tillers to enable them to photosynthesise sufficient energy" (Lunt *et al.* 1998). *T. triandra* grassland not burnt for greater than 6 years is now thought to senesce in this way (Morgan and Lunt 1999, Lunt and Morgan 2002), rather than reach a steady state (Lunt and Morgan 2002). Low soil fertility and moisture levels may sometimes prevent such senescence (Kirkpatrick *et al.* 1995), so on less productive sites *T. triandra* senescence requires considerably longer periods or may never occur. O'Shea (2005 p. 161) stated that on productive sites, the phenomenon requires 10-11 years: "the canopy collapses upon itself and forms a thick layer of dead thatch over the soil surface, allowing only minimal seedling recruitment and preventing new tiller initiation". According to Muyt (2005 p. 3), the dense *T. triandra* thatch "undermines the growth of [the grass] itself; plants become increasingly brittle and subject to collapse". After burning *T. triandra* usually regains high cover quickly, returning to pre-fire biomass levels in 2-4 years (Morgan 1994, McDougall and Morgan 2005) and can form a complete dense canopy in as little as 3 years. Death of the dominant grass results in a major nutrient pulse in the soil, resulting primarily from decay of *T. triandra* crowns and roots, and this enables invasion by exotic plants (Wijesuriya 1999, Wijesuriya and Hocking 1999). Weedy exotics are now generally pervasive in these systems, so what would happen in the absence of exotic seed sources after *T. triandra* die-off is not clear.

The senescence dieback phenomenon has been widely reported worldwide for other dominant temperate and subtropical C_4 tussock grasses adpated to fire (Bond *et al.* 2008). Although often described under different rubricks (e.g "detritus accumulation" – Knapp and Seastedt 1986) the effect is the same: accumulation of standing dead litter shades out and kills the shade-intolerant new tillers (Knapp and Seastedt 1986; Everson *et al*. 1988, Uys *et al.* 2004). Fire frequency is thus one of the most important determinants of the grass species composition in C_4 grasslands: "fire-dependent grass species, typically members of the Andropogoneae ... are fire-dependent in the sense that they decrease in, or disappear from, a sward in the absence of frequent burning" (Bond *et al.* 2008 p. 1747). Lunt and Morgan (1999a) reported a 70% decrease in *T. triandra* tussock density and a 58% decrease in live tiller density in rarely burnt areas. Similar changes are indicated by Uys *et al*. (2004) who found that the cover of *T. triandra* in a mesic (735 mm per annum) South African grassland decreased from c. 70% when annually burnt to < 5% after fire exclusion for 4 or more years, and the plant effectively disappeared from mesic and montane sites that were unburnt..

In southern Brazilian mixed C_3 and C_4 tussock grasslands dominated by C_4 grasses, Overbeck and Pfadenhauer (2007 p. 35) observed that "without periodic removal of biomass ... shading by dead [grass] biomass inhibits survival and tillering and higher humidity under the litter may cause death and decay of underground plant parts within a few years". Post-fire effects that increase the vigour of tussocks have been recorded for a number of dominant species in other parts of the world, including increased photosynthetic activity, growth rates and sexual reproduction (Overbeck and Pfadenhauer 2007).

The *T. triandra* senescence phenomenon may be compared with 'normal' grass senescence, which occurs in all Poaceae in response to drought (Norton *et al.* 2008) and is a mechanism to reduce plant mortality from water stress, by the gradual 'abandonment' of foliage. Senescence dieback of *T. triandra* swards after extended periods of biomass accumulation might possibly be the result of altered water relations, rather than the postulated 'self-shading': the underlying mechanisms require further investigation. But like other dominant C_4 grasses worldwide, accumulation of large quantitites of dead biomass by *T. triandra* is apparently an adapted strategy that enables it to perpetuate its dominance by providing appropriate conditions for frequent burning (Hocking and Mason 2001). The high C:N ratio of C_4 grass foliage means the leaves have low nutritional quality and limited palatability to herbivores (Moore 1993, Moretto and Distel 2002) so a higher proportion die without being eaten than leaves of C_3 grasses, and the litter is more resistant to microbial breakdown than that of non-C_4 plants (Wedin 1999, Groves and Whalley 2002) so more of it can accumulate.

Senescence dieback of *T. triandra* increases the soil available nutrients, probably as a result of increased rates of decay of both above and below ground vegetation, due to increased moisture and temperature under the thatch of dead leaves, and by reduced nutrient uptake by living biomass (Hocking and Mason 2001). However utilisation of the nutrient pulse by other plants is not possible until the high cover of dead grass decays or or is removed by fire or other biomass reduction. When this occurs major weed growth usually follows (Hocking and Mason 2001).

Effects of *T. triandra* biomass accumulation on other species

Commonly, in the absence of of regular biomass reduction by fire, grazing or mowing, litter accumulation by exotic or native perennial grasses results in the suppression of the smaller intertussock native vascular plant species (McIntyre 1993, Kirkpatrick *et al.* 1995, Morgan 1998e). Entire populations of perennial forbs can disappear within a short period in the absence of fire (Morgan 1998e). In *T. triandra* grassland unburnt for >5 years the cryptogam crust also degenerates due to litter accumulation, shading and increased earthworm activity (Scarlett 1994). However bryophyte diversity in areas burnt at 1-2 year intervals is reduced compared to longer unburnt areas (Morgan 2004).

Periodic biomass reduction is required to maintain the vascular flora, a large proportion of which have soil seed banks which disappear after 1 year (Lunt 1990c 1995a, McIntyre 1993, Stuwe 1994). Morgan (1995b) for example found that 90% of *Rutidosis leptorhynchoides* seed germinated within a few weeks of autumn rains. Endangered species that are threatened when fire frequency in *T. triandra* grasslands is too low include *Senecio macrocarpus* (Hills and Boekel 1996) and *Rutidosis leptorrhynchoides* (Morgan 1995a, Humphries and Webster 2003). Sharp (1997) experimentally confirmed the hypothesis that litter removal is required to facilitate establishment and reduce suppression of the smaller native grasses and the low-growing and small forb components in ACT grasslands. Lack of fire or some other management regime with similar effects is therefore a threat to the continued existence of the more mesic, *T. triandra* dominated grasslands, both in terms of the keystone species (*T. triandra*) and most of the other plant components. Suppression of other native species by the dominant grasses is not generally a problem in grasslands on shallow rocky soils and the more xeric inland plains, and fire is not necessary to maintain their indigenous vascular plant diversity (Kirkpatrick *et al.* 1995).

Effects of fire on *Themeda triandra*

T. triandra is well adapted to survive fire but mortality nevertheless occurs. Stafford (1991) reported that very few four-year-old *T. triandra* plants survived an intense wildfire in Cleland Conservation Park, South Australia, and a fire at Organ Pipes National Park, Victoria, in April 1997 before a severe drought resulted in substantial mortality and a dramatic cover decline (McDougall and Morgan 2005). However biennial autumn burning at Organ Pipes usually did not inhibit an already established trend of increased *T. triandra* frequency and cover (McDougall and Morgan 2005). Burning generally does not kill *T. triandra* tussocks (Henderson 1999) nor the very high proportion of other grassland plants which are fire-adapted hemicryptophytes, geophytes etc., i.e. perennial plants with perennating buds protected underground (Morgan 1996, Lunt 1990a 1990c.). *T. triandra* usually regains high cover quickly, returning to pre-fire biomass levels in 2-4 years (Morgan 1994). At Evans St., Sunbury, cover reached 43% after 9 months and was predicted to reach 100% after 2-3 years (Morgan and Rollason 1995). Creation of bare ground along with an ash bed probably enhances seedling establishment for most native species (Stuwe and Parsons 1977), but these are favourable conditions for most exotic vascular plants as well.

In South African grassland Uys *et al.* (2004) recorded declines of *T. triandra* related to longer fire frequency but continued persistence at a semi-arid (550 mm per annum) site 26 years post fire.

Fire also enables *T. triandra* regeneration from seed. In *T. triandra* establishment experiments, Stafford (1991) found that burning of areas to which a close thatch of whole *T. triandra* culms had been applied resulted in immediate seed germination, with an estimated seedling density of c. 1000 m^{-2}. Areas thatched in December and burnt 10 months later produced seedlings at the end of October, the most successful of which produced seed the following February. However fire kills *T. triandra* seeds that have not worked their way into the soil (Hocking pers. comm.).

Effects of fire on other vascular plants

Particular forb species may be negatively effected by regular burning during a particular season. The late-flowering native pea *Glycine labrobeana* (Meisn.) Benth. is very susceptible to regular fires in late spring-early summer, which destroy its flowers and seeds (Scarlett and Parsons 1993). *Cullen* spp., also late flowering peas, may be rare in rail reserves for the same reason (Morgan 1994). *Thesium australe*, once widespread in native temperate *T. triandra* grasslands, is short-lived and highly dependent on annual seedling recruitment, is probably eliminated by annual burning (Scarlett and Parsons 1993), apparently germinates well without fire and after fire, but seems to require open conditions for growth (Scarlett *et al.* 2003).

As previously noted, Morgan (2004) found that more frequent fires reduced bryophyte diversity in Victorian basalt plains grasslands by loss of species, mostly mosses, although none of the 150 m^2 quadrats he surveyed had a richer moss and liverwort flora than the total of 990 m^2 surveyed at the frequently burnt Evans St. Sunbury site by Morgan and Rollason (1995). Presumably the greater exposure and dessication resulting from frequent fire destroys mosses and removes suitable habitat, including the shade and increased humidity of dense cover provided by *T. triandra*. Slow recovery and recolonisation of mosses post-fire has been widely reported in other ecosystems, and, as for vascular plants, frequent burning of native grasslands through ecological time has probably eliminated the most fire-sensitive species long ago (Morgan 2004). Fire damage to soil cryptogam crusts can also facilitate grass invasion (Milton 2004).

Fire effects on weeds

Moore (1993 p. 351) argued that *Themeda* grasslands remained “remarkably stable” under regimes of marsupial grazing and periodic burning, and if otherwise undisturbed were “not invaded by introduced species”. Fire results in temporary increases in nutrient availability and this fluctuation of resources may enhance invasion by exotic plants (Hobbs 1989). In general burning of south-eastern Australian native grasslands promotes post-fire colonising plants, most of which are exotic annuals that recruit from a large soil seed bank (Lunt 1990b, Lunt and Morgan 2002). However Stuwe and Parsons (1977) found a smaller proportion of the vascular flora consisted of alien species at regularly burnt (railway) sites than in grazed or unmanaged *T. triandra* grasslands, while Dodd *et al.* (2007) found that sites burnt less frequently had higher exotic seed banks, and considered regular burning to be detrimental to the exotics. Burning of some degraded *T. triandra* grasslands has been reported to lead to major increases in cover and density of exotic annuals, which then slowly decline (Lunt 1990b 1990c, Morgan 1998d). Scarlett’s (1994) view was that regular burning of sites with a long history of grazing and trampling rarely has any major impact on exotic annuals, an effect he linked to the poor re-establishment of the cryptogam crust.

Fire is often considered to provide advantages in reducing weed populations, but may promote or inhibit particular weed species or functional groups. Fire is demonstrably an effective tool to greatly reduce the cover of exotic invasive grasses when the invasives are not fire adapted, and to restore native plant cover (e.g. MacDougall and Turkington 2007). In temperate Australian grasslands spring fires might reduce or prevent seed set in exotic annual grasses (Stuwe 1986) but late autumn burning promotes their regeneration along with *Romulea rosea* (L.) Eckl. (Iridaceae) (Lunt 1990c). Burning can reduce the density of the exotic grasses *Briza maxima*, *Cynosurus echinatus* L., *Lolium rigidum* Gaudin, *L. perenne* and *Bromus hordeaceus* in *T. triandra* grasslands but promotes a range of others including *Aira* and *Vulpia* spp. (Lunt 1990c, McDougall 1989, Adair 1995).

As with the native plants, seasonality of the fire may determine the effect on particular exotics (see Morgan 1996), while the impacts on propagule production and seed bank levels are obviously important factors. According to Adair (1995) no clear evidence was then available that the season of burning has a significant effect on introduced grasses and forbs. Exotics are likely to be advantaged if they account for a high proportion of the soil seed bank, which is generally the case (Kirkpatrick *et al.* 1995, Morgan 1998c, Dodd *et al.* 2007). Robertson (1985) found similar densities of exotic annuals after autumn and spring burns at Gellibrand Hill. Stuwe (1994) among others argued that biomass-reduction burning now facilitates the growth of both native and exotic plants, while Lunt (1990b), based on seed bank studies at Derrimut, argued that burning is likely to promote exotics more, or at least as much as natives. Dodd *et al.* (2007) argued that exotic dominance of the seed bank is partly due to removal of fire, which along with exotic dominance in the surrounding landscape matrix, is likely to result in increased weediness of remnants.

Decisions about the desirability of burning need to be based on an understanding of the contents of the soil seed bank and the phenology of the above ground cover at each site in order to predict whether a burn would be beneficial for the flora. Determining an appropriate fire regime even at a single small site can thus becomes prohibitively difficult. Most native grasslands contain a mix of weeds with different life strategies, so fire cannot be used as a general tool to favour the native species (Lunt 1990c).

Stuwe (1994) warned that burning of areas with a *N. neesiana* seed bank should not be undertaken unless follow up herbicide treatment could be undertaken. However there appear to have been no studies on the specific effects of fire timing and intensity on *N. neesiana* populations in native grasslands. No information appears to be available about the comparable fuel loads of grasslands with and without *N. neeesiana*, so it is difficult to speculate about whether *N. neesiana* infestations increase or decrease the frequency and intensity of fires.

In relation to vascular plants of native grasslands, there is a general consensus that the interaction between fire and grazing is the major factor involved in the abundance of most native species, including threatened taxa, and that low fire frequency is detrimental to most species (Scarlett and Parsons 1993). Frequent burning (a fire every 2-5 years) is necessary to maintain grasslands dominated by *T. triandra*, but other Victorian grassy ecosystems (*E. camaldulensis* and *E. melliodora* grassy woodlands in the Grampians and Sandplain Grassland in the Mallee) appear not to require burning to maintain their vascular plant diversity (Lunt 1991). In *T. triandra* grasslands, long intervals between fires results in loss of forb diversity (Stuwe and Parsons 1977, Lunt 1990c, Lunt and Morgan 1999). Morgan (1998c) found no correlation between seed bank species richness and fire history for five grasslands in the Victorian volcanic plains. However fires do not generally lead to significant seedling recruitment of native plants (Henderson 1999, Lunt and Morgan 2002), possibly because of severe depletion of the seed bank resulting from prior affects of long-term livestock grazing on seed production (Lunt 1990b 1990c). *T. triandra* is more sensitive to grazing shortly after fire (Groves and Whalley 2002).

Effects of fire on animals

Combinations of positive and negative effects of fire also occur with other organisms. Fire can change the abundance, range (spatial and temporal), fecundity and dietary choice of other organisms by altering the provision of food, shelter and habitat (Low 2002). Fire directly results in the elimination of many animal populations, although many sedentary species survive underground.

According to Yen (1995 1999) the effects of fire on temperate Australian grassland invertebrates were unknown, while Driscoll (1994) noted that they were ‘yet to be investigated’. Studies from other ecosystems tend to be equivocal, with few lessons for grasslands (Driscoll 1994). Edwards (1994) argued that fire often causes local extinction, but recolonisation from unburnt areas is usual, so in a situation where an invertebate is dependent on a community that is scarce and highly fragmented, recolonisation is often impossible. This appears to be the case with *Synemon* spp. (Edwards 1994) and with xanthorhoine moths (McQuillan 1999), although with organisms like *Synemon* that spend a major part of their lifecycle underground, the precise timing of the fire with respect to the above-ground stages would appear to be critical.

Removal of dense cover by fire and the creation of open ground will radically alter temperatures at the ground surface. Lunt (1995a) quantified temperature differences between the canopy surface in *T. triandra* grassland, the ground surface temperature and soil temperatures at 3 cm depth, in areas where the canopy was closed and in open gaps from July to April. The canopy provided excellent insulation with temperatures on the surface similar to those in the soil. Temperatures in gaps were generally

>5°C warmer than under the canopy and much larger differences occurred in summer. Such contrasts will substantially affect the behaviour and activity levels of invertebrates.

Farrow (1999) found no clear differences in the diversity of canopy-living insects in small burnt patches and unburnt areas in ACT grasslands and suggested that recolonisation occurred within 6 months of fire. Nearly twice as many individual insects were present in summer in areas burnt 6 months prior to sampling than in unburnt areas, and more than three times as many in the following spring. Species that benefit from more open ground, like many ants, probably commonly proliferate. Maintenance or periodic refreshment of plant diversity by fire will benefit a wide range of herbivorous taxa with particular food plants, and maintenance of the forb components will benefit nectar and pollen feeders. Maintenance or enhancement of animal diversity at the primary consumer level will flow on to higher tropic levels, benefitting the diverse array of predators and parasitoids. Greenslade (1994) found litter removal by fire was likely to markedly reduce Collembola diversity for at least two years. Other detritivores dependant on plant litter would be expected to be similarly disadvantaged.

Any beneficial effects on fire on plant diversity may or may not flow on to invertebrates, depending, in part on whether source populations of new and recolonising species exist (Tscharntke and Greiler 1995). Driscoll (1994) concluded that some species may be completely intolerant of fire, while others may require it for survival. Any species that spend part of their lifecycle underground are probably relatively resistant to fire, while those that do not are likely to be more highly vagile and have an ability to recolonise from unburnt areas. Sedentary, non-subterranean species are probably most vulnerable to extinction, but there are unlikely to many of them in fire adapted vegetation. As with vascular plants (Stuwe 1994) and bryophytes (Morgan 2004), the indigenous invertebrate flora of grasslands that have been subject to periodical fire over many thousands of years must consist largely of fire-adapted species, whether or not they are fire survivors or recolonisers.

Fire regime management in Victoria now incorporates the goal of providing the conditions necessary for the persistence of the indigenous biota (Mansergh *et al.* 2006b) but implementation of this idealfor the various biotic elements, including animals, is difficult and is bound to produce contradictory results because different valuable elements of the biota may be advantaged or harmed by the same fire cycle. The difficulty for managers is to evaluate and juggle the often contrary needs and tolerances of the various components in each grassland remnant.

Nutrients and soil factors

Lowland native grassland in Australia is found on relatively fertile, organic-rich, cracking clay soils on substrates of volcanic rocks (basalt and dolerite), fine-grained sedimentary rocks (including limestone) or recent alluvium (Kirkpatrick *et al.* 1995). In the past, temperate grasslands have erroneously been characterised as low in nutrients, based on analysis of soils. Mott and Groves (1994 p. 376) state that "Australian grassland soils are of very low fertility, particularly of nitrogen and phosphorus, by comparison with those of grasslands elesewhere". Sharp (1997) lists low soil nutrient content as one important factor determining the distribution of native grassland in the ACT. Australian soils have in general been considered to be nutrient deficient (e.g. Roberts *et al.* 2006). However, like tropical rainforest, much of the system nutrients are held in the plants.

Above- and below-ground biomass

In temperate herbaceous communities 60-80% of vascular plant biomass is underground (see Reynolds 2006 p. 57). In grasslands up to 90% is below-ground (Wijesuriya and Hocking 1999) and it is usual for a high proportion of total plant biomass to be represented by roots and buried crowns. More of the energy captured in photosynthesis in grasslands is directed to below-ground parts than those above-ground and most of the nutrient circulation occurs below ground (Soriano *et al.* 1992). In Australian grasslands most of the biomass is contained in the dominant grasses (Groves 1965). *T. triandra*- and *Poa*-dominated communities are more productive (i.e. produce more biomass) than the *Austrodanthonia* and *Austrostipa* grasslands that predominate in drier areas (Lunt and Morgan 2002). The mean root: shoot ratios in North American grasslands varies from 13 to 2, being higher in cooler climates (Tscharntke and Greiler 1995). Cooler and drier grasslands generally have ratios between 13 and 6, while warmer, more humid grasslands have ratios between 6 and 2 (Soriano *et al.* 1992). A ratio of 2.6 was calculated for one Argentinean pampas grassland (Soriano *et al.* 1992). Rodríguez *et al.* (1995) measured below-ground biomass down to 10 cm depth in five grazed grassland communities in Spain and found that 61-68% of the total biomass was below ground, of which 49-68% was in crowns and the remainder below 1 cm depth. Groves (1965) found that the root:shoot ratio of a *T. triandra* grassland had very high seasonable variability but that root biomass was generally 2 to 4 times that of above-ground parts, i.e. 66-80% of the biomass of the overwhelming dominant grass was below ground. In one Pampas grassland 65% of the underground biomass was located above 10 cm, 85% above 30 cm and 100% above 70 cm, a similar distribution to most temperate, subhumid grasslands (Soriano *et al.* 1992).

Underground net primary productivity in one Pampas grassland was estimated to be about 5000 kg ha^{-1} yr^{-1}, just 17% less than productivity above ground, with a below-ground: above-ground productivity ratio of 0.9 (Soriano *et al.* 1992).

Soil nutrient levels

The soils of Australian native grasslands usually have low nutrient levels (Table 8), and a high organic matter content with organically bound N and P (Wijesuriya and Hocking 1999). However most of the nutrients in the system are locked up in the biomass of the grasses. In the Victorian basalt plains, soils derived from sediments have higher nutrient levels than those derived from basalt, and soils on stony rises have the highest fertility (Williams 2007).

Table 8. Typical nutrient levels in Australian grassland soils. Source: McIntyre and Lavorel (2007).

Vegetation	**N**	**P (mg kg^{-1} ha^{-1})**
Natural grasslands	low	1-3 (low)
Native pasture	medium	1-3 (low)
Fertilised (improved) pasture	high	20 (high)
Sown pasture	high	20 (high)
Enriched grassland	medium	medium

Moore (1973) suggested that nitrate levels in the surface soils rarely exceeded a few parts per million at any time of year. In grasslands in general a "small active fraction" of soil organic matter dominates both C respiration and N mineralisation (microbial conversion of N into the plant-available nitrate and ammonium forms) (Wedin 1999 p. 194). Roberts *et al.* (2006 p. 148) stated that pasture productivity may be limited when P falls below 25 mg/kg (Colwell), but that "native pastures ... tend to be more tolerant of lower P levels than those dominated by introduced species".

Weed invasion and nutrient enrichment

Nutrient enrichment by legumes, application of fertiliser, runoff, deposition of atmospheric pollution etc. is a major cause of alien grass invasion worldwide (Milton 2004) and experimental addition of nutrients often rapidly leads to weed invasion (Carr 1993). Eutrophication, particular with N and P, is a major cause of plant diversity decline in terrestrial ecosystems (Hobbs and Heunneke 1992, Hautier *et al.* 2009). Grasses tend to be particularly favoured by nutrient inputs, and biodiversity losses are usually associated with their increasing productivity and dominance (Hobbs and Heunneke 1992).

Australian soils have generally been characterised as nutrient impoverished, particularly in relation to phosphorus, but also in nitrogen, minor nutrients and organic matter (Leeper 1970). Because most Australian native plants are adapted to these low nutrient levels, nutrient enrichment favours the establishment of exotic weeds that are better adapted to high levels of fertility (Brereton and Backhouse 2003). Cale and Hobbs (1991) found a strong positive correlation of nutrient gradients across roadsides with exotic plant diversity and suggested that nutrient enrichment may increase their competitiveness. Cover of exotics increased from <1% in reserves to nearly 25% on roadsides while mean exotic diversity showed a 25 fold increase, corresponding with tripling of P levels and a 150% increase in soil nitrates. Superphosphate addition to *Austrodanthonia* grasslands in the South East of South Australia encouraged the invasion of exotic annuals including rosette forming dicots, *Trifolium* spp., *Holcus lanatus*, *Lolium rigidum* and *Vulpia* spp. and within a few years severely affected a diverse array of small native perennial forbs (Specht 2000). Drainage into grassland remnants from adjacent fertilised agricultural land often results in dominance of exotics in the runoff areas. "Circles of exotics form" where rubbish with a high nutrient concentration or animal carcases are dumped (Kirkpatrick *et al.* 1995 p. 81). Fertilisation of grasslands increases their above-ground biomass in the short term, and may have some benefits for biodiversity, but in the long term, the biodiversity effect of the resulting high productivity is negative (Tscharntke and Greiler 1995).

Changes in N cycling were reported in 22 of 30 studies of alien grass invasion examined by Rossiter *et al.* (2006). The particular effects are dependent on pre-existing conditions and other ongoing changes as well as characteristics of the grass species. Different areas invaded by the same species can show opposite changes in the status of soil N pools and there is often pronouced temporal variation. Decreases in total soil N were more commonly reported than increases, soil inorganic N mostly showed no change but could be increased or decreased, while changes in mineralisation rates also were variable. Altered N status of the soil may persist for many years after exotic grass removal and continue to interfere with restoration activities (Rossiter *et al.* 2006).

Native grasses can respond to fertiliser applications by increasing their production, e.g. Groves *et al.* (1973) found that *P. labillardieri* outcompeted *T. triandra* at increased P and N levels compared to their growth in monoculture, but both species appeared to be generally less responsive than exotic grasses. In pot trails Groves *et al.* (2003a) found that native perennial grasses were less competitive than four common introduced annual and perennial grasses as complete nutrient levels were increased. Grown alone, *T. triandra, P. labillardieri*, *Austrodanthonia carphoides* and *Vulpia bromoides* produced maximum biomass per unit area at nutrient levels double the normal level of nutrient solution, and decreased biomass production at higher nutrient levels. Some seedlings of *T.triandra* and *A. carphoides* died at high nutrient levels, which were "presumably toxic". The exotic pasture grasses *Dactylis glomerata*, *Hordeum leporinum* and *Lolium perenne* reached biomass production peaks or plateaus at quadruple nutrient levels. *T. triandra* was the most productive species at the lowest nutrient level (0.156 x normal). When grown all together *H. leporinum* and *L. perenne* continued to increase yield up to levels 16 x normal, but the other species had yield optima between 0.24 x and 2 x normal nutrient level. Biomass production by *T. triandra* relative to the the most productive species in monoculture declined steadily with increasing nutrient levels, while *A. carphoides* and *P. labillardieri* showed maximum responses at intermediate levels and declined at high levels. When grown all together the three native grasses "hardly managed to survive at high nutrient levels" (Groves *et al.* 2003a p. 495).

Invasions of exotic grasses are often favoured by high levels of available nutrients in the soil. In temperate Australia, exotic grasses proliferate in deliberately fertilised areas of native grassland (Lunt 1991) and deliberate addition of phosphorus fertilisers favours cool season annuals grasses such as *Hordeum* spp. (Groves *et al.* 2003a). O'Dwyer (1999) found that concentrations of available soil P above 14µg/g in *Austrodanthonia* grasslands were associated with weedy sites. Huenneke *et al.* (1990) fertilised Californian grasslands on low-nutrient, serpentine soils with N, P and a complete fertiliser and recorded a resulting increase in exotic annual grass biomass after one year, and invasion and dominance of these grasses in patches previously dominated by native annual forbs after two years, corresponding with decline in native plant species richness (loss of annual forbs and legumes). Accumulation of dense, standing, dead biomass of the grasses in year 1 probably had a major suppressive effect on subsequent germination of the native plants. Barger *et al.* (2003) found that fertilisation with P and K resulted in higher germination of invasive*Melinis minutiflora* seeds and survival of seedlings in a Brazilian grassland, and that additions of N, P and K greatly increased seedling growth.

Nitrogen dynamics of competing C_3 and C_4 grasses

C_4 grasses are superior competitors in undistrurbed grassland because of they way they use and sequester N and extraneous addition of soil N benefits alien annual grasses and decreases species richness of native flora that evolved under conditions of low soil N (Milton 2004).

Moore (1973) suggested that the success of *T. triandra* as a warm-season C_4 grass in southern latitudes is due to an ability to sequester N and other nutrients as they are mineralised. Short term increases in N mineralisation after fire in ungrazed *T. triandra* grassland therefore advantage the dominant grass. N appears to be the key nutrient determining the balance between C_4 and C_3 grasses (Wedin 1999, Groves and Whalley 2002, Groves *et al.* 2003a). Soils are more commonly deficient in it than any other nutrient, and plants growing in N-deficient soils usually have a high root-shoot ratio (Salisburyand Ross 1992). Plant growth is believed to be primarily limited by the availability of N in the soil (Eschen *et al*. 2007). Unlike other nutrients, N has little interaction with inorganic soil minerals and its plant-availability is almost totally regulated by biotic processes (Wedin 1999). The amount of plant-available soil N is determined by mineralisation from organic matter by soil microbes, immobilisation in microbial and plant biomass, deposition (external fertilisation) and external losses (denitrification and leaching) (Moretto and Distel 2002). Soil inorganic nitrogen content largely reflects the balance between mineralization of N and immobilisation of N by soil microbial biomass (Andrioli and Distel 2008). Most soil N is contained in the humus, locked in C-N bonds that are energetically very expensive for decomposer organisms to break (Wedin 1999). High lignin concentrations and high C:N ratios in plant litter commonly immobilise the N pool and result in low available N in the soil (Moretto and Distel 2002). C_4 grasses use N more efficiently than C_3 grasses (Monson 1989, Bouchenak-Khelladi *et al.* 2009) and therefore have roots and leaves with higher C:N ratios and litter of a lower quality. For example the ratio in *Schyzachyrium scoparium* (Michx.) Nash (C_4) roots was 100 and leaf litter 110 (Andrioli and Distel 2008) compared to roots c. 39-59 and leaf litter c. 40-60 in four *Nassella* spp. assessed (Andrioli and Distel 2008). *T. triandra*, as a C_4 species, produces a relatively high amount of biomass, low in protein, compared to co-occurring native C_3 grasses (Moore 1993, Nie *et al.* 2009), and its litter has a high C:N ratio, so it can be conceived of as a climax species in grassland succession, where the climax is characterised by a stable species assemblage, with low levels of available soil N and relatively high biomass (Moore 1993).

Higher quality plant litter decomposes more rapidly and results in net mineralisation of N, whereas lower quality litter decomposes more slowly and results in net immobilisation of N (Andrioli and Distel 2008). Andrioli and Distel (2008) found little difference between the litter quality of several *Nassella* spp. (not including *N. neesiana*) in semiarid (mean annual rainfall 400 mm) Argentina and no differences in their influence on soil inorganic N content or potential N mineralisation. Variation measured within the *Nassella* spp. was low in comparison to C_4 grasses. Presumably *N. neesiana* has similar higher quality litter, that markedly differs in its biodegradibiltiy to the low quality *T. triandra* litter.

Mineralisation of soil N in temperate Australian takes place during the summer, reaching a peak at the end of summer (Moore 1993). The nitrate content of the top 10 cm of soil under *T. triandra* grassland at the end of summer has been found to not exceed 5 ppm, in comparison to >36 ppm under *Austrodanthonia* C_3 grasses (Moore 1993). Soils under the cool season native grasses therefore had large pools of labile N when the winter growing season commenced, facilitating invasion by cool-season annuals, while intact *T. triandra* was resistant to invasion: “By growing when mineralisation processes are actually or potentially active, and utilising or otherwise limiting the accumulation of labile nitrogen in the soil surface, *Themeda*, seemingly, gives stability to the grassland community” (Moore 1993 p. 352).

When the C:N ratio of grass litter is more than 30:1, the rate of decomposition of the litter is slow, microbial decomposers are N-limited, N is largely immobilised, and there is little or no release of nitrate and ammonium into soil solution (Wedin 1999, Groves and Whalley 2002, Moretto and Distel 2002). In such situations with a low rate of N mineralistation, species with a high N use efficiency, usually the C_4 grasses, have a competitive advantage, and are able to efficiently deplete the low soil nitrate pools. The C:N ratio of litter and roots of such grasses is generally much greater than 30:1, and they immobilise the N, and buffer against N pulses created by disturbance, so perpetuate their own dominance (Wedin 1999, Groves and Whalley 2002). *T. triandra* is a more efficient user of N than *N. neesiana*, and healthy *T. triandra* stands lock up system pools of N in high-C biomass. This array of N-related mechanisms explains the resistance to invasion by exotic species of *T. triandra* grasslands reported by Hocking (1998) and Wijesuriya and Hocking (1999).

When disturbance results in the death of *T. triandra*, levels of available N are increased and this results in changes in the floristic composition of the grassland (Moore 1993). Disturbances including continuous grazing, fertiliser addition and cultivation, result in increased rates of N mineralisation and higher soil nitrate and ammonium levels (Wijesuriya and Hocking 1999, Groves and Whalley 2002). Soil disturbance involving digging and homogenisation of soil of *T. triandra* grassland thus results in a major increase in the above-ground biomass of dicot weeds and annual grasses. Wijesuriya and Hocking (1999) found that approximately 90% of a total of 60 kg ha^{-1} dry weight above ground in late spring, 70 days after such disturbance, consisted of exotic annual grasses, “thistles” and “flat weeds”. This reflected a simultaneous nearly ten-fold increase in the amount of plant-available soil N and an approximate doubling of available soil P. Addition of c. 25 kg ha^{-1} of both N and P fertiliser, combined with digging and homogenisation of the soil, produced total above ground biomass over the same period of c. 150 kg ha^{-1} dry weight, of which approximately 90% again consisted of these exotic weeds (Wijesuriya and Hocking 1999).

These authors demonstrated that addition of N and P to *T. triandra* grassland at rates of c. 25 kg of N or P ha^{-1} resulted in weed flushes and that cultivation resulted in rapid mineralisation of organic matter and a consequent ‘pulse’ of N. In experiments on basaltic clays at Derrimut, Victoria, after 14 days, the rate of mineralisation of N in soil dug out, homegenised to very small particle size and replaced in plots was 4.7 times that of undisturbed soil, while the rate for P was not significantly different to undisturbed soil. Total available soil N continued to increase in the disturbed soil for 70 days, at which time it was approximately 10 times that of undisturbed soil. Available P was also significantly higher in the dug soil after 70 days. These authors also compared plots in which there was no soil disturbance with those in which soil was dug out, homogenised and returned, and subsequently unfertilised, fertilised with N, P, both N and P, or treated with sucrose (as a C source). In early summer, 70 days after disturbance, >95% of plant biomass in disturbed plots consisted of exotic weeds, mainly annual Asteraceae and annual Poaceae, with the Poaceae accounting for about half the biomass of the dicotyledonous species. Undug plots carried >90% *T. triandra*. Species diversity was similar in plots dug and treated with N and P, or both N and P, but annual grasses produced sigificantly more biomass when fertilsed with P than when fertilsed with N or not fertilised, and annual dicots were significantly more numerically dominant in plots receiving both nutrients. Annual grasses had significantly higher numbers when the dug soil was treated with both nutrients than when treated with N alone, but not P alone. Total biomass was significantly greater in plots receiving both nutrients. Addition of sucrose resulted in increased microbial activity and rapid, near complete exhaustion of soil nitrates. Biomass of dicot weeds and annual Poaceae was significantly lower in the sugar treatments than in disturbed, unfertilised plots.

Small scale spatial and temporal N mineralisation fluxes across the C:N degradation threshold "are probably common in even strongly N-limited grasslands and may play a role in maintaining grassland diversity" (Wedin 1999) as well as offering limited opportunities for exotic plant invasion. However disturbances involving death of *T. triandra* produce major nutrient pulses in the soil, which strongly facilitate invasion of weeds. Elimination of *T. triandra* tips the competitive balance in favour of C_3 grasses, which produce litter with low C:N ratios, below the threshold that limits microbial breakdown, increase the mineralisation rate and perpetuate their own dominance. If *N. neesiana* happens to be one of those weeds, the cycling of N in the system is permanently altered. *N. neesiana* litter, produced largely in the summer after flowering, breaks down more rapidly than that of *T. triandra* so presumably gives rise to soil nutrient fluxes at a time of year more suitable to its own needs than that of *T. triandra*. Levels of plant-available nutrients will remain higher than in *T. triandra* swards, so conditions for the growth of other exotic weeds will be enhanced. Thus, once *N. neesiana* becomes established it too would appear to be able to perpetuate its own dominance. Grassland N cycling processes therefore explain both the original persistence and abundance of *T. triandra* and the permanent change from C_4 (*T. triandra*) to C_3 grass dominance (whether native or exotic) that have resulted from European grazing regimes and addition of chemical fertilisers (Groves and Whalley 2002, Groves *et al.* 2003).

Nutrient enrichment, nutrient reduction and grassland restoration

Species richness of native forbs declines with increasing P levels (McIntyre andLavorel 2007). Morgan (1998d) compared native and non-native species richness and cover in a *T. triandra* grassland and found a strong positive correlation between soil P (unstated method, unclear if this was Olsen 'available P') and the number and cover of non-native species, and a negative association for native species. There was more than twice the level of soil P at the edge of the grassland than in its centre (30-50 m from the edge) and the edges were also enriched with ammonium and organic C. There were weak positive correlations between ammonium, soil pH, % organic C and exotic richness, and a weak negative correlation between soil pH and native richness, but no significant relationships for nitrate and sulfur. Non-native, perennial, high-biomass Poaceae were most dependent on high levels of soil nutrients and were suggested to be resource limited in undisturbed soils.

Various endangered native plants are only known from areas where superphosphate has not been applied, but usually there are compounding disturbance factors such as soil cultivation that have probably played a role in reducing population sizes. *Amphibromus pithogastrus* is only known from unploughed sites to which superphosphate has not been applied (Ashton and Morcom 2004 p. 2). Cultivation destroys the deep-rooted native perennials, although "there are several instances of the re-establishment of native grassland after ploughing" (Kirkpatrick *et al.* 1995 p. 80). Weed invasion is enhanced more by nutrient addition than by cultivation alone (Kirkpatrick *et al.* 1995).

There are potentially large nutrient additions to small vegetation remnants from farmland via windblown fertiliser, soil and plant material (Hobbs 1989) and 'run-on' of nutrient enriched water (Sharp 1997) that could significantly enhance weed invasion (Hobbs 1989). Proximity to urban development presumably has similar risks, particularly in regard to nutrient enrichment by atmospheric nutrient deposition. N enrichment is occurring globally in the atmosphere, water and soils. As much as 70% of the reactive nitrogen in the global system is the result of human activity and deposition rates in industrialised countries increased 500% in the last 100 years (Hooper 2006) and are expected to double globally by 2050 (Mooney *et al.* 2006). The increases have been largest in agricultural lands, where native grasslands are mostly found (Aguiar 2005). The N comes from various sources: fossil fuel combustion, agricultural fertilisers, use of agricultural legumes, mobilisation of soil nitrogen by soil disturbance, and ammonia from livestock and human sewage being the most important. Much reactive N enters the soil from acid rain and particulate deposition and this is largely ammonium or ammonia (Heil *et al.* 1988, Hooper 2006). Wind-blown dust contains high amounts of N (Eldridge and Mensinga 2007) and increased dust deposition has likely been a feature of the landscape associated with increased agricultural development. Heil *et al.* (1988) measured bulk and throughfall ammonium deposition in a Netherlands grassland and found that a significant proportion is captured by the canopy and assimilated by the plants. Total deposition was estimated to be 5.9 kg ha^{-1} over the 3.5 month growing period in undisturbed grassland with a leaf area index of 2.0-5.7 m^2 m^{-2}, and 2.5 kg ha^{-1} over the same period in mown grassland with a leaf area index of 1.8-3.2 m^2 m^{-2}. Assimilation in the canopy was calculated to be 4.7 kg ha^{-1} in the undisturbed grassland and 1.2 kg ha^{-1} in the mown grassland. Such increases in ammonium availability are more than sufficient to alter competitive relationships between plants and enable fast-growing species to outcompete slow-growing ones. Grasslands as a whole are not greatly N-limited and are expected to be in the intermediate range of affected ecosystems, but N addition has been demonstrated to have profound effects on grassland biodiversity, promoting dominance of a few species, generally fast-growing with high shoot-root ratios, and the suppression of many (see Tilman 1987, Aguiar 2005).

Long term N fertiliser application is also associated with increased soil acidity (Aguiar 2005), which in turn is likely to have differential effects on grassland species, *Austrodanthonia* spp. for example having low tolerance to acidic conditions than *Microlaena stipoides* (Sharp 1997). Fertilisation of grasslands also decreases species diversity of native invertebrates across a wide range of taxa and simplifies the trophic web, although normally a few species benefit (Driscoll 1994).

Increased atmospheric CO_2 improves N use efficiency of C_3 grasses (Milton 2004 see her ref.). A meta-analysis indicates that under CO_2 enrichment, C_3 species increased their biomass by 44% while C_4 species increased theirs by 33%, so elevated levels are expected to have a relatively high impact in mixed C_3/C_4 grass systems, although experimental findings have so far been mixed (Aguiar 2005). Higher water use efficiency by plants with increased CO_2 levels should decrease transpiration and increase soil water content (Aguiar 2005). Increasing concentration of CO_2 is also likely to increase rates of microbial denitrification in the soil (Hooper 2006).

Water enrichment may also favour exotic grasses over native grasses. Stafford (1991) found that *Lolium perenne* was highly competitive with *T. triandra* in cultivation when irrigated, but that cessation of mid-summer watering allowed *T. triandra* to dominate. Seasonal disturbances in the water regime may be important as well as changes to water tables. Grassland restoration may also require management of the water regime and water tables.

Restoration of grasslands to a semi-natural state involves transition from fertilised to low-fertility states (Oomes 1990, Kirkpatrick *et al.* 1995, McIntyre and Lavorel 2007, Eschen *et al*. 2007). Weedy species remain dominant as long as nutrient availability remains high. Reduction in plant available N appears to be the key prerequisite (Eschen *et al*. 2007) but other nutrients may be important. Particular species may be limited by low P or K levels when available N is adequate for their needs. Techniques to achieve long-term reductions are poorly developed, and the process is generally prolonged (Kirkpatrick *et al.* 1995, Eschen *et al*. 2007). Some existing management strategies may be successful because they achieve this objective. Oomes (1990) suggested that the first stage of such management should aim to reduce annual above-ground dry matter production to 4-6 t ha^{-1}. Appropriately managed grazing can also remove nutrients if the grazing animals are harvested. Annual crops have been used to reduce nitrate leaching from farm land, and species with proven abilities to sequester N, such as *Secale cereale* L. could be grown and harvested in some highly degraded situations to reduce nutrient levels (Sheley and Rinella 2001).

Oomes (1990) reported on the restoration of fertilised grassland withdrawn from agricultural use on sand and clay soils in the Netherlands to more species-rich grasslands by mowing twice annually over periods of 14 and 11 years respectively, and removing the harvested biomass. On the sand substrate, dry matter production fell from 10.2 t ha^{-1} to 6.5 t ha^{-1} after 4 y and after 9 y was similar to that of comparable unfertilised grassland (4.1 t ha^{-1}) at which time N and P yields in the vegetation and soil were still higher than unfertilsed grassland, but K yields were similar, indicating that K was then the limiting nutrient. On clay, dry matter yield decreased from 10.2 t ha^{-1} to 5.0 t ha^{-1} after 3 y, but increased again after 6 y. After 10 y low soil N concentration was probably limiting biomass production but low P may have been having a similar effect.

One promising method of nutrient reduction involves applications of C via sugar (sucrose), sawdust and woodchips, to manipulate grassland species compostion. These C sources are believed to feed or provide substates for soil microbe populations that can temporarily 'mop-up' available soil N, and decrease rates of N mineralistation and nitrification. Eschen *et al.* (2007) found that C addition affected the concentration of nitrate, but not that of ammonium and that effects varied between different microbial components and at different sites. Sucrose stimulates microbial activity, probably mostly of bacteria, within hours while sawdust acts more slowly and wood chips more slowly still, probably largely on fungi. Little is known about the the dynamics of the soil microbial community components in relation to C addition (Eschen *et al.* 2007). The soil microbial population may increase, or if it's biomass remains stable, its N content may increase or microbe consumer populations may increase. The method has been used effectively to reduce the competitive ability of invasive plants and above-ground biomass. Grass biomass is reduced more than that of legumes, the root:shoot ratio of grasses is significantly increased, annuals are more affected than perennials, and more bare ground is created (Eschen *et al.* 2007). The effects of a single application reduce over time, rapidly with sugar and more slowly with wood, and inorganic N pools may be replenished by decay of the mircobial biomass. Crushed brown coal, as used by McDougall (1989) as a mulch, similarly increases microbial activity and may have similar effectiveness. McDougall (1989) found that 3.5 kg m^{-2} of crushed coal applied over a mulch of *T. triandra* culms significantly improved establishment and later the flowering of the *T. triandra*, but did not measure any soil nutrient parameters or directly test its effects on weeds.

Soil disturbance by animals

Disturbance to the soil surface by animal grazing, burrowing and foraging creates the conditions required for the establishment of many plants, including invasive species (Hobbs and Heunneke 1992). Increases in the availability of safe sites for establishment is probably the most important effect (Hobbs and Heunneke 1992). Soil disturbance by introduced livestock and rabbits in Australian native grasslands is a very important contributor to the establishment and survival of weed populations, but may also benefit native species. Livestock trampling often destroys the cryptogam crust, favouring exotic plants (Kirkpatrick *et al.* 1995). But the digging and burrowing of animals (biopedturbation) appears also to be a critical factor in maintaining diversity of vascular plants in native grasslands, by creating favourable microsites for germination and seedling survival (Reynolds 2006, Kirkpatrick 2007). These disturbances generally modify soil structure and destroy the soil crust (Eldridge and Rath 2002). When vertebrate diggings are associated with resting sites, rather than foraging sites, they are likely to also have higher concentrations of dung and urine, which can improve the chances of plant establishment (Eldridge and Rath 2002). Biopedturbation alone may increase nutrient availability, as well as reducing competition from existing plants (Hobbs and Heunneke 1992). Pits made by burrowing animals increase water infiltration and water holding capacity of the soil, trap litter and seeds, and otherwise alter soil properties in ways that can enhance seed germination and seedling survival (Noble 1993, Eldridge and Mensinga 2007, James *et al.* 2009). Major effects of bioturbation can persist long after the animals that caused them have disappeared from the landscape (Villarreal *et al.* 2008).

Vertebrate burrows and warrens generally result in nutrient enrichment of the soil, particularly with total and available N (Garkaklis *et al.* 2003, Villarreal *et al.* 2008). In semi-arid Australian rangelands biopedturbation results in long-term changes to structure and spatial patterning of surface soils and to alterations in microtopography (Noble 1993). Even the shallow hip holes constructed by *Macropus* spp. as resting places can significantly alter soil erodibility and water infiltration rates, and concentrate plant litter, dung and nutrients, notably N and S (Eldridge and Rath 2002). James et al. (2009) found that litter accumulation and seedling emergence at an Australian desert site was almost entirely restricted to vertebrate foraging pits. Pits acted as resource sinks and their effectiveness was possibly releated more to their capability of retaining trapped material than capturing it. A variety of small pits were possibly as effective as few, large pits. Vertebrate biopedturbation can also have opposite effects including increased runoff, reduced litter concentrations and physical compaction of the soil, depending on the particular soil, the nature of the disturbance and environmental factors (Eldridge and Rath 2002). In Tasmania, marsupial and aboriginal biopedturbation created "a widespread ... frequently renewed, regeneration niche" (Kirkpatrick 2007 p. 222) which is now absent in many areas.

Fossorial vertebrates are or were once a feature of the indigenous fauna of temperate grasslands worldwide. Darwin (1845 p. 51) reported that "considerable tracts" of grassland of the Maldonada region in Uruguay were undermined by the extensive shallow burrowing of the root-feeding Tucotuco *Ctenomys brasiliensis* Blainville (Rodentia: Ctenomyidae), while the commonest mammal in grasslands between the Rio Negro and Bahía Blanca in Argentina was the burrowing Agouti or Mara (*Dolichotis patagonum* Zimmerman) (as *Cavia patagonica*) (Caviidae). Another burrowing rodent, the Viscacha (or Plains Vizcacha) *Lagostomus maximus* (Desmarest) (Chinchillidae), larger than the Agouti, lives in large groups in the pampas between the Uruguay and Rio Rivers, makes deep, multi-chambered burrows with large soil mounds, known as viscacheras, and forages at night on grasses and herbs. It is considered a"key ecosystem engineer" whose grazing and burrowing activities change the structure and composition of the vegetation over extensive areas (Villarreal *et al.* 2008 p. 701). This speices remained abundant at least until the early 1970s (Soriano *et al.* 1992). Rheas were abundant in the grasslands of Bahía Blanca, and live on "roots and grass" (Darwin 1845 p. 89). Burrowing mammals have been implicated in significant changes in microtopography (soil mounds) in Argentina (Noble 1993). The effects of *L. maximus* activities cascade through the ecosystem, and include altered plant biomass distribution, nutrient cycling (primarily by deposition of faeces and urine in the burrow), nutrient content of plants and fire regimes (Villarreal *et al.* 2008).

Other small mammals in the regions where *N. neesiana* is found include a group of *Necromys* mice (Rodentia: Cricetidae) of open areas (D'Elía et al. 2008). *N. lactens* (Thomas) is found in high altitude grasslands (over 1500 m) in north-western Argentina and southern Bolivia including Catamarca, south Jujuy and Tucuman; *N. obscurus* onthe Atlantic coast of Uruguay and in areas around the La Plata River and *N. lasiurus* is very widely distributed including southern Buenos Aires Province (D'Elía et al. 2008). The oldest *Necromys* fossils are 3.5-4 million years old from southern Buenos Aires Province and the group probably radiated in the Pampean region during the late Pliocene (D'Elía et al. 2008).

The biopedturbation activities of mammals now extinct or rare in temperate Australian grasslands probably played a critical role in the maintenance of forb diversity (Reynolds 2006). The mechanisms include alteration to the spatial distribution and cycling of soil nutrients and water infiltration (Garkaklis *et al.* 2003). Bettongs, potoroos, bandicoots, bilbies and rodents are amongst the most important digging and burrowing groups (Garkaklis *et al.* 2003). Bilbies are powerful burrowers, prefering soft soils such as sand dunes (Noble 1993). Reptiles, including goannas, may also be important, and the feral animal diggings, including those of rabbits, may function in a similar fashion to those of native vertabrates (James *et al.* 2009).

Bettongia species probably mostly feed on underground fungi and may be opportunistically insectivorous and omnivorous (Seebeck and Rose 1989). They sometimes bury and store seed, "which are eaten later, often after germination" (Seebeck and Rose 1989 p. 721). The Rufous Bettong *Aepyprymnus rufescens* (Gray) is primarily rhizophagous buts eats fungi throughout the year (Seebeck and Rose 1989). Foraging activities of *Bettongia penicllata* Gray for hypogeous fungi commonly cover the ground with small diggings of a range of different sizes and ages. In plan they are elliptial with a spoil heap at one end and a steep wall to a depth of 10-15 cm at the other. These excavations accumulate litter, leading to concentrations of buried fungal hyphae which become water repellent lenses in the soil after gradual infill of the excavations. The increased water infiltration in the excavations is the probable cause of decreased available nitrate and sulfur found in the soil of old, simulated diggings, while decreased ammonium may be due to rapid nitrification (Garkaklis *et al.* 2003).

The Burrowing Bettong *Bettongia lesueur* is considered to be the most fossorial of the potoroids (Strahan) and constructed warrens up to 30 m in diameter that could contain over 100 entrances or were simple structures with only one or two entrances, the former sometimes associated with rock caps and the latter sometimes on plains (Noble 1993, Noble *et al.* 2007). It is "a powerful burrower ... capable of penetrating the underlying rock" (Noble 1993 p. 60) and its activities probably significantly promoted landscape heterogeneity and plant diversity (Noble *et al.* 2007). *B. lesueur* "may have helped maitain vast areas as grassland by eliminating shrubs" (Noble *et al.* 2007 p. 335).

Among the native mammals still present in some temperate Australian native grasslands, the biopedturbation activites of the Short-beaked Echidna may be the most significant. Much of the foraging activity of the Echidna requires digging to obtain invertebrates, and the animals shelter in temporary digs and prepared tunnels (Menkhorst 1995c). Nursery burrows are shallow and 1-1.5 m long (Menkhorst 1995c) while foraging disturbances range from nose-poke holes, through shallow scrapes to deep digs and extensive bulldozing (Eldridge and Mensinga 2007). In semi-arid woodlands with a grassy understorey this soil disturbance has been found to make a large contribution to landscape patchiness (Eldridge and Mensinga 2007). The foraging pits accumulated greater quantities of plant litter than undug areas, have moister and more porous soil, are cooler and have a different suite and greater abundance of soil micro-arthropods than the surface soil. Contrary to expectations, increased litter in pits did not result in increases in total or active C, total N and available P, although the N was probably largely immobilised in the litter. Ultimately, echidna pits probably influence plant germination and establishment (Eldridge and Mensinga 2007).

The hip hole diggings of *Macropus* spp. are constructed so as to assist the animals to cool, and are generally located in the shade of trees or shrubs (Eldridge and Rath 2002), so may be of little significance in grasslands.

Biopedturbation by invertebrates may be more important than that of vertebrates. Ants and earthworms are probably the most important groups. Ants are a prominent feature of temperate south-eastern Australian grasslands. Many species construct surface mounds of excavated material around their nest entrances, associated with tunnels that may descend well under the surface. When the effects of their activity is quantified over the long term they can be viewed as ecological engineers whose activities restructure the landscape, generate heterogeneity, and affect soil structure and porosity, the distribution of soil nutrients and regeneration of the flora (Richards 2009). The vertical tunnels of Underground Grass Caterpillars *Oncopera fasciculatus* (Walker) (Hepialidae) reach a depth of up to 23 cm at maturity, depending on the ease with which the soil can be dug, and the excavated soil is deposited around the tunnel entrance and on the larval feeding runways (Madge 1954). Many other insects have larvae which live beneath the soil surface and contribute to biopedturbation. Earthworm activity in temperate Australian grasslands can also be substantial. However there appear to be no published studies of the effects of bioturbation by invertebrates in temperate native grasslands.

Native temperate grasslands of south-eastern Australia and their conservation status

According to the Australian Native Vegetation Assessment 2001 (Cofinas and Creighton 2001), 60,214 km^2 of the pre-European area of 589,212 km^2 of tussock grasslands in Australia had been cleared or substantially modifed by grazing by c. 2000. The category includes grasslands dominated by *Astreleba*, *Sorghum* etc., mostly in Queensland (282, 547 km^2) and the tussock grasslands of the dry inland, the largest proportion by far of which was in the north of the continent. Of all the major vegetation groups, grasslands are among the most affected by clearing in Victoria, ACT and NSW (See Table 9). The Victorian Midlands, Victorian Volcanic Plains (Victoria and South Australia) and the South East Coastal Plain (Victoria) had less than 30% of their orginal native vegetation remaining (Cofinas and Creighton 2001).

Table 9. Areal extent (km^2) of tussock grasslands in the ACT, NSW and Victoria pre-European settlement and c. 2000. Source: Cofinas and Creighton (2001).

State/Territory	Pre European	c. 2000	% remaining
Australian Capital Territory	207	91	44
New South Wales	40,790	19,318	47
Victoria	19,175	614	3

Thus it is the native temperate grasslands along with neighbouring grassy woodlands that are among the most threatened ecosystems in Australia, and amongst the most inadequately represented in reserves (Lunt 1991, Eddy *et al*. 1998). Whole grassland ecosystems have therefore been afford threatened status in south-eastern Australia (Table 10).

Table 10. Threatened grassland communities in south-eastern Australia. CE = critically endangered, E = endangered, U = unlisted, - = not present

Community	ACT	NSW	Vic	References
Natural Temperate Grassland	E	U		Sharp and Shorthouse 1996, ACT Govt 1997
Native Vegetation on Cracking Clay Soils of the Liverpool Plains (partly Western Slopes Grasslands)	-	E	-	Keith 2004
Natural Temperate Grassland of the Victorian Volcanic Plain	-	-	CE	DEWHA 2008

In 1971 there were no areas >4,000 ha in conservation reserves (Groves 1979). In the late 1970s the possibility of conserving moderately large areas seemed remote, because only small remnants were then known to exist (Groves 1979). By the early 1990s natural temperate grasslands had declined by 99.5% since European settlement (McDougall and Kirkpatrick 1994, Sattler and Creighton 2002). The 0.5% estimated to remain included remnants in “semi-natural condition” (Kirkpatrick *et al.* 1995 p. v). By the late 1990s, in all areas of south-eastern Australia, less than 1% remained of the grasslands and grassy woodlands that once existed (Lunt *et al.* 1998). Widespread extinctions occur when habitats are reduced by 90% and extinctions of vertebrates are continuing to occur in southern Australia in areas where native vegetation is reduced by 70-80% (Traill and Porter 2001).

Existing remnants of southern Australian temperate grassland on public land are mostly small and isolated (Lunt and Morgan 2002). Those on private land are generally larger, but are of lower quality, and all have a history of grazing (Kirkpatrick *et al.* 1995). Sattler and Creighton (2002) identified the NSW South Western Slopes, Riverina and Victorian Volcanic Plain as bioregions with the highest priority for improvement of reservation status. These areas cover a high proportion of the land once occupied by native grasslands.

The extreme fragmentation of the conserved elements (Eddy *et al.* 1998, Groves and Whalley 2002) means that they are subject to inundation or impoverishment by the surrounding ‘cultural steppe’, an immature ecosystem with a higher proportion of energy going into production than into maintenance, rapid accumulation of biomass, reduced litter production, increased excrement production and reduced species diversity with most species being *r* strategists (rapid intrinsic rates of population increase, little food specialisation, etc.) (Matthews1976). Nutrients, biomass, pollutants, exotic organisms, native pests and other ecological disrupters may be flushed in (Hobbs and Heunneke 1992), while native organisms or their propagules, water, etc. are extracted. Many environmental changes that may substantially affect the composition and functioning of small remnant grasslands have rarely received any consideration, including altered climatic regimes, light availability and noise profiles.

Thus ‘fragmentation’ as an outcome of development needs to be contrasted to with the increased connectivity that also results. Utility infrastructure including power lines, fences, drains and traffic corridors have provided a new network of corridors that facilitate dispersal of a different set of organisms and allow the movement of a range of non-biological resources between remaining grassland remnants (Aguiar 2005). A series of small grasslands may nevertheless sustain more diversity than a large patch with an equivalent total area, because different species may dominate in small patches, there are more edges and transitional habitats (Hobbs and Heunneke 1992) and a greater liklihood of heterogeneity in disturbance regimes.

Victoria

In simplistic terms, the major plant formations of southern Victoria are determined by geology: heathlands on sands, *Eucalyptus* forests and woodlands on sedimentary rocks, and grasslands on clays of volcanic origin (Patton 1935). Victorian grasslands occur mainly on relatively young geological materials, such as Tertiary volcanics and Pleistocene and Holocene sediments

(Rosengren 1999). Approximately one third of Victoria (c. 8 million ha) was probably occupied by grassy ecosystems, including grasslands and grassy woodlands, at the time of European occupation, of which less than 0.5% remains (Lunt 1991). All Victorian native grasslands are severely depleted (DNRE 1997) and all are now listed as threatened communities (DSE 2009a), that is Central Gipssland Plains Grassland Community, Northern Plains Grassland Community, Plains Grassland (South Gippsland) Community and Western (Basalt) Plains Grassland Community.

"Plains Grassland" is one of 28 Broad Vegetation Types recognised in Victoria, occurring on fertile plains with 300-1000 mm annual rainfall, on heavy clay soils of basaltic origin (Western Volcanic Plains), outwash clays (Sale Plains) and alluvial silts and clays (Northern Plains, Wimmera and West Gippsland). The category does not include coastal grasslands of *Austrostipa stipoides*, dune grasses and sedges. Pre-1750 this formation is estimated to have covered 1,882,411 ha or c. 8.2% of the State, of which 8277 ha (0.44%) was considered to be extant in the early 1990s. Only 2504 ha (30%) was in conservation reserves, while 4938 ha (60%) was on private land (Traill and Porter 2001). These estimates are similar to those of DNRE (1997) (Table 11). Ecological Vegetation Classes (EVCs) are a more accurate categorisation of actual vegetation types present in the State. The grassland EVC on the Western Volcanic Plains is Western Plains Grassland, in Gippsland it is Gippsland Plains Grassland and in the north is Northern Plains Grassland. In general, much higher proportions of these Plains Grasslands EVCs have been lost than of other grassland formations (Table 12).

Table 11. Bioregional pre-European areal distribution of grassland complexes in Victoria and proportion remaining. Source: DNRE (1997). 'Area remaining' derived by calculation from the '% remaining'.

Region	**Victorian Bioregion**	**Pre-European area (ha)**	**Area remaining (ha)**	**% remaining**
Victorian Mallee	Murray Mallee	51,512	52	0.1
	Wimmera	329,737	1319	0.4
Victorian Volcanic Plain	Victorian Volcanic Plain	826,402	1652	0.2
Midlands	Dundas Tablelands	79,694	80	0.1
	Goldfields	4,601	0	0.0
Victorian Riverina	Victorian Riverina	444,713	3113	0.7
Coastal Plains	Gippsland Plain	133,547	1870	1.4
Total		1,870,206	8086	0.4

All Victorian grasslands are presumed to have lost significant biodiversity since European occupation. Native vegetation and species disappeared locally and regionally in many areas before any detailed records were made (Mansergh *et al.* 2006a). Exotic plants have been reported to comprise 29% of the Southern Victoria grassland vascular flora (Kirkpatrick *et al.* 1995).

Gippsland Grasslands

The West Gippsland plains consist largely of uplifted marine and fluviatile sediments and swamp deposits at Koo-wee-rup (Hills 1967). The largest areas of grasslands on the Gippsland Plains at the time of European settlement were between Stratford, Rosedale and Sale, north of the Latrobe River with some onthe floodplains of the Latrobe and Macalister Rivers, in coastal South Gippsland east of Yarram between Seaspray and Welshpool, and north of Westernport around Kooweerup Swamp (DNRE 1997, Lunt *et al.* 1998, Rosegren 1999). The Central Gippsland grasslands occur on leached sandy soils in areas with perched watertables and an abundance of swamps and small lakes (Rosegren 1999). In the Nambrok-Denison area, between the Latrobe and Thomson Rivers, grassland occupied areas with heavy loam topsoil over heavy clay on flat, alluvial plains 3.5-7 m above the floodplain of the Thomson, and were infrequently flooded (Kirkpatrick *et al.* 1995). Moore (1993) mapped the coastal plain from Sale to Lakes Entrance as Temperate Shortgrass (*Austrodanthonia- Austostipa-Enneapogon*). To the north, in primarily forested country he mapped a wide zone of Temperate Tallgrass (*Themeda-Poa-Dichelachne*) continuous up the east coast to north of Sydney,west across Victoria to the Hamilton area and inland to Rutherglen and the ACT.

The historical extent and nature of Gippsland grasslands is very poorly known. Indeed, Gullan *et al.* (1985) did not recognise the presence of any natural grassland community in South and Central Gippsland, and Moore (1993) mapped the whole of West and South Gippsland except Wilsons Promontory (!) as an area without native grasslands. However many secondary grasslands derived from grassy woodlands currently exist in the region (Lunt *et al.* 1998) and several remnant native grasslands have recently been recognised.

Kirkpatrick *et al.* (1995) briefly described two Gippsland grassland communities: 1. South Gippsland *Themeda* Grassland, a closed tussock formation, occasionally with significant amounts of *Hemarthria uncinata* R.Br. (Poaceae) and a variety of other grasses and rushes, found in the Welshpool-Seaspray areas; and 2. Central Gippsland *Themeda* Grassland, also a closed tussock formation, but with abundant Asteraceae, Liliaceae and Orchidaceae and scattered trees at some sites, found on alluvial plains between Traralgon and Johnsonville and derived originally from woodland or open forest.

Substantially different grasslands have recently been identified in the Westernport and Mornington Peninsula regions. These have been described and delineated by inspections of the very restricted remnants that remain, and by analysis of early survey maps, plans, fragmentory historical records, aerial photographs and other sources (Cook and Yugovic 2003, Yugovic and Mitchell 2006, Sinclair 2007). They include c. 12 km^2 north of Tooradin (Cook and Yugovic 2003) and small areas (< 6 km^2) at Safety Beach (Sinclair 2007). *Poa labillaredieri* was the major grass, dominating the wetter areas, with *T. triandra* on drier sites (Yugovic and Mitchell 2006). The Westernport grasslands were occasionally flooded, but aboriginal burning probably prevented them being overrun by *Melaleuca ericifolia* Sm., which also may have been constrained by soil factors (Lunt *et al.* 1998, Yugovic and Mitchell 2006). The Safety Beach grasslands are on alluvial clays, were seasonally swampy, and are dominated by *Poa poiformis* (Labill.) Druce (very close to or identical with *P. labillardieri* var. *(Volcanic plains)*) and *Notodanthonia semiannularis* (Labill.) Zotov, along with *T. triandra*, and are also considered to be Gippsland Plains Grasslands (Sinclair 2007). Similar grasslands once occurred at Carrum (Sinclair 2007). Both the Westernport region and Safety Beach grasslands included *Acacia melanoxylon* R.Br. in the overstorey in some areas, and were transitional into grassy woodlands and *Melaleuca ericifolia* swamp scrub.

Table 12. Areal extent and conservation and reservation status of grassland and grassy woodland Ecological Vegetation Classes in Victoria by bioregion. Source: Traill and Porter (2001), June 2000 data from Department of Natural Resources and Environment. Conservation status: X = extinct, E = endangered, V = vulnerable, R = rare, D = depleted, LC = least concern; Reservation status: X = EVC not reaching reservation target, Y = reaches reservation target. Excludes swamp and wetland categories and tree or shrub dominated formations including a grassland component.

Ecological Vegetation Class	**Bioregion**	**% of Bioregion mapped**	**Conservation Status**	**Reservation Status**	**Pre-1750 area (ha)**	**2000 Extent (ha)**	**Proportion existing (%)**
Plains Grassland	Central Victorian Uplands	100	E	X	10490	219	2
	Gippsland Plain	75	E	X	37327	291	1
	Glenelg Plain	100	E	X	46214	944	2
	Goldfields	99	E	X	1560	0	0
	Murray Mallee	4			7862	3	0
	Otway Plain	100	E	X	2064	76	4
	Victorian Riverina	77	E	X	168816	579	0
	Victorian Volcanic Plain	100	E	X	220073	2291	1
	Wimmera	41			24612	3	0
Plains Grassland/Stony Knoll Shrubland	Victorian Volcanic Plain	100			761	0	0
Plains Grassland/Plains Grassy Woodland Mosaic	Victorian Volcanic Plain	100			456163	3326	1
Riverina Plains Grassy Woodland/Plains Grassland Mosaic	Central Victorian Uplands	100			2799	241	9
	Goldfields	99			1696	5	0
	Murray Mallee	4			12314	1	0
	Victorian Riverina	77			6808	16	0
	Victorian Volcanic Plain	100			8873	333	4
	Wimmera	41			3607	3	0
Wimmera Plains Grassy Woodland/Plains Grassland Mosaic	Goldfields	99			90	4	4
	Murray Mallee	4			2549	1	0
	Wimmera	41			6739	2	0
Riverina Plains Grassy Woodland/Plains Grassland/Gilgai Plain Woodland Mosaic	Goldfields	99			11307	24	0
	Victorian Riverina	77			415	0	0
Black Box Chenopod Woodland/Plains Grassland Mosaic	Wimmera	41			190	0	0
Swamp Scrub/Plains Grassland Mosaic	Gippsland Plain	75			22218	0	0
Plains Grassland/Gilgai Plain Woodland/Wetland Mosaic	Victorian Riverina	77			16180	87	1
Creekline Tussock Grassland	Victorian Volcanic Plain	100	X		2591	0	0
Coastal Tussock Grassland	Otway Plain	100	V	X	249	176	71
	Otway Ranges	100	V	Y	62	54	86
	Gippsland Plain	75	R	X	744	522	74
	Victorian Volcanic Plain	100	V	X	30	20	68
	Warrnambool Plain	100	R	Y	198	160	81
Coastal Headland Scrub/Headland Coastal Tussock Grassland Mosaic	Otway Plain	100			253	193	76
Mangrove Shrubland/Coastal Salmarsh/Berm Grassy Shrubland/Coastal Tussock Grassland	Otway Plain	100			61	26	43
Coastal Headland Scrub/Headland Coastal Tussock Grassland Complex	Warrnambool Plain	100			1094	490	45
Coastal Dune Grassland	Gippsland Plain	75	R	X	32	32	100
Scree-slope Grassland/Woodland	Greater Grampians	100			32	7	22
Calcareous Swale Grassland	Gippsland Plain	75	R	Y	558	310	55
Montane Grassland	Highlands - Northern Fall	100	E	X	2013	52	3
Montane Grassy Woodland/Montane Grassland Mosaic	Highlands - Northern Fall	100			1867	1	0
Sub-alpine Grassland	Highlands - Northern Fall	100	R	Y	879	879	100
	Highlands - Southern Fall	100	R	X	987	983	100
	Victorian Alps	100	LC	Y	13925	13492	97
Sub-alpine Wet Heathland/Sub-alpineGrasslandMosaic	Highlands - Northern Fall	100			315	285	90
	Highlands - Southern Fall	100			696	696	100
	Victorian Alps	100			2643	2437	92

Grasslands of the Gippsland Plains have substantially disappeared and are now largely restricted to small linear remnants (DNRE 1997) (Tables 11 and 12). Those at Safety Beach are on small urban blocks destined for housing (Sinclair 2007). Threats include weed invasion, livestock grazing and roadworks (DNRE 1997). Exotic grasses are the most serious weeds at Safety Beach and include *Anthoxanthum odoratum*, *Paspalum dilatatum*, *Pennisetum clandestinum*, *Holcus lanatus*, *Festuca arundinacea*, *Sporobolus africanus*, *Phalaris* spp. and *Stenotaphrum secundatum* (Walter) Kuntze (Sinclair 2007). Fire is now believed to be less frequent and more intense than in pre-European times (DNRE 1997).

Northern Plains Grasslands

Much of the Murray Valley Riverine Plains were reputedly covered with grassland at the time of European settlement. The Victorian Riverina plains grasslands are ecologically similar to those on the floodplains of the Lachlan and Murrumbidgee Rivers in New South Wales. The Northern Plains Grasslands largely occupied gently sloping, Quaternary alluvial stream deposits, often very deep, built of sedimentary and igneous materials derived from the Victorian highlands, deposited on flat plains with residual volcanic hills (Hills 1967, Rosengren 1999).

The soils are <10,000 years old (Jones 1999b) and although not of basaltic origin, the proportion of fine grained material (<0.05 mm, i.e. silt to clay) is high, exceeding 50% (Patton 1930). The Northern Plain extended eastwards from Charlton in the Wimmera, to the Wodonga and Wangaratta areas in the Victorian Riverina, occupying approximately 25,000 km^2 (Hadden 2002). Grassland and grassy woodland occurred on the higher and drier ground away from seasonally inundated areas, but grassland was typical on the poorly drained clay soils (Hadden 2002).

Some grasslands in the Victorian Wimmera and Murray Mallee are secondary formations resulting from timber harvesting and grazing by livestock and feral animals (DNRE 1997), while some former grasslands were transformed into woodlands by agricultural development (Conner 1966). In the west almost all the grasslands have been destroyed but in the north, remnant grasslands have been relatively well conserved, although they are susceptible to high grazing pressure and weed invasion. In the south, only small remnants exist, and these areas are threatened by edge effects and continued clearing (DNRE 1997).

Grasslands in the Wimmera once occupied large areas but have largely been cleared for agriculture (DNRE 1997). This is the case, for example with *Austrostipa*/*Austodanthonia* grasslands in the Horsham area (Connor 1966). Extensive grasslands occurred in the Wimmera on the grey cracking clays and are believed to have been dominated by *Austrodanthonia*, *Austrostipa* and *T. triandra* (Lunt *et al.* 1998). In the eastern Wimmera grasslands formerly existed in a large area known as the Kalkee Plain between Pimpinio, Horsham, Dooen and Jung and through to the north of Kalkee, on the Lallat Plain east of Rupanyup, and in an area between Murtoa and Rupanyup (Connor 1966). These all occurred on heavy textured grey and brown soils, the Kalkee Plains being “extremely self-mulching” gilgai soils with slight variation in microtopography and high lime content (Connor 1966 p. 641). Connor (1966) was unable to find any *T. triandra* in remnants in the Horsham region and characterised these grasslands as a ‘*Stipa-Danthonia*’ association. According to Kirkpatrick *et al.* (1995), the Wimmera grasslands were represented by two extant remnant communities: 1. on red-brown cracking soils on aeolian sediments near Birchip, dominated by *Calocephalus citreus* Less. (Asteraceae), *Austrodanthonia duttoniana* (Cashmore) H.P. Linder and *A. caespitosa* and 2. on alkaline clay between Hosham and Donald, a tussock grassland dominated by *Austrostipa* spp. or occasionally a herbland dominated by *Calocephalus citreus* (Asteraceae), with other characteristic species including *Arthropodium minus* (Liliaceae) and chenopods.

In the Goldfields Region grasslands were confined to the north and were essentially continguous with those in the Wimmera and Victorian Riverina. These were confined approximately to the 350-450 mm annual rainfall belt, bounded to the south (i.e. in wetter areas) by Plain Grassy Woodlands complexes, and to the north and west (drier areas) by Mallee complexes and Wimmera/Mallee woodland (DNRE 1997 – pre-1750 broad vegetation types map).

The Riverina grasslands essentially occupied the floodplains of the major watercourses, in Victoria the Broken, Goulburn, Campaspe and Loddon Rivers (Lunt *et al.* 1998). Unlike the derived grasslands of the NSW Riverina, they appear to have been mostly treeless at the time of European settlement (Lunt *et al.* 1998), although this is contentious. The Victorian Riverina contained the second largest area of grasslands in Victoria prior to European occupation, but these grasslands are now highly depleted and restricted to small fragments, many of which are on private land (DNRE 1997) where they are managed largely by grazing.

The northern Victorian grasslands are dominated by *Austrodanthonia* and *Austrostipa* sp. with a mixture of herbs from the Asteraceae, Chenopodiaceae and Fabaceae (DNRE 1997). *Austrodanthonia setacea* is the most frequent dominant, especially on grazing lands (Kirkpatrick *et al.* 1995). Low saltbushes are a typical component (Lunt *et al.* 1998). Chenopods were more common in the northern areas and *Atriplex nummularia* was possibly once a dominant in the lowest rainfall areas towards the Murray River (Kirkpatrick *et al.* 1995). McDougall (1999) considered that many remnants, like those in neighbouring areas of New South Wales were structurally herblands, i.e. not dominated by grasses, while some were chenopod shrublands, while Kirkpatrick *et al.* (1995) thought that the vegetation of the Mitiamo, Echuca and Serpentine areas was very similar to that of the NSW Riverina. Hadden (1998) found that the major floristic difference between long-grazed Northern Plains and Basalt Plains grasslands she surveyed was the presence of native annuals in the former and their absence in the latter. The exotic flora of the Northern Plains consists mostly of annual species (Foreman 1997). Some of the rare and threatened flora occur also in *T. triandra* grasslands (Kirkpatrick *et al.* 1995). Peak flowering perod for most of the forbs is mid to late September, the grasses usually seed by November or early December, and the soil has largely dried by early summer (Kirkpatrick *et al.* 1995).

Kirkpatrick *et al.* (1995) briefly described the following communities present in the Northern Plains Grasslands:

1. *Austrodanthonia setacea – Enteropogon acicularis – Sida corrugata* Riverine Plains Grassland. Usually a tussock grassland but sometimes dominated herbs or chenopods. Occurs on lime-rich clays and clay loams in areas with less than 470 mm annual rainfall. Also in the NSW Riverina.

2. *Calocephalus citreus – Austrodanthonia duttoniana – A. caespitosa* Wimmera Herbland/Grassland, then known only from a single site near Birchip on aeolian sediment with c. 370 mm annual rainfall. *Maireana* spp. were common.

Foreman (1997) investigated the effects of livestock grazing, cultivation and burning on a long-grazed species-rich remnant. Only the diminutive annual species were not grazed and they increased in abundance under grazing by exploiting the increased gaps. Cultivation increased the abundance and species richness of exotic species, and the abundance of some native annuals (probably because they had a soil seed bank). Fire reduced the abundance of exotics, particularly annuals, presumably by destroying surface seeds. He also found that drought had a very significant effect on the flora, causing a substantial drop in above-ground species richness and abundance, and that native annuals were more abundant when winter rainfall was high.

Irrigated agriculture is the major landuse in the Riverina and salinity is a widespread problem, while other threats include cultivation, irrigation, inappropriate grazing and fire regimes, weed invasion, feral animals and increased fertiliser use (DNRE 1997).

The Northern Plains Grasslands are listed as a threatened community under the *Flora and Fauna Guarantee Act*. (Department of Sustainability and Environment 2009a). Terrick Terrick National Park near Mitiamo, a former grazing property, is the largest and most important conserved remnant of this ecosystem in Victoria (Lunt *et al.* 1998).

Victorian Basalt Plains Grasslands

The grasslands of the Victorian basalt plains were a very large area of grassland at the time of European settlement (Tables 11 and 12). The grassy ecosystems of the plains extended from Melbourne to Hamilton (Stuwe and Parsons 1977) or to “beyond the South Australian border, broken only in a few places by deeply dissected ranges” (McDougall 1987 p. 17), at altitudes from less than 100 m to over 600 m (Stuwe and Parsons 1977). The Volcanic Plains as a land unit occupies c. 22,000 km^2 of which about 37% or 8,260 km^2 (or over 10,000 km^2 according to Williams 2007) was occupied by grassland complexes and most of the remainder by grassy woodland (28%) and herb-rich woodland (14%) complexes (DNRE 1997, Barlow and Ross 2001). Numerous other vegetation types occurred, including wetland, forest and swamp scrub, forming a complex mosaic, in which, judging by the maps of early surveyors, “treeless areas occurred as discrete ‘openings’ in the landscape”, which they identifed as “Plains” (Barlow and Ross 2001 p. 26).

The majority of the Victorian Volcanic Plains terrain is composed of Newer Volcanics, a series of lava flows and tuff plains with extinct volcanic cones (commonly scoria cones but also lava domes) aged from 46 million years ago, peaking at about 2.4 million years and ceasing about 7,000 years ago, i.e. Middle Pliocene to recent (Hills 1967, Dahlhaus *et al.* 2003), although radiocarbon evidence indicates that the most recent volcanic activity was >20,000 years ago (Rosegren 1999). The most recent lava flows are represented by stony rises of ropy lava (Hills 1967). Smaller volcanoes, such as Mt Cottrell, produced the majority of the geological material, mostly highly fluid, basalt lava, that spred in thin sheets 20-200 cm thick, with overlapping flows to 60 m thick in some areas (Rosengren 1999). Eruptions were infrequent and there was little pyroclastic material and ash in most areas, so vegetation would have survived widely beyond the edges of the lava flows (Rosengren 1999).

Despite common parent materials, the soils are highly variable, ranging from gradational clayey chocolate soils and kraznozems on the younger basalts, to coarsely structured duplex soils on the older rocks (Dahlhaus *et al.* 2003). Much of the lava plains was “originally rough and stony, resulting in an irregular topography with many small depressions” (McDougall 1987). In areas that have not been worked, there is still abundant surface rock (Hills 1967), and in areas with developed soils, basalt corestones (‘floaters’) are common at the surface. Much of the rock in developed areas has been cleared, and many kilometres of dry stone walls were built (Patton 1935). The rock is fine-grained, blue-grey in colour and not very hard (Patton 1935) and underlying rock is very close to the surface in many areas (Sutton 1916-1917). The development of watercourses is generally poor, with lava flows often resulting in blockages and substantial areas of internal drainage to ephemeral wetlands, swamps and lakes (Dahlhaus *et al.* 2003), many of which have been drained (McDougall 1987) Waterlogging is widespread (Dahlhaus *et al.* 2003), partly because the soils are so shallow (Patton 1935), but much of the area is well drained due to strong fracturing of the underlying rocks (McDougall 1987).

The eastern areas are Miocene to recent lava plains, with two dominant soil types, formed *in situ*: grey cracking clays, Northcote classification Ug 5.2, and hard alkaline red soils Northcote classification Dr 2.13, ranging in surface texture from sandy loam to clay, but mostly clay loams or light clays, and in colour from black to grey, brown and reddish brown (Stuwe and Parsons 1977). Patton (1935) thought the darker soils characteristic of more low-lying areas, the colour attributable to leaching or organic matter from upslope, and considered that soils higher up the slope had lower clay content. The clays have a high water-holding capacity (45% according to Patton 1935) and high shrink:swell ratio so become waterlogged with poor aeration in winter and deeply cracked in summer (Stuwe and Parsons 1977). With a moisture content of 19%, the soil is “definitely sticky” (Patton 1945 p. 185). Patton (1935) provided a generalised soil profile of a red-brown earth on the Keilor Plains and noted that the B horizon, extending from c. 40-85 cm depth, is not generally penetrated by roots and rests directly upon bedrock. It contains abundant calcium carbonate giving it a white colour. “Most of the richest aricultural and pastoral land in the Western District is composed of ... recent tuffs” (Hills 1967). For Australian soils, the clays are relatively nutrient rich, particularly in phosphorus (Barlow and Ross 2001).

The Victorian Volcanic Plain has average annual rainfalls of 500-700 mm (Dahlhaus *et al.* 2003) and western Victorian grasslands between 450-850 mm (Jones 1999b) , with some areas in the east in rain shadow (between Melton and Werribee) receiving slightly less (Dahlhaus *et al.* 2003), the areas between Anakie and Melbourne with a range of c. 400-600 mm (McDougall 1987), and areas at higher altitude receiving up to 1000 mm, and is evenly distributed throughout the year (Stuwe and Parsons 1977) or with a late winter peak (Jones 1999b). Eight major droughts occurred in the eastern area between 1887 and 1987 (McDougall 1987). Average monthly temperatures are 7-20ºC (Jones 1999b). February is hottest, with maxima sometimes exceeding 40ºC and annual frost days in the eastern area range from 16 to 53 (McDougall 1987). Evaporation is very high in the summer (December to February). The precipitation to evaporation ratio appears to have fallen over the last 100 years, so the area seems to be drying (Dahlhaus *et al.* 2003). Much of the western area is severely affected by rising water tables and dryland salinity, predicted to dramatically worsen (Dahlhaus *et al.* 2003). Mean daily minimum and maximum temperatures are 5-12ºC in July and 12-26ºC in January (Stuwe and Parsons 1977).

Victorian western plains grasslands a result of both soil and climate factors, not aboriginal burning (Cook and Yugovic 2003). Treelessness is explained by seasonal aridity,cold temperature and heavier clay soils (Willis 1964 p. 398). Fires and ash falls resulting from vulcanism would have periodically impacted on the vegetation (Rosegren 1999). Some secondary grasslands are present, resulting from tree removal or suppression of tree regeneration by livestock, notably on stony rises (Kirkpatrick *et al.* 1995).

Grasslands in the Victorian Midlands are included in this category. Little is known about the original extent and composition of the Midlands grasslands. They were mostly in the Dundas tablelands, an undulating area west of the Grampians, 90% of which has now been cleared and which currently supports sheep and cattle grazing (DNRE 1997). The principal areas were in the Glenelg and Wannon catchments west of Hamilton. Smaller areas were present in the Goldfields and Central Victorian Uplands Bioregions. Remnants are are often degraded (DNRE 1997). Prior to European occupation the heavy clays in the Wannon region, near the western end of the Volcanic Plains, were often occupied by grasslands (Lunt *et al.* 1998).

The flora of the Victorian volcanic plains as a whole is the most highly modified vegetation in the State (Willis 1964). The grasslands were the first areas of Victoria occupied by squatters in the 1830s and 1840s for sheep and cattle grazing (Willis 1964, Turner 1968) and "conversion of tribal territory to sheep-runs was rapid and decisive" (Mulvaney 1964 p. 427). These areas "were especially valuable because they required little or no clearing" (Wadham and Wood 1950 p. 84). According to Marshall (1968 p. 165) "the native flora was virtually exterminated over hundreds of square miles". Nevertheless there is still high diversity in the area as a whole. Carr (1999) provided a checklist of the Victorian Volcanic Plains indigenous flora, listing the conservation status of each taxon and the vegetation formations in which they occur. Treeless grasslands and grassy woodlands were not considered to be separate formations. Stony Rise Complex, in many ways a similar floral assemblage to the grasslands, was treated as a separate entity. Asteraceae and Poaceae were by far the richest families (Table 13). McDougall (1987) provided a list of the common vascular plant species in the basalt plains tussock grassland in the eastern section of the Plains (Melbourne region) and a list and brief description of 32 remnant sites on private and public land.

Table 13. Number of plant taxa in plant families with the greatest number of taxa in Victorian Volcanic Plains grasslands and grassy woodlands. Derived from Carr (1999). Taxa doubtfully occuring in this vegetation formation are recorded as "Uncertain". Liliaceae is the combination of Carr's Anthericaceae, Asphodelaceae, Colchichaceae, Hypoxidaceae and Phormicaceae.

Family	**No. of taxa**		
	Known	**Uncertain**	**Total**
Asteraceae	61	9	70
Poaceae	56	7	63
Orchidaceae	18	20	38
Liliaceae	23	1	24
Fabaceae	19	1	20
Chenopodiaceae	16	2	18
Cyperaceae	13	1	14
Juncaceae	10	1	11

Two main types of grassland occur, dominated respectively by *T. triandra* in the drier eastern portion and by *Poa labillardieri* in the higher rainfall western portion, and grassy wetlands occurred in areas subject to seasonal inundation (Lunt *et al.* 1998, Barlow and Ross 2001). The daisies *Rutidosis leptorhynchoides* and *Senecio macrocarpus* have been identified as subdominant herbs on red-brown earth soils (Hills and Boekel 2003). *T. triandra* was the original main dominant over a high proportion of the area, with subdominant *Austrodanthonia* and *Austrostip*a spp., forming discrete tussocks with a range of herbs in the intertussock spaces (Lunt 1990a). In the eastern area *Austrodanthonia* spp. are occasionally locally dominant, and low lying areas are dominated by this genus or *P. labillardieri* and are "usually species rich", while *Themeda*-dominated areas may be depauperate due to dense cover (McDougall 1987 p. 17).. The *T. triandra* tussocks are rarely taller than 30 cm (not including panicles) and have a basal diameter of 5-15 cm (Specht 1970).

Kirkpatrick *et al.* (1995) considered that most of the basalt plains grassland was a *T. trindra – Eryngium ovinum – Schoenus apogon* association, with other characteristic species including *Acaena echinata* (Rosaceae), *Leptorynchos squamatus* (Labill.) Less. (Asteraceae) and *Convolvulus* spp., and at drier sites, *Calocephalus citreus* Less. (Asteraceae). Other areas were dominated by a *T. triandra - Austrodanthonia setacea* community, similar to, and possibly a degraded form of the former. Stony rises were occupied by a community dominated by *T. triandra*, *Austrostipa semibarbata* and *Poa sieberiana*, sometimes with scattered shrubs of *Bursaria spinosa* or small trees (*Acacia melanoxylon* R.Br. and *Allocasuarina verticillata* (Lam.) L.A.S. Johnson), possibly derived from woodlands. Another *T. triandra* community, occurring in the Merri Creek Valley and on the Keilor Plains, is characterised by sparse shrubs of *Acacia paradoxa* DC., and commonly *Austrostipa mollis* (R.Br.) S.W.L. Jacobs and J. Everett and *Austrodanthonia carphoides* Kirkpatrick *et al.* (1995). McDougall (1987) found that many early maps referred to occasional 'Honeysuckle' trees in the grasslands to the north-west and west of Melbourne and concluded that these were probably *Banksia marginata* Cav. (Proteaceae), a species which no longer existed in this formation in the region. Barlow and Ross (2001) expanded this interpretation and considered this formation to be a *Banksia marginata* Cav./*Allocasuarina verticillata*/*Acacia implexa* Benth. woodland, none of which survived into modern times (Barlow and Ross 2001).

The grasslands formed a complex mosaic with other vegetation types, including wetlands and riparian areas, grassy woodlands, shrublands and herblands, which have been similarly degraded or destroyed (McDougall 1999, Barlow and Ross 2001). In the western part of the plains, Grassy Woodland dominates wherever rainfall exceeds c. 700 mm per annum and trees naturally occured on the most rocky areas througout the region (Kirkpatrick *et al.* 1995) and on scoria cones (Barlow and Ross 2001).

Willis (1964) considered that the flora of the Volcanic Plains to have the fewest species of higher plants of all the major vegetation provinces in Victoria (543 spp.), similarly for mosses (c. 85 spp.), lichens and fungi, but probably not for terrestrial and aquatic algae. This "floristic deficiency" (Willis 1964 p. 397) was not, in his opinion, due to degradation. McDougall (1987) calculated that the Melbourne area *T. triandra* grasslands had a total of 183 indigenous vascular species. Of the 108 taxa detected by Stuwe and Parsons (1977) in 59 remnants across the plains, 39 were exotics of which 52% were annuals, whereas annuals comprised only 10% of the native species and 76% of the annuals were alien species, while of the 151 species at Evans St., Sunbury, grassland 101 were native and 50 exotic.

The Keilor Plains (Little, Werribee and Maribyrnong River catchments, along with some creeks that enter the lower Yarra River) at the eastern end of the Volcanic Plains is a rainshadow area with grasslands containing a larger component of 'dry country' species, typically found in the Northern Plains (Sutton 1916-1917, Lunt *et al.* 1998). The Keilor Plains and the plains between Geelong and Cressy "are and always have been open, dry tussock grassland, without any arboreal growth or even tall shrubs" (Willis 1964 p. 398 – except the *Banksia* (see above)) and with floristic and numerical dominance of Poaceae and Asteraceae, which together comprise nearly one quarter of the vascular plant species (Willis 1964). At least 40 species of native grass and about 150 other native plants are found on the Keilor Plains (Scarlett *et al.* 1992). These grasslands are also characterised by the absence of perennial plants that are obligate seed regenerators (Lunt and Morgan 2002). They are notable for the large areas of 'bare' ground between the plants ('intertussock spaces') (Willis 1964),75-80% of the areas at Derrimut treated by by annual or biennial burning or grazing and 85-97% at Laverton North (Henderson 1999), but this space disappears as the grassland ages and the biomass of the dominant grass increases, leading to loss of the intertussock species, through shading, increased seed predation, etc. (Lunt and Morgan 2002). Frequent destruction or natural sparseness of the grass canopy is needed to maintain floristic diversity (Lunt and Morgan 2002).

Stuwe and Parsons (1977) sampled 59 remnants in 1976 with wide variation in climate, substrate and position in the landscape, and found remarkable uniformity in floristic composition, which was most affected by the current management regime. Railway sites, burnt annually, usually in late spring and often with slow, patchy fires had significantly greater mean species richness, with abundant intertussock space. Roadsides, once commonly grazed, but then "virtually unmanaged" (Stuwe and Parsons 1977 p. 473) generally were depauperate, with dense, litter-rich *T. triandra* stands and no bare ground. Pastures grazed by sheep, cattle and horses contained open, species poor vegetation. Morgan (1998c) examined five grasslands on the volcanic plains and found that vascular plant richness varied more between sites than within them, i.e. sites were internally homogeneous.

Most of the flora commences growing from dormant buds after soaking rains in late autumn or winter, blooms in spring (October and November), sheds seeds in summer (December and January) and dies back to dormant buds with very limited growth in the driest period of the year (December to April) (Willis 1964, Lunt and Morgan 2002).

By the mid 1970s only remnants remained, the richest and least weed-infested being along railway lines, managed by annual burning, with roadsides, largely unmanaged or burnt annually or less frequently by local fire brigades, and native pastures having lower plant diversity, the former dense and the latter relatively open (Stuwe and Parsons1977, Morgan 1998c). By the 1990s most intact *T. triandra* grasslands on the Victorian volcanic plains were no longer grazed or were subjected to minimal vertebrate grazing (Morgan 1998c 1998d) but the largest remnants had been degraded by long-term livestock grazing, generally contained few rare species, had low native plant diversity and in some instances a weed dominated soil seed bank (Lunt 1990b 1990c).

Over 95% of all native vegetation on the Victorian Volcanic Plain has been cleared (Sattler and Creighton 2002). According to Sattler and Creighton (2002) 78 Ecological Vegetation Classes (EVCs) have been mapped in the region, 15% of which are probably extinct and 78% threatened. Barlow and Ross stated that 48 EVC occurred on the Volcanic Plain, as determined by direct observation or modelling. According to Dahlhaus *et al.* (2003 citing Ross *et al.* 2002) 115 EVCs, including mosaics and complexes occur in the region. Plains Grassland and Grassy Woodlands originally occupied three quarters of the region and only about 1% remains, much of it degraded (Sattler and Creighton 2002). Nature conservation reserves occupy approximately 1.3% of the region and contain approximately 40% of the EVCs, and biodiversity conservation is heavily reliant on private land, road and rail reserves and other public land (Sattler and Creighton 2002).

Barlow and Ross (2001) cautioned that the several attempts to determine the area of grasslands currently existing in the region were beset with methodological problems, including the difficulty of identification where vegetation was highly altered. Using DNRE (1997) data, they concluded that grassland complexes had been reduced to an area of 1671 ha by 1997, an estimated 0.2% of the pre-1750 extent. But a more complete estimate was suggested to be 5000-6000 ha, or 0.6-0.7%. In the early 1990s possibly <500 ha was considered species rich and minimally weed invaded (Morgan and Rollason 1995 citing McDougall *et al.* 1992), although Barlow and Ross (2001) estimated that "less than 1000 ha" was in this condition. 44% of the remnant sites identified by Stuwe (1986) had been severely degraded, destroyed, or were under threat of immanent destruction by 1992 (Kirkpatrick *et al.* 1995). 80% of Victorian volcanic plains grassland plant species were unrepresented in conservation reserves in 1992 (Morgan and Rollason 1995 citing Scarlett *et al.* 1992). By 1997 grasslands were conserved in "only a handful of small ... reserves" (DNRE 1997). A *Flora and Fauna Guarantee Act* Action Statement for the Western (Basalt) Plains Grassland Community was first prepared in 1994 (Muir 1994).

The Victorian Volcanic Plains Grasslands are one of the most threatened vegetation formations in Australia. The Western (Basalt) Plains Grassland Community is listed as a threatened community under the Victorian *Flora and Fauna Guarantee Act 1988* (Muir 1994). 65 nationally threatened taxa and 173 taxa threatened in Victoria (15 mammals, 61 birds, 4 reptiles, 1 frog, 8 fish, 2 invertebrates and 93 plants) have been recorded in the Victorian Volcanic Plain bioregion (Sattler and Creighton 2002). Environmental weed invasions and modification of fire regimes are amongst the major threatening processes (Sattler and Creighton 2002).

Despite recognition of the importance of these grassland remnants Williams (2007) found that extensive destruction has continued into very recent times, primarily driven by social (including economic) factors. Of the 880 ha that existed in his study area in 1984, 29% had been destroyed by 2004. Road reserve grasslands were reduced by 36% (169 ha), private grasslands by 32% (67 ha) and Crown land grasslands by 14% (18 ha). Grasslands with a high conservation ranking had the lowest probability of destruction but unranked grasslands and those with lower conservaton rankings were more likely to be destroyed. Grasslands on basalt duplex soils had the highest probablity of destruction but also supported the largest number of grasslands. These are more readily cultivated than stony and uniform soils and are relatively high in nutrients. In terms of the road class of the nearest roads, grasslands on local roads had the highest probability of destruction, followed by patches on highways, possibly because local roads are more likely to be grazed, illegally cropped or sprayed with herbicides. In terms of land tenure, grasslands on Crown land were most likely to have been destroyed (mostly by weed invasion), those on private land were less likely to have been destroyed than those on roadsides, and no railway line grasslands were lost. However the number of private grasslands in 1984 was severely underestimated, and it is likely that in reality large numbers were probably destroyed during the period. Country Fire Authority brigades also had a major impact on destruction: those brigades area where management of grasslands had changed from burning to managment using herbicides experienced the highest levels of destruction.

McDougall (1987) argued that management requirements for remnants needed to be site specific, depending on the particular weed problems and specific conservation requirements, and that much remained to be learned. He acknowledged that the effects of fire on the inter-tussock herbs was then largely unknown, but recommended burning at 3-5 year intervals between early October and mid-December to reduce weeds and prevent overdominance by *T. triandra*, except at sites with spring-flowering rare or endangered species, for which late summer or autumn fires were appropriate. The main management issues for these grasslands currently include inadequate knowledge of threatened taxa, management of introduced grasses, prevention of new weed incursions and generalised ecosystem degradation (Groves and Whalley 2002).

Loss of unreserved remnants continues through development for housing and agriculture. Degradation of ‘protected’ remnants also continues, including decline in quality, loss of species etc., as a result of invasive species, pollution at the local and global levels (e.g. N and CO_2 enrichment of the atmosphere), alteration of hydrological processes, other changed ecological processes, and inappropriate or inadequate management.

South Australia

South Australia once had immense areas of temperate native grassland and grassy woodland in what is now the agricultural zone (Davies 1997). The grassy vegetation in that State occurred mainly on plateaus and in broad valleys on lower slopes from the Orroroo and Peterborough areas in the southern and western Flinders Ranges through the Mount Lofty Ranges to Peterborough and Murray Bridge. Smaller areas occurred on the sub-coastal plain of the South East between Bordertown and the Victorian border, on the southern Eyre Peninsula, the Yorke Peninsula, and on basalt soils near Mount Gambier (Lunt *et al.* 1998). However their composition and previous distribution is unclear (Davies 1997). As in Victoria, recognition that grasslands existed in some areas has been slow in coming. Lange (1983) failed to acknowledge the existence of grasslands in the South East. The grasses there, he noted, “do not form savannah; usually they grow sparsely” (p. 99). In the mid 1990s half of the significant South Australian remnants were on private land, one third on roadsides and one sixth on Crown land (Kirkpatrick *et al.* 1995). Exotic plants have been reported to comprise 30% of the South Australian temperate grassland vascular flora (Kirkpatrick *et al.* 1995).

Moore (1993) mapped these grasslands as Temperate Shortgrass (*Austrodanthonia-Austrostipa-Enneapogon*) formations, extending from south of Adelaide through the Mount Lofty Ranges to north of Port Augusta, and in parts of the South East.

Two extant temperate grassland communities are under threat or inadequately conserved*: Lomandra effusa*/*Lomandra multiflora* subsp. *dura* (open) tussock grassland (co-dominant with *Austrodanthonia* and *Austrostipa* spp.), known as Mat-rush Grassland (Scented Mat-rush and Stiff Mat-rush *Lomandra dura* according to Lunt *et al.* 1998), or Irongrass communities (Carter *et al.* 1993) and *Austrodanthonia*/*Themeda* tussock grassland. The former occurs on similar soil types and under similar ecological conditions to other temperate grassland communities in Australia, so despite the dominants not being grasses, the formations are considered in ecophysiological terms to be temperate grasslands (Carter *et al.* 1993). It is most common on skeletal soils in the eastern Mount Lofty Ranges and the Mid North (Kirkpatrick *et al.* 1995). Both communities were mainly found in the Mid North, in the Clare-Port Pirie-Peterborough region but have largely been destroyed by cropping and grazing. Grass dominated communities may have occurred near Adelaide and more widely in the lower South East, but are extremely poorly conserved (Lunt *et al.* 1998, Davies 1997).

Areas of *T. triandra* grassland are “suspected to have existed” in the lower South East, “primarily on basalt soils (e.g. around Mount Schanck and Mount Gambier)”(Foulkes and Heard 2003 p. 48). These areas were described by early settlers as lighted wooded with *Acacia melanxoylon* R.Br, and eucalypts.

A number of other grassland community types are present in South Australia, including *Austrostipa* grasslands and Murray Lakes grasslands (Davies 1997). The *Austrodanthonia caespitosa – Enchylaena tomentosa* Marsh Margin Grassland occurred on the margins of the Murray lakes, and “only survives in small roadside fragments” (Kirkpatrick *et al.* 1995). A *Themeda-Geranium retrorsum-Arthropodium strictum* community occurs in the Mount Lofty Ranges in the Mid North (Kirkpatrick *et al.* 1995). Mathison (2004) stated that South Australian native grasslands are not climax communities but transitional states and can radically change their nature when there is a change in the management regime. Stafford (1991) provided some descriptive information on secondary grassland (transitional to woodland) developed in the East Torrens district after cessation of cropping and grazing. This probably constituted ‘enriched grassland’ in the sense of McIntyre and Lavorel (2007).

Approximately half of the 20 most abundant vascular plant species in South Australian grasslands are exotic and annual grasses including *Avena* spp. *Bromus* spp. and *Vulpia* spp. are amongst the most invasive (Lenz *et al.* 2003)

Tasmania

As in other areas of southern Australia, the natural grasslands of Tasmania were rapidly occupied by European settlers (Benson and Redpath 1997), however they are better reserved than mainland grasslands (Kirkpatrick *et al.* 1995). Tasmanian non-alpine grasslands occur mostly on valley bottoms, on heavy clays or alluvial soils and lower slopes on shallow rocky soils, mostly in the drier Midlands” (Lunt *et al.* 1998). Moore (1993) mapped a narrow band of Temperate Shortgrass (*Austrodanthonia-*

Austrostipa-Enneapogon) from around New Norfolk to south of Launceston. Frequent frosts appear to be the main cause of treelessness (Lunt *et al.* 1998). Secondary grasslands resulting from tree clearance are present in near-coastal areas where frequent burning prevent encroachment by *Melaleuca ericifolia* (Lunt *et al.* 1998). *Poa labillardieri* grasslands on Cape Barren and Flinders Islands were probably formed by repeated burning of forest (Kirkpatrick *et al.* 1995). *Austrodanthonia*, *Austrostipa*, *Poa*, *Microlaena stipoides* and *T. triandra* are the dominant grasses, the latter probably the major dominant at the time of European settlement (Lunt *et al.* 1998). Almost all of Tasmania's remnant are grazed by livestock (Kirkpatrick 2007). Exotic plants have been reported to comprise 23% of the grassland vascular flora (Kirkpatrick *et al.* 1995).

Several plant communities comprise the Tasmanian grasslands (Kirkpatrick *et al.* 1995):

1. *Austrodanthonia – Astroloma humifusum* East Coast Tasmanian Grassland, a derived formation dominated by sparse *A. caespitosa* (Gaudich) H.P. Linder, *A. pilosa* (R.Br.) H.P. Linder and *A. racemosa* (R.Br.) H.P. Linder with other grasses, and intertussock spaces occupied by herbs and the epacrid *A. humifusum* (Cav.) R.Br.

2. *Poa labillardieri – Lomandra longifolia – Acaena novae-zelandiae* Tasmanian Valley Grassland, mainly in the Midlands, dominated by *P. labillardieri* and *L. longifolia* Labill. (Xanthorrhoeaceae), with various components including *Juncus* spp. and *A. novae-zelandiae* Kirk (Rosaceae).

3. *P. labillardieri – Microlaena stipoides – Solenogyne dominii* Tasmanian Valley Grassland, characterised by sparse *Poa* tussocks interspersed with grasses and herbs including the Flat Daisy, *S. dominii* L.G. Adams.

4. *P. labillardieri – Juncus – Hypericum japonicum* Tasmanian Flood Plain Grassland, with large Poa tussocks, found on alluvial flats.

5. *Poa rodwayi – Astroloma humifusum* Tasmanian Rock Outcrop Grassland, found on shallow sandy clay loams around dolerite outcrops.

6. *Themeda – Hibbertia hirsuta – Astroloma humifusum* Tasmanian Grassland, widespread in the Midlands and on the east coast, much of it probably derived from grassy woodland.

7. *Themeda – Stipa stuposa – Chrysocephalum apiculatum* Tasmanian Grassland, on fertile, well-drained sites in the Midlands.

8. *Themeda – Solenogyne gunnii – Microlaena stipoides* Tasmanian Grassland, also in the Midlands and on the east coast, many remnants probably derived from woodlands.

New South Wales and Australian Capital Territory

For convenience, discussion of the NSW and ACT native grasslands is subdivided into three geographical regions. This ignores the occurrence of Temperate Montane Grasslands in outliers around Braidwood, Goulburn, Bathurst and the Albury area, and the whole *Austrostipa aristiglumis*-dominated Western Slopes Grasslands on the North West and Central West Slopes and Plains (Keith 2004). The previous extent of 'natural' grasslands in New South Wales remains controversial. There are large areas of derived grassland. Based on a survey of 126 selected landholders Garden *et al.* (2000) estimated that nearly 1.4 m ha (40%) of Central, Southern and Monaro Tablelands pastures (excluding the ACT) contained significant amounts of native perennial grasses, representing 48%, 31% and 40% respectively of the area of these regions. It was assumed that "cleared and undisturbed areas were essentially dominated by native perennial grasses" and that timbered areas and areas disturbed by cultivation or hebicides to sow pastures or crops were not (Garden *et al.* 2000 p. 1085). The figures probably significantly underestimate the true extent of native grass dominance, since many disturbed area have been recolonised and some sowing of exotic pastures has occurred amongst native grasses (Garden *et al.* 2000). Groves et al. (1973) considered that except for frost hollow areas the *Themeda*/*Poa* grasslands of south-eastern NSW were derived from woodland, and maintained by sheep grazing and regular burning.

Compared to other States, large areas of native grassland in New South Wales exist in Travelling Stock Routes and Reserves, linear reserves up to 400 m wide, that are leased by Rural Land Protection Boards for grazing (Kirkpatrick *et al.* 1995).

Southern Tablelands (NSW and ACT)

The Murrumbateman (South Eastern Highlands 6) bioregion covers the Australian Capital Territory and surrounding areas in NSW and includes the Monaro Tablelands. Grassy woodlands are the major native vegetation type in the region but grasslands occurred throughout, especially on clay substrates in lower rainfall areas, in frost hollows and land with poor drainage (Lunt *et al.* 1998). The soils are typically fertile clays and are derived from basalt, limestone or other sedimentary rocks (Keith 2004). The grasslands in the region are included in Benson's (2004) and Keith's (2004) Temperate Montane Grasslands, which include the grasslands of the ACT, Southern Tablelands and Monaro Plains. According to Keith (2004) they occur at 550-1500 m altitudes in areas with 500-750 mm annual rainfall and are closely related to Tableland Clay Grassy Woodlands, widespread on both the Northern and Southern Tablelands of NSW. On clay soils they are dominated by *T. triandra* and *Poa* spp., on lighter soils and drier upper slopes by *Austrostipa*, *Austrodanthonia* and *Bothriochloa* and along drainage lines by *Poa labillardieri*. The inter-tussock spaces are occupied by erect, scrambling and rosette herbs, and geophytes including orchids and lilies (Keith 2004).

Benson (2004) and to a lesser extent Keith (2004) include alpine grasslands dominated by *Poa* spp. in this class, although Keith acknowledges a gradation into *Poa costiniana* Vickery alpine herbfield/grassland. Temperate *Themeda*/ *Austrodanthonia*/ *Austrostipa* grassland was one of the dominant ecosytems in the region (Lunt *et al.* 1998, Sattler and Creighton 2002), with pre-European extent in the ACT of about 14,000 ha, or 20,000 ha if sparsely treed areas (<10% cover) are included, and approximately 250,000 ha in the whole of the Monaro Tablelands (Sharp 1997, Keith 2004). The natural grasslands of the Monaro have mostly been considerably modified by grazing and other agricultural practices (Garden *et al.* 2000). The natural temperate grasslands in the ACT are found mainly in the northern half, in areas with <600 mm annual rainfall and usually below 600 m in valleys or lower slopes (Chan 1980, Sharp and Shorthouse 1996). Their treelessness has been explained as the combined effects of low nutrient, cracking clay soils, relatively dry and cold conditions, a frost hollow effect and regular aboriginal burning (Sharp and Shorthouse 1996). Cold air accumulates in valley floors to a depth corresponding to the treeline

(Chan 1980). The region also contains large areas of native pasture and secondary grasslands (Sharp and Shorthouse 1996, ACT Government 2005).

Despite the relatively high altitude of these tablelands grasslands, their vascular plant composition is more similar to the grasslands of the Victorian Volcanic Plains than to alpine grasslands (Lunt *et al.* 1998). *T. triandra*, *Austrodanthonia auriculata*, *A. caespitosa*, *A. carphoides*, *A. laevis*, *Austrostipa bigeniculata*, *A. scabra*, *Bothrichloa macra*, *Poa labillardieri* and *P. sieberiana* are generally the dominant native grasses (Sharp 1997). *B. macra* was dominant in some areas in the late 1970s (Groves 1979). Areas of the Monaro tablelands not dominated by *Poa sieberiana* were probably dominated by *T. triandra*, which was largely replaced under bovid grazing by less palatable *Austrostipa* spp. from the mid 1840s (Kirkpatrick *et al.* 1995). Similar to other areas, pasture improvement intensified dramatically from the 1940s, resulting in widespread losses of native grasslands or major modification of their components and structure, including massive incursions of weeds (Keith 2004). Exotic plants have been reported to comprise 29% of the Monaro grassland vascular flora (Kirkpatrick *et al.* 1995). Unlike the Victorian Volcanic Plains, rocks are not a common feature (Melbourne 1993, Kukolic 1994).

Kirkpatrick *et al.* (1995) briefly described the following lowland grassland communities in the region: 1. *Poa labillardieri – Austrostipa – Bothrichloa macra* Monaro Basalt Grassland, a widespread, dense-tussock formation on clays in the ACT and NSW; 2. *Poa sieberiana – Carex appressa – Juncus* Monaro Grassland, probably best thought of a highland community; 3. *Austrostipa scabra – Enneapogon nigricans* Monaro Grassland, a mid-dense tussock grassland found mainly on upper slopes and ridges; 4. *Themeda triandra – Poa sieberiana – Bulbine bulbosa* Monaro Grassland, found on valley floors or slopes with a southerly aspect; 5. *Themeda triandra – Eryngium ovinum – Carex inversa* Canberra Grassland, largely confined to the ACT in valleys on limestone;

Sharp (1997) provided an analysis of the floristic associations present in the ACT (Table 14) and previous floristic classifications. The *Austrodanthonia* association occurred on sites subject to historical levels of moderate to high disturbance on well drained clay soils with low nutrient levels, and had the largest areas of bare ground. A wet *Themeda* association occurred in areas with moderate to high historical disturbance regimes, on poorly drained (seasonally wet) sites with higher soil P and acidity levels. A dry *Themeda* assocation occurred on well drained sites with low levels of disturbance, and had high litter cover of c. 40% and low soil P (7.9 ppm). About 70% of vascular plant species present were forbs, with Asteraceae an important component (Sharp and Shorthouse 1996). No community had consistently higher exotic richness, but the wet *Themeda* association had the highest exotic cover in spring, and the dry *Themeda* association the lowest (Table 14).

Table 14. Floristic characteristics of natural grassland floristic associations in the ACT from a survey of 39 sites (Sharp 1997).

Association	**Mean spp. richness (per 10 m^2)**			**Mean spp. richness (sites)**			**% exotic cover (spring)**
	Native	**Exotic**	**Total**	**Native**	**Exotic**	**Total**	
Austrodanthonia	24.7	12.4	37.1	33.2	21.7	54.9	32.8
Wet *Themeda*	25.3	13.7	39.0	36.3	23.2	59.5	35.5
Dry *Themeda*	21.8	8.6	30.4	41.8	23.6	65.4	11.1

Remnant grassland on the Southern Tablelands is highly fragmented and adequate reservation was considered unlikely to be achievable (Sattler and Creighton 2002). Remaining remnants are in various states of degradation and exist in a matrix of exotic pasture (Keith 2004). Approximately 5% of the original 20,000 ha of grasslands in the ACT were in more of less natural condition (florisitically and structurally intact, with low weed cover) in 1996, with an additional 550 ha of low quality grassland (Sharp and Shorthouse 1996, Sharp 1997). Sharp and Shorthouse (1996) provided a map of the pre-European distribution and remaining remnants and estimated that c. 70% of the grasslands identified in the late 1970s had subsequently been destroyed by urban development, conversion to pasture or invasion by exotic plants. Less than 3% of the pre-European area remained in reasonable condition by 2005, reduced from 11% of the region pre-1750 to about 1% in 2000 (ACT Government 2005). Most had been destroyed by intensive agriculture and urban growth, and existing remnants were threatened by inappropriate management. Remaining sites were mostly <5 ha, with a range from <1 to 300 ha (Sharp 1997).

Examples with high-biodiversity are very poorly reserved in NSW but better represented in the ACT conservation network (ACT Government 2005), although the ACT remnants are highly fragmented and their composition and structure have been markedly changed by weed invasion and management (Sharp and Shorthouse 1996). In NSW the most intact examples exist in cemetries and on travelling stock routes not subjected to heavy grazing (Keith 2004). Natural temperate grassland was listed as an endangered ecological community in the ACT in c. 1996 (Sharp and Shorthouse 1996).

Little grassland in the ACT has been deliberately burnt since European occupation and current management is primarily by livestock grazing, while many of the larger grasslands are intensively grazed by kangaroos. An action plan for the region's grasslands has been prepared only for the ACT, under the *Nature Conservation Act 1980* (ACT Government 1997) and recently a comprehensive conservation strategy (ACT Government 2005).

Keith (2004) provided a list of indicative species for the Temperate Montane Grassland formation.

Northern Tablelands (NSW)

According to Johnson and Jarman (1975 p. 26), the explorer Thomas Oxley, the discoverer of the New England Tablelands, and early settlers described the country as "open park-like tussock grassland, irregularly and fiercly burned by aborigines". Much of the area was probably open woodland. However, West of Glen Innes, Cameron (1975 p. 19) judged that "the only open country when the white man came ... was on the floor of the valleys". Benson and Redpath (1997) thought that treeless natural grasslands were mainly restricted to cracking clay soils and alluvial soils derived from basalt in a small proportion of the southern section of the Tablelands. Keith (2004 p.108) considered them Temperate Montane Grasslands, and mentioned their occurrence in "valleys around Guyra". Most of the existing grassland is currently recognised as formation derived from Tableland Clay Grassy

Woodlands and New England Grassy Woodlands (Benson 2004), by tree clearing and livestock grazing (Trémont 1994). Frequent aboriginal burning is believed to have opened up the woodlands and maintained grassy vegetation (McIntyre and Lavorel 1994b). The map of Moore (1993) included most of the Northern Tablelands as aTemperate Shortgrass (*Austrodanthonia-Austrostipa-Enneapogon*) community. The grasslands occur on soils derived from basalts, granite or sedimentary rocks, at altitudes from <1000-1400 m (McIntyre and Lavorel 1994a). The plant species composition of the basaltic grasslands, both native and exotic, clearly differs from grasslands on the other substrates, although very few species are specific to a particular geological substrate. Altitude and topographic position has little effect on their composition (McIntyre and Lavorel 1994a).

The New England Tablelands were discovered in 1812, the first settlers arrived with sheep in 1832, 66 stations were occupied by 1840 and all of the best grazing land had been taken up by 1848 (Johnson and Jarman 1975). Woodlands were cleared from the 1850s onwards, and the native pastures that resulted consisted mainly of summer-growing species that proved to be inadequate for livestock (Davidson 1981). Graziers instituted a new fire regime, regular burning in late winter (Johnson and Jarman 1975). Annual fires encouraged *T. triandra* and did little to eliminate unpalatable *Poa* tussock grass (Davidson 1981) but contributed to an alteration in the “tussocky nature of the grassland” (Johnson and Jarman 1975).

A government bounty was offerred for large macropods in the 1870s and many tens of thousands of kangaroos were killed annually (Cameron 1975, Johnson and Jarman 1975). Bounties were extended in the 1880 to rat kangaroos (Johnson and Jarman 1975). The Armidale Pasture Protection Board first put the European hare on the bounty list in 1902 and the European rabbit in 1905, having “first treated [it] with complacency” (Johnson and Jarman 1975 p.30). In the Armidale region bounties paid on hares peaked in 1905 at c. 135,000 animals, while those for rat kangaroos peaked in 1909 at c. 20,000 animals (Johnson and Jarman 1975). The Armidale Board appointed its first rebbit inspector about 1909, the rabbit problem having then become serious. Sheep and cattle numbers increased rapidly from 1900 leading to “the final disappearance of tussock grasslands under grazing pressure or pasture improvement” (Johnson and Jarman 1975). After stock numbers plateaued early in the 20th century, *Bothrichloa* became the dominant native grass, with exotic *Vulpia* and *Hordeum* providing cool-season feed (Davidson 1981). Use of superphosphate commenced about 1950 along with sowing of *Trifolium* spp. and then introduced grasses (Davidson 1981), leading to massive increases in the number of sheep and a lesser increase in cattle and horses through to 1975 (Johnson and Jarman 1975).

The native grasslands of the Northern Tablelands are still most commonly dominated by *Poa* spp. and *T. triandra* (McIntyre 1993). They are often on the most elevated areas, so it is somewhat misleading to include them in the ‘lowland’ category (Carter *et al.* 2003). Detailed studies of these grasslands include those of Trémont (1994) and Trémont and McIntyre (1994).

South West Slopes and Riverina (NSW)

The extent of grasslands in central and southern New South Wales prior to European settlement continues to be controversial. Grasslands were formerly widespread in the NSW Riverina (Lunt *et al.* 1998). The South West Slopes of NSW include part of the NSW Riverina which extends into the South West Plains. Small areas of treeless grassland occurred on the South West Slopes but their “composition and persistence is unknown” (Lunt *et al.* 1998). Cluff (2001) argued that treeless grasslands extended from the Liverpool Plains to Lake George and that much of the Central West and Central Tablelands were not forested. Benson (2004) described the NSW Western Slopes Grasslands as dominated by *Austrostipa aristiglumis* (F. Muell.) S.W.L. Jacobs and J. Everett, lacking many of the plant genera typical of the more temperate grasslands and much drier than the temperate montane grasslands of the south-east.

The Riverine Plain is a vast plain covering over 90 million ha, covered wtih alluvial material and extending from north of Bendigo, Victoria to Ivanhoe in the far west of NSW, and from Balranald to Narrandera, in the south-west of NSW (Leigh and Mulham 1965). In NSW the grasslands occur in the more mesic south-easterly section of the Plains, the Riverina, between the Murray and Murrumbidgee Rivers. Grasslands in the NSW southern Riverina are similar in composition to those of adjacent areas in northern Victoria (Lunt *et al.* 1998) (see ‘Northern Plains Grasslands’, above). McDougall (1999 p. 50) suggested calling the whole formation “the eastern Riverina plains”. The Riverina grasslands occur on clay and clay loam soils, and are dominated by *Austrodanthonia* spp., *Austrostipa* spp. and *Chloris truncata* (Benson 2004). *Austrodanthonia setacea* is frequently the dominant species (Kirkpatrick *et al.* 1995). Seasonally wet depressions are occupied by grassy wetlands including blown grasses and *Austrodanthonia duttoniana* (Lunt *et al.* 1998). Moore (1993) mapped most of this region as Temperate Shortgrass (*Austrodanthonia-Austrostipa-Enneapogon*), bounded to the north-west from north of Deniliquin to Griffith and further north by a band of “Xerophytic Midgrass (Southern)” dominated by *Austrostipa*, *Chloris* and *Aristida*. Much of the western Riverina was considered “Saltbush Xerophytic Midgrass”, dominated by *Atriplex*, *Maireana* and *Austrostipa*.

The Riverine Plains have “long been considered one of the finest sheep-rearing areas in Australia” but continuous heavy stocking grazing from the 1880s resulted in “dramatic retrogressive changes in botanical composition” including a lack of dry season fodder (Leigh and Mulham 1965 p. ix). According to Mulham and Moore (1970 p. 105) the dominant grasses on the lighter soils were originally summer-growing *Eragrostis* sp. and *T. triandra* but these were eliminated or much reduced by continuous grazing, and replaced by winter-growing *Austrostipa* spp. In the wetter areas of the south and east these speargrasses are strong perennials but in the drier western areas are “more ephemeral”. Leigh and Mulham (1965 pp. 29-30) thought that *T. triandra* “originally covered vast areas of the Riverine Plain, particularly on loam soils” but was then rare and found only in in areas from which livestock had been excluded for long periods. Despite the former predominace of *T. triandra*, the modified flora has few similarities with that of the more mesic *T. triandra* grasslands of south-eastern Asutralia and contains a large proportion of arid zone species (Kirkpatrick *et al.* 1995). Exotic plants have been reported to comprise 32% of the Riverine Plains grassland vascular flora (Kirkpatrick *et al.* 1995).

A higher proportion of the region’s grasslands are secondary than of any other region in south-eastern Australia (Lunt *et al.* 1998). Much of the existing grassland is derived from shrubland dominated by *Acacia pendula* A. Cunn. ex G. Don. and *Atriplex nummularia* Lindl., with shrubby Aizoaceae widely present in the understorey, as a result of heavy grazing (Benson and Redpath 1997, McDougall 1999, Benson 2004). According to Leigh and Mulham (1965 p. ix) grazing practically eliminated the larger chenopod shrubs, including *A. nummularia*, *A. vesicaria* Heward ex Benth., *Maireana aphylla* (R.Br.) Paul G. Wilson, *M.*

pyramidata (Benth.) P.G. Wilson and *M. sedifolia* (F. Muell.) P.G. Wilson that were originally dominant over most of the area, and resulted in their replacement by low-growing, spiny, unpalatable *Sclerolaena* spp., or by "degraded grassland vegetation ... of annual, and to a lesser extent perennial, grasses and herbs". Kirkpatrick *et al.* (1995) thought that the original vegetation before livestock grazing might best be characterised as chenopod shrubland with a grassy ground layer, and suggested that drought, fire or rabbit grazing may have destroyed the original shrubland, rather than livestock grazing which merely prevented regeneration of woody species. According to Moore *et al.* (1973 p. 236) no stands of the original vegetation then existed, but observations suggested that the trees had been up to 9 m high, the shrub layer was well-developed but discontinuous, that *Atriplex* predominated on grey and brown clay soils and the *Acacia* was dominant on red-brown earths. The other main shrubs were the chenopods *Rhagodia spinescens* R.Br., *Enchylaena tomentosa* R.Br. and *M. aphylla*. The grassy ground layer varied in composition according to soil texture. *Chloris truncata* and *Austrostipa* "*variabilis*" (= *A. scabra/A.nodosa*) were then common on light-textured soils. *Austrodanthonia caespitosa* and *C. truncata* were the main species on clays, although *Austrostipa artistiglumis* was probably once more common or dominant. Leigh and Mulham (1965) considered the latter species to be found on most soil types and to often occur in dense, localised stands. Other common and widespread native grasses included *Chloris ramosus* B.K. Simon, *Eragrostis* spp., *Eriochloa pseudoarcrotricha* (Stapf ex Thell.) J.M. Black, *Panicum* spp., *Sporobolus caroli* Mez, (Leigh and Mulham 1965). Other common native species included *Bulbine bulbosa* (R.Br.) Haw., *Lomandra effusa* (Lindl.) Ewart, *Hypoxis glabella* R.Br., other *Atriplex* spp., *Chenopodium* spp., *Disphyma crassifolium* (L.) L.Bolus, *Swainsona* spp., *Sida* spp., *Haloragis* spp., *Plantago varia* R.Br., *Asperula conferta* Hook. f., *Wahlehbergia* spp., herbaceous *Goodenia* spp. and a large suite of small daisies (Leigh and Mulham 1965).

Leigh and Mulham (1965) provided an illustrated compendium of the important pastoral plants of the Riverina grasslands.

Grassland fauna

The fauna of temperate Australian native grasslands is very poorly known. Much of the vertebrate fauna, particularly the mammals, was eliminated during the early years of European occupation, and the invertebrate fauna has received limited attention, apart from a few agricultural pests and iconic native species, some exploratory inventory studies in Victoria and the ACT, and several detailed studies in the ACT. Australian grasslands have been said to have relatively few specialist animal species and "a modest but distinctive array of animals that feed on on the foliage or the seeds of grass" (Keith 2004 p. 104).

Grasslands are characterised by high rates of herbivory compared to many other terrestrial ecosystems, with consumption efficiencies generally c. 25% compared to c. 5% in forests (Tscharntke and Greiler 1995). High root: shoot ratios in temperate grasslands means there is a large subterranean plant biomass to support soil fauna, and the subterranean standing crop consumed by insects is 2-10 times higher than the above-ground crop (Tscharntke and Greiler 1995). Thus an underground life stage is typical in grassland insect genera (McQuillan 1999).

The seral stage of *T. triandra* grassland affects its suitability for animals. Biomass of the grass determines the floral composition of the grassland, presence of food plants, amount of shade and the structure of habitat. Watson (1995 cited by Lunt and Morgan 2002) "found substantial seed predation beneath a dense grass cover, but little in burnt open areas".

In this review, the vertebrates are first examined, with a particular emphasis on the extinct mammalian fauna, then invertebrates, with a particular emphasis on insects, including an examination of several rare and threatened taxa, and a detailed review of what is known about the fauna of grasses.

Vertebrates

Many of the mammals and birds that forage in grasslands require structural habitat features for shelter, nesting, etc. that grasslands do not provide (Keith 2004), this being the case for example with insectivorous bats. But today, and in geologically recent times, the often complex vegetation mosaics around or within south-eastern Australian grasslands have meant that vertebrates dependent on woodland and shrubland for shelter etc. have been widely able to use grasslands to meet some of their requirements.

Vertebrate species can be detrimentally or beneficially impacted by the floristic and structural vegetation changes caused by weeds, including alterations to food supply and foraging potential, nest sites, cover, predator protection, etc. (Brown *et al.* 1991). Conversely, the activities of vertebrates may hinder or facilitate weed populations by bioturbation, defecation and urination, feeding and other activities.

Mammals

Grassland mammal assemblages are characterised by the lack of arboreal species and of browsers, and restricted diversity of grazers (Webb 1977). Australian grasslands were once occupied by a marsupial megafauna, which disappeared, like similar faunas in North and South America, during the Miocene and the end of the Pleistocene (Webb 1978). The major extinction phase in Australia occurred in the late Pleistocene, possibly mostly c. 26 kbp and continuing to c. 18-15 kbp, and has been associated with general continental drying (Kershaw et al. 2000). The marsupial megafauna occurred in 250-750 mm rainfall zones, and one of three groups was specifically adapted to southern grasslands (Kershaw et al. 2000). Aboriginal Australians may have played little part in their disappearance, since fossil evidence suggests coexistence for at least 20,000 years, although recent redating appears to have markedly reduced this overlap period (Kershaw *et al.* 2000) and consensus now favors hunting as the major cause of extinctions (Flannery 1994, Johnson 2009). Subsequent to the extinction of the megafauna, another set of medium sized animals largely disappeared from south-eastern Australian grasslands, mainly during early historical times (Table 15).

According to Lunt *et al.* (1998), 8 of 26 mammal species (excluding bats), mostly rodents and small to medium sized marsupials, once found in the grassy plains of south-eastern Australia are now no longer present. In the South East of South Australia the mammals that have disappeared since European occupation have been those that "lived mainly in woodlands and grasslands" (Aitken 1983 p. 127). Numerous species have been lost in Victoria including Potoroidae (Bettongs *Bettongia* spp., Rufous Bettong *Aepyprymnus rufescens* Gray), Macropodidae (e.g. Eastern Hare-wallaby *Lagorchestes leporides* (Gould), Bridled Nailtail Wallaby *Onychogalea fraenata* (Gould), Toolache Wallaby *Macropus greyi* Waterhouse, Tasmanian Pademelon

Thylogale billardierii), Peramelidae (bandicoots) and Muridae (Rabbit Eared Tree Rat *Conilurus albipes* (Lichtenstein)) (Wakefield1964b, Menkhorst 1995a). Many grassland mammals have also become exinct in New South Wales, including *L. leporides*, Tasmanian Bettong *Bettongia gaimardi* Desmarest, Western Barred Bandicoot *Perameles bougainville* (Quoy and Gaimard), *C. albipes* and Plains Mouse *Pseudomys australis* Gray (Muridae) (Keith 2004).

Bats are relatively common crespusclar and nocturnal foragers over native grasslands. The insectivorous Verpertilionidae are the dominant group in south-eastern Australia but their persistence is dependent on the availability of roosting and maternity sites in tree hollows, to which they must return on a daily basis, and the ongoing loss of old hollow-bearing trees is a threat to their continued existence (Mansergh *et al.* 2006b).

Table 15. Grassland mammals that have disappeared from south-eastern Australian grasslands since European settlement. E = globally extinct, E(MSE) = extinct in mainland south-eastern Australia, En(Vo) = endangered in Victoria, only present in Victoria. 'Mainland south-eastern Australia' excludes Queensland and the Northern Rivers district of NSW. N.B. Grasslands were not a habitat of *Leporillus apicalis*, *Dasyurus viverrinus* and *Phascogale calura* according to Menkhorst (1995a).

Species	**Common Name**	**Family**	**Current Status**	**References**
Dasyurus viverrinus (Shaw)	Eastern Quoll	Dasyuridae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998
Phascogale calura Gould	Red-tailed Phascogale	Dasyuridae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998
Chareropus ecaudatus (Ogilby)	Pig-footed Bandicoot	Peramelidae	E	Menkhorst 1995a, Lunt *et al.* 1998
Perameles bougainville (Quoy and Gaimard)	Western Barred Bandicoot	Peramelidae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998
Perameles gunnii Gray	Eastern Barred Bandicoot	Peramelidae	En(Vo)	Menkhorst 1995a, Backhouse and Crossthwaite 2003
Aepyprymnus rufescens (Gray)	Rufous Bettong	Potoroidae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998
Bettongia gaimardi (Desmarest)	Tasmanian Bettong	Potoroidae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998
Bettongia lesueur (Quoy and Gaimard)	Burrowing Bettong	Potoroidae	E(MSE)	Noble 1993
Bettongia penicillata Gray	Brush-tailed Bettong	Potoroidae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998
Lagorchestes leporides (Gould)	Eastern Hare Wallaby	Macropodidae	E	Wakefield1964b, Menkhorst 1995a
Macropus greyi Waterhouse	Toolache Wallaby	Macropodidae	E	Menkhorst 1995a
Onychogalea fraenata (Gould)	Bridled Nailtail Wallaby	Macropodidae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998
Thylogale billardierii (Desmarest)	Tasmanian Pademelon	Macropodidae	E(MSE)	Williams 1995
Conilurus albipes (Lichtenstein)	White-footed Rabbit-rat	Muridae	E	Menkhorst 1995a, Lunt *et al.* 1998
Leporillus apicalis (Gould)	Lesser Stick-nest Rat	Muridae	E	Menkhorst 1995a, Lunt *et al.* 1998
Pseudomys sp.	rat	Muridae	E	Lunt *et al.* 1998
Pseudomys australis Gray	Plains Rat	Muridae	E(MSE)	Menkhorst 1995a, Lunt *et al.* 1998, Mansergh andSeebeck 2003

Information on the orginal habitat preferences and populations densities of the species that have dramatically declined are difficult to obtain (Noble *et al.* 2007). Opinions differ on whether some were grassland inhabitants. Seebeck and Mansergh (2003 p. 2) considered the extinct *Lagorchestes leporides* to be an arid zone species, "limited to the central and southern sections of the Murray-Darling basin", and the former range of the extinct *C. albipes* to be unclear. Hope (1994) argued that 30-12 kybp cave sediment fossils from south-western Victoria were of desert animals. But Wakefield (1964b) reported subfossil remains of *L. leporides* at Mt Hamilton and of *C. albipes* from Mt Eccles, Byaduk Caves and Mt Hamilton, while Seebeck and Mansergh (2003) mentioned historical records of *C. albipes* from the Port Phillip region and the Portland area. *L. leporides* was known in the South East of South Australia where it was last recorded near Naracoorte in 1870, and *C. albipes* was reported from the South East only before 1843 (Aitken 1983). Frith (1973 p. 76) considered both *Lagorchestes* and *Onychogalea* to have been "abundant in more open woodlands and savannahs". Brown (1987) considered that three species of bandicoots extinct in Victoria were restricted to the semi-arid north-west of the State. Wakefield (1963a p. 328) stated that there is "evidence that *C. albipes* survived [in Victoria] until well after European settlement". Williams (1995) stated that *Thylogale billardierii* was "apparently common" in coastal forest and scrub in southern Victoria before 1900, but recorded a specimen from Werribee in 1881.

Pseuodmys australis, extinct in Victoria and NSW but still present in central Australia, is considered to have once inhabitated the Western Plains Grasslands of Victoria, "where it constructed large, shallow, complex burrow systems", but there is no reliable (i.e. specimen based) evidence that it occurred in the State at the time of European occupation (Mansergh and Seebeck 2003).

Wakefield (1964b) reported subfossil remains of the *Bettongia gaimardi* from Mt Hamilton and the Burrowing Bettong *B. lesueur* (Quoy and Gaimard) from Mt Hamilton and Bushfield (8 km north of Warrnambool). The former was probably present in the South East of South Australia during the period of early settlement (Aitken 1983) and probably became extinct on mailand Australia about 1900, but is still extant in Tasmania (Mansergh and Seebeck 2003). The latter, at the time of European settlement, was found across all regions of native grassland in western and northern Victoria, the NSW Riverina and South Australia, but not the NSW Southern Tablelands (Aitken 1983, Seebeck and Rose 1989, Noble 1993, Noble *et al.* 2007), and had the widest distribution of all native mammals (Noble *et al.* 2007), but became extinct on the mainland. Population densities of 14-35 km-2 have been estimated in arid and semiarid areas (Noble *et al.* 2007). The Brushtailed Bettong *B. penicillata* was once common across southern Australia (Garkaklis *et al.* 2003), although Seebeck and Rose (1989) indicated a former range inland of current temperate grasslands, except in South Australia. The Rufous Bettong *Aepyprymnus rufescens* prefers "open grassy woodland and forest", but in northern NSW the vegetation consisted of "only tall native grasses" and individuals have been observed feeding in pasture (Seebeck and Rose 1989 p. 726). It's decline on the northern tablelands of NSW was partly the result of destruction as vermin and partly from extinction of its tussock grassland habitat (Seebeck and Rose 1989). Bettongs were considered to be agricultural pest species during early European settlement (Seebeck and Rose 1989, Noble *et al.* 2007).

Wakefield (1964a p. 277) listed other species found as subfossils in caves near Byaduk and Mt Eccles that are not found in the Western Plains Grasslands today but were "Presumably ... present on the basalts of south-western Victoria at the time of European occupation ...". These included the extinct *Pseudomys auritus* which was present "in the recent past ... eastward, apparently in abundance, to central Victoria" (Wakefield 1964a p. 278) and was "once widespread in western Victoria" (Wakefield 1963b p. 44).

Perhaps at a more distant time the Western Basalt Plains were also inhabited by the Tasmanian Devil *Sarcophilus harrisii* (Boitard) and the Thylacine *Thylacinus cyanocephalus* (Harris). Wakefield (1963a) reported sub-fossil remains of both these large predators, extinct on mainland Australia, from lava caves at Mount Hamilton. Remains of of *S. harrisii* appeared to be "quite modern" with one mandible having "pieces of dried tissue adhering to the bone", while the few remains of *T. cyanocephalus* appeared to be "not ... very old" (Wakefield 1963a p. 324). Remains of the latter species are known also in Victoria from Gisborne, while remains of *S. harrisii* in Victoria have been radiocarbon dated to 550 ±200 years B.P. (Wakefield 1963a). Dixon (1989 p. 557) noted that *T. cyanocephalus* was well known from the main area of natural open grasslands in Tasmania, the midland plains region, and that most captures of the animal occured in "farmed flat areas", where it was considered a serious predator of lambs. Loss of 'top predators' has serious cascade effects in food webs, and probably contributed greatly to the collapse of grassland ecosystems.

Bandicoots are primarily nocturnal and crepuscular, rat to rabbit sized marsupials, which, along with bilbies (Thylacomyiidae) have sufferred more negative impact from European occupation than any other marsupial group except Potoroidae (Brown 1987) and the thylacine. The extinct Pig-footed Bandicoot *Chaeropus ecaudatus* (Peramelidae) was a grassland species which required "lush growing tips of grasses and herbs", so livestock grazing is probably the major factor in its extinction (Menkhorst 1995a) along with habitat destruction by rabbits and predation by introduced mammals (Seebeck and Mansergh 2003). Seebeck and Mansergh (2003), on the other hand, considered it to be an arid zone species, restricted in the historical period in Victoria to the Mallee. Sheep grazing is also probably the major factor in disappearance of the Bridled Nailtail Wallaby (Menkhorst 1995a). Losses of such a large proportion of the native herbivores likely had a profound effect on plant diversity (Bloomfield and McPhee 2006).

Studies of more arid and northern regions of/Australia, and other areas of the temperate pastoral zone show similar losses of medium sized (35 g to 55 kg) ground dwelling marsupials and murid rodents (Burbidge and McKenzie 1989, Short and Smith 1994, Short and Turner 1994, Noble *et al.* 2007). Various factors in combination are blamed including hunting, increased predation from foxes and cats, rabbit and livestock grazing, habitat clearance and fragmentation, land use change and altered fire regimes (Recher and Lim 1990, Short and Smith 1994). Rat kangaroos (Potoroidae) never recovered from hunting under a bounty system on the Northern Tablelands of NSW (Johnson and Jarman 1975), although they were present "in plague proportions" in the 1880s and 1890s (Cameron 1975 p. 21). Altered fire regimes are possibly the most important: in areas where it has been possible to study the losses, in Central Australia, they are temporally correlated with the departure of aboriginal people and the cessation of regular aboriginal burning (Short and Turner 1994, Flannery 1994). The absence of regular burning resulted in decreased rates of nutrient recycling and the absence of new lush vegetation, creating a nutritional crisis for the more specialised feeders (Flannery 1994). A general increase in biomass of vegetation coupled with decreased patchiness meant that a fire, when it did arrive, burnt much more widely and intensely than previously, creating large areas with no food, nor shelter from predators, and later a uniform, even-aged vegetation (Flannery 1994). However a test of the mosaic burning decline hypothesis (Short and Turner 1994) found that mosaic scale had no significant effect on survival of three species in the critical weight range, and that declines on mainland Australia and survival on off-shore islands was better explained by the presence or absence of exotic predators (foxes and cats) and herbivores (rabbits and livestock). More generally, Burbidge and McKenzie (1989) found that the diverse effects of diversion of environmental production to human uses effectively resulted in a general trend to environmental aridity, that differentially affected moderately sized mammals with limited mobility, relatively high daily metabolic requirements and more specialised feeding strategies.

Victorian grasslands now support little native mammalian diversity. Victorian mammals adapted to grasslands and grassy woodlands are one of Menkhorst's (1995b) five groups of mammals requiring specific managment to secure their future. They include the Fat-tailed Dunnart *Sminthopsis crassicaudata* (Gould), Eastern Barred Bandicoot *Perameles gunnii* and Common Wombat *Vombatus ursinus*. The latter occurred throughout the volcanic plains in the 1800s but is now extinct in western Victorian grasslands. Another widespread species not threatened on a State or national basis, the Eastern Grey Kangaroo *Macropus giganteus* was once common in the Victorian basalt plains (Sutton 1916-1917, Coutts 1982) but is now rare in the region (Lunt *et al.* 1998) although some large populations exist (e.g. at Woodlands Historic Park). In the South East of South Australia it was restricted to four colonies by 1983, one in woodland with associated grassland (Aitken 1983). The Western Grey Kangaroo *M. fuliginosus* (Desmarest) was still common and included grassland in its habitat (Aitken 1983). This species prefers areas with heathy understorey but forages in grassland (Bennett 1995).

In the South East of South Australia *S. crassicaudata* was considered common in grassland, including pasture, while *V. ursinus* was reduced to remnants, including populations in coastal grassland and sedgeland (Aitken 1983).

Perameles gunnii, incorrectly said to be endemic to the Victorian Volcanic Plain (DNRE 1997), was formerly widespread and abundant across the Plains from near Melbourne north to Beaufort and west to Coleraine in Victoria and into the South East of South Australia, but is now critically endangered on mainland Australia (Aitken 1983, Brown 1987, Brown *et al.* 1991, Backhouse and Crossthwaite 2003). The mainland and Tasmanian populations are distinct, undescribed subspecies (Backhouse and Crossthwaite 2003). *P. gunnii* is "specifically adpated to grassland and savannah woodland" (Brown 1987). *P. gunnii* digs small conical burrows in the soil when foraging for its invertebrate prey. Earthworms are important in the diet in wetter months. Cockroaches (Blattidae), earwigs (Forficulidae), beetles, both larval and adult especially larval Scarabaeidae, Lepidoptera larvae and *Romulea rosea* bulbs are other common dietary items (Brown 1987).

Its original habitat on the mainland "included" *Austrodanthonia*, *Austrostipa*, *Poa labillardieri* and *Themeda triandra* grasslands and it requires dense ground cover for shelter, and open areas with relatively short grass in which to forage (Brown *et al.* 1991 p. 150). Replacement of native grasses by exotic pasture grasses and weeds has reduced protective cover, but other factors including habitat destruction, predation by introduced vertebrates and exotic disease appear to be of much greater importance than weeds in its decline (Brown *et al.* 1991, Backhouse and Crossthwaite 2003). One important factor is probably soil compaction by bovid livestock (Brown 1987). It was last recorded in South Australia nearr Mt Gambier in 1890 (Aitken1983). Several colonies possibly still existed in the Victorian Western District in the late 1940s but it probably survived only in the Hamilton and Penshurst districts in the 1960s (Brown 1987). From c. 1971 the last remaining wild population on mainland Australia continued to exist in a highly modified environment "almost totallydominated by exotic plant species" at Hamilton rubbish tip, being able to escape predation by hiding in old car bodies and thickets of gorse *Ulex europaeus* L., and foraging in surrounding paddocks (Backhouse and Crossthwaite 2003 p. 3).

Hadden (2002) surveyed 24 remnant grassland sites on the Victorian Western Volcanic Plains and Northern Plains by pitfall trapping and systematic and opportunistic searching from January 1995 to February 1996. She evaluated habitat by measuring cover of cool- and warm-season perennial grasses, native herbs, exotic grasses, exotic herbs, bare ground, dry litter, total floristic composition (native/exotic), sheep grazing pressure and invertebrate richness. Three mammal species were captured in c. 7500 trap nights. *Sminthopsis crassicaudata* (Gould) was found at all sites in the Northern Plains and 7 of 12 sites in the Western Plains. One inidividual of the Common Dunnart *S. murina* (Waterhouse) was captured at a Western Plains site, the first Victorian grassland record. The introduced House Mouse *Mus musculus* L. was found at 5 of the Western Plains sites and 8 Northern Plains sites. Rabbits *O. cuniculus* and European Hare *Lepus capensis* were almost ubiquitous in Northern Plains sites but were observed at approximately half the Western Plains sites. No mammals were recorded at five of the Western Plains sites. *S. crassicaudata* was abundant at some floristically rich sites and also in degraded remnants and exotic pastures. It was relatively more abundant at sites that were lightly grazed, at sites with more open vegetation and floristically rich sites. It is an active hunter, mainly of invertebrates, and may require open areas for foraging, as well as tussock cover as a protection from predators. It was found living in rock piles and stone walls, and utilised wolf spider burrows on the Northern Plains. This species has disappeared from grasslands near Melbourne where it was once common. The almost ubiquitous *M. musculus* was relatively more abundant on heavily grazed sites, was absent from lightly grazed sites on the Western Plains, was more abundant at densely vegetated sites on the Western Plains and lightly vegetated sites on the Northern Plains, and was more common on floristically poor sites. Two other species, the introduced Brown Rat *Rattus norvegicus* (Berkenhout) and native Swamp Rat *R. lutreolus* (Gray) have been recorded in Victorian grasslands in recent historical times.

Mus musculus is a threat to some grassland plants. Mouse predation of tubers of *Diuris fragrantissima* is believed to have been responsible for mortality of perhaps 70% of plants at its single extant site during the mid-1980s (Webster *et al.* 2004).

The Short-beaked Echidna, *Tachyglossus aculeatus* (Shaw), occurs widely in grasslands (Menkhorst 1995c) but appears to be absent from most of the smaller remnants, particularly in areas of closer settlement.

The highly depauperate mammalian faunas or remnant grasslands means that biodiversity components directly dependent upon mammalian activities are also threatened or lost. Obvious dependents include dung beetles (Scarabaeidae: Scarabaeinae and most Aphodiinae) that require a dung resource, and a range of ectoparasites (fleas, etc.) and endoparasites (Nematoda, etc.) that require their host for survival. The complex consequences of the loss of native grazing species and mammalian plant-predators have only recently begun to be explored and very little is known about the ramifications. However absence of soil disturbance by mammals has probably had a strong negative impact on regeneration of many native forbs (Reynolds 2005) and the dispersal opportunities for plant seeds must have been radically altered.

Birds

Few Australian birds are restricted to grasslands and by necessity they are ground-nesting species. In New South Wales, populations of many grassland species that forage and nest on the ground have disappeared or shrunk to very low levels (Keith 2004). In Victoria the most significant regions for threatened bird species include the Northern Plains and the Wimmera Plains, and few threatened species occur in the Western Volcanic Plains or the Gippsland Plains (Robinson 1991). Threatened birds in Victoria are more likely to be woodland or grassland species that are seed eaters or vertebrate predators, and to nest in tree hollows or on the ground (Robinson 1991). A number of species once common in native grasslands have declined markedly or disappeared from grasslands as the area of habitat has shrunk, however only two species that are more or less restricted to grasslands have endangered status (Table 16).

Table 16. Endangered bird species of south-eastern Australian temperate native grasslands. U = unlisted,V= vulnerable, E = endangered, CE = critically endangered, T = threatened, X = extinct.

Species	**Common Name**	**ACT**	**NSW**	**SA**	**Vic**	**References**
Ardeotis australis(J.E. Gray)	Australian Bustard	X			CE	Sharp and Shorthouse 1996, Venn and Menkhorst 2003, Department of Sustainability and Environment 2009a
Pedionomus torquatus (Gould)	Plains Wanderer	X			V/T	Baker-Gabb 2003, Department of Sustainability and Environment 2009a

Emus *Dromais novaehollandiae* (Latham) were once common in the Victorian basalt plains (Sutton 1916-1917, Coutts 1982) and the grasslands of NSW (Keith 2004). Marshall (1968 p.76) reported observations by the Rev. James Backhouse in 1837 that emus in the Melbourne area were then "fast retiring before the white population and their flocks and herds". They are now rarely reported on the volcanic plains (Lunt *et al.* 1998) and have disappeared or markedly declined in NSW grasslands (Keith 2004), their extermination probably having followed very similar lines to those reported by Marshall (1968): shot for food, oil and as vermin, but road deaths have probably also caused substantial populations losses.

Of the threatened birds mentioned by Robinson (1991) the following may be the most restricted to grassland habitats: Australian Kestrel *Falco cenchroides* Vigors and Horsfield, Little Button Quail *Turnix velox* (Gould), Red-chested Button-quail *T. pyrrhothorax* (Gould), Singing Bushlark *Mirafra javanica* Horsfield, Rufous Songlark *Cincloramphus mathewsi* Iredale, Brown Songlark *C. cruralis* (Vigors and Horsefield), and possibly Southern Whiteface *Aphelocephala leucopsis* (Gould) (Blakers ***et al.*** 1984). Notable subjects of conservation concern are the Plains Wanderer *Pedionomus torquatus* Gould, Australian Bustard *Ardeotis australis* (J.E. Gray), Bush Thick-knee or Stone Curlew *Burhinus grallarius* (Latham) and Painted Button-quail *Turnix varia* (Latham) (Lunt ***et al.*** 1998), although the Painted Button-quail reportedly lives only in heath, woodland and eucalypt forest (Blakers ***et al.*** 1984). Loyn and French (1991) discussed the diets of Stubble Quail, a relatively common species also found in grasslands, and Plains Wanderer in relation to exotic plant invasions.

The Bush Thick-knee is mainly a woodland bird (Blakers ***et al.*** 1984), usually living in Victoria on farmland remnants of lightly-timbered, lowland grassy woodlands, most commonly treed with *Eucalyptus microcarpa* (Johnson and Baker-Gabb 1994). The bird is classified as Vulnerable in Victoria, where it has sufferred widespread regional extinction in the south due to habitat clearing and alteration. It is a long-lived, sedentary, nocturnal, cursorial ground-nesting bird, requiring low, sparse groundcover (10-70% bare ground, grasses 67% <15 cm high, *Austrodanthonia* spp. usually dominant) as habitat, fallen coarse woody debris for camouflage and invertebrate food (Johnson and Baker-Gabb 1994). The vegetation of 95 day shelters investigated by Johnson and Baker-Gabb (1994) was often dominated by exotic annual grasses, notably *Critesion murinum* and *Bromus hordeaceus* with large populations of *Romulea rosea* and *Trifolium* spp. The grass cover in foraging areas is taller (<30 cm) than in resting areas. Birds "methodically probe ground plants and debris, disturbing and catching prey as it emerges", insects being the predominant food (determined by analysis of faeces and regurgitated pellets) and ground-dwelling Coleoptera being most frequently eaten of a wide range of Coleoptera, Orthoptera, Hymenoptera, larval Lepidoptera and spiders (Johnson and Baker-Gabb 1994 pp.27-28).

The Plains Wanderer is a threatened species, the sole member of the Pedinomidae and found only in south-eastern Australia (Baker-Gabb1993) with strongholds in the Riverina of NSW, North Central Victoria (Blakers ***et al.***1984) (about 500 on the Northern Plains of Victoria, concentrated in the Mitiamo area – Baker-Gabb 2003) and south-western Queensland (Baker-Gabb 2003). It was formerly common in south-western Victoria, south-eastern South Australia and eastern NSW (Baker-Gabb 2003). On the Northern Plains of Victoria, Maher and Baker-Gabb (1993) reported that suitable habitat then existed on only a single large property and in a few scattered paddocks. The bird is a small, diurnal, ground-dwelling species of sparse grasslands (Baker-Gabb 2003) and formerly of chenopod shrublands (Maher and Baker-Gabb 1993), and requires open spaces in low vegetation (<5 cm with some taller plants for concealment) to walk and forage for seeds and insects, so any invasive plant that restricts these spaces may assist in its decline (Loyn and French1991, Maher and Baker-Gabb 1993). Weed invasion of native grassland has been specifically mentioned as one of the lesser threats to the species (Maher and Baker-Gabb 1993, Baker-Gabb 2003). The decline of the Plains Wanderer is emblematic of the destruction of south-eastern Australian grasslands. Cultivation of grasslands and overgrazing by livestock are the major threatening factors, as are tall-growing invasive plants and fire (Maher and Baker-Gabb 1993, Baker-Gabb 1993). According to Baker-Gabb (1993) diverse native grassland is the preferred habitat, as long as the vegetation is not too dense, but Blakers ***et al.*** (1984) state that unimproved pastures and cereal paddocks 1-3 years after cropping provide suitable habitat. A high proportion of areas occupied in the Northern Plains are long-grazed bovid pastures (Baker-Gabb 2003). Particularly favourable habitat consists of areas with topsoil erosion exposing red clay subsoil, with c. 50% bare ground, c. 10% litter and foliage height largely <5 cm and with the highest stratum rarely >30 cm tall being important for concealment (the bird is c. 15 cm tall when standing on tip-toes) (Baker-Gabb 1993 2003). Plants comprise about 60% of its diet, seed of grasses and saltbush being the most important components, while invertebrates make up the remaining 40% or a larger proportion in spring. Beetles, ants, bugs and caterpillars are the most frequently consumed insects (Baker-Gabb 1993 2003).

The Australian Bustard is a large ground dweller up to 80 cm high, formerly widespread in all Australian mainland States but now seriously reduced and rare or totally absent in south-eastern Australia, due primarily to shooting, habitat destruction and predation by feral animals (Marshall 1968, Blakers ***et al.*** 1984, Venn and Menkhorst 2003). A "wide range of open vegetation communities can support populations" (Venn and Menkhorst 2003). In Victoria it was once widespread in grasslands and grassy woodlands in the Riverina, Western Volcanic Plain and Gippsland Plain regions and is classed as critically endangered. A.J. North once counted 83 within one mile of Murdeduke Station at Winchelsea, Victoria (Marshall 1968). It is an omnivorous species with Orthoptera, small reptiles and *Mus musculus* being common dietary items (Venn and Menkhorst 2003).

Reptiles

Reptiles have been less effected by anthropogenic environmental degradation than mammals because they are better able to survive periods of low food availability by aestivation, and to escape predation by introduced predators by living underground (Flannery 1994). Recher and Lim (1990) considered their greater resilience in Australia to be just a matter of degree, and predicted future declines of similar magnitude to mammals. A number of species are confined to the grasslands of south-eastern Australia and several are endangered (Table 17).

Table 17. Endangered reptile species in south-eastern Australian native temperate grasslands. U = unlisted,V= vulnerable, E = endangered, T = threatened.

Species	Common Name	ACT	NSW	SA	Vic	References
Delma impar Fischer	Striped Legless Lizard	V	V/E	E	V	Coulson 1990, Kukolic 1994, Sharp and Shorthouse 1996, Eddy *et al.* 1998,Webster *et al.* 2003, Keith 2004, O'Shea 2005, Department of Sustainability and Environment 2009a
Tympanocryptis pinguicolla (Mitchell)	Grassland Earless Dragon	E	E		E	Sharp and Shorthouse 1996, Eddy *et al.* 1998, Brereton and Backhouse 2003, Keith 2004, ACT Government 2005, Department of Sustainability and Environment 2009a
Eulamprus tympanum marnieae (Lvnnberg and Andersson)	Corangamite Water Skink	-	-	-	T	Department of Sustainability and Environment 2007
Aprasia parapulchella Kluge	Pink-tailed Worm Lizard, Pink-tailed Legless Lizard	E or V	E		T	Sharp and Shorthouse 1996,Eddy *et al.* 1998, Keith 2004, Department of Sustainability and Environment 2009a
Suta flagellum	Eastern Whip Snake	E or V	E or V			Eddy *et al.* 1998
Varanus rosenbergii	Rosenbergs Monitor	E or V	E or V		T	Eddy *et al.* 1998, Department of Sustainability and Environment 2009a

Delma impar, Striped Legless Lizard (Pygopodidae)

Delma impar Fischer is one of 38 species in the Pygopodidae, a family of mostly surface active, fossorial or semi-fossorial, arthropod-eating lizards, endemic to Australia except for two species in Papua New Guinea, and most closely related to diplodacytline Geckonidae (O'Shea 2005). It is the most southerly occurring of the 17 *Delma* spp., is considered to be a diurnal, semi-fossorial species, active from September to late March or April (O'Shea 2005). It is slow growing, and could live for up to 20 years (O'Shea 2005). According to Hadden (1995) *D. impar* had been recorded at 125 sites from the South East of South Australia, through eastern and northern Victoria to southern NSW and the ACT, of which possibly 45 were then considered still capable of supporting it. Additionally O'Shea (2005) mapped recent records from the South East of South Australia. The lizard's rarity was considered to be due to its specificity to lowland grassland habitat and the widespread loss and degradation of such habitats. Western (Basalt) Plains Grassland was the major vegetation type occupied in Victoria (Webster *et al.* 2003). Population densities were reportedly highest in dense, relatively undisturbed native grassland, although capture rates were relatively high in an area dominated by *Nassella trichotoma* and total grass cover appeared to be the best predictor of population density (Coulson 1990). Most of the extant sites (Hadden 1995) were native perennial tussock grasslands, either *T. triandra* in Victoria or *T. triandra* and *Austrostipa bigeniculata* in the ACT (Kukolic 1994), but a few were dominated by the exotic perennial *Phalaris aquatica*, while sites then dominated by *Nassella* spp. were found to no longer harbour the species (Hadden 1995). Kukolic (1995) recorded pitfall trap captures in *T. triandra* grasslands with mixed native and exotic grasses and in areas more dominated by exotic grasses at Yarramundi Reach, ACT. Hadden (1995) found that tussock cover >50% was usual at the majority of extant sites and tussocks were considered important for shelter and as basking sites. *D. impar* utilises deep cracks in clay soils for shelter, breeding and refuge, and surface rocks may be similarly used, but are not a necessary habitat component (Hadden 1995). Fire was considered an unknown risk, while livestock grazing was considered acceptable since it occurred on nearly half the known extant sites (Hadden 1995). Kukolic (1994) recommended that fire not be used to manage the habitat, mentioning finds of dead individuals at Derrimut, Victoria, after control burns. Webster *et al.* (2003) noted that fires in spring represented a clear risk to Victorian populations because soil cracks were seasonally unavailable. Weed invasion was listed as one of numerous threats to its habitat (Webster *et al.* 2003). O'Shea (2005) found that the population at Iramoo Grassland, Victoria, was present in areas dominated by *N. neesiana* and *N. trichotoma* as well as *T. triandra* areas, and persisted well in 0.5 ha areas that were deliberately burnt. She argued that grassland structure (presence of perennial tussocks) rather than floristic criteria determined suitable habitat.

Spiders, larval Lepidoptera, Black Field Crickets *Teleogryllus commodus* (Walker) (Orthoptera: Gryllidae) and cockroaches (Blattodea) are the most frequently recorded prey items (O'Shea 2005). Coulson (1990) reported that the majority of faecal pellets obtained from individuals at Derrimut Grassland, Vic., from mid January to early February contained unidentified larval Noctuidae (Lepidoptera) and *T. triandra* fragments which were presumed to have been larval gut contents. Faecal pellets studies by Wainer (1992) indicated prey 10-30 mm in length including locusts (Acrididae), an earwig, an ant, adult moths, as well as items already mentioned. Invertebrates common in the habitat that were not eaten included millipedes, slaters, slugs, bugs (Hemiptera) and beetles (Coleoptera). He also found unidentified grass seeds in the scats. Kutt *et al.* (1998) reported that nocutid larvae consistuted a high proportion of the diet from November to January and crickets were predominant from December to February, corresponding with the abundance of these taxa. The lizard appears to have a flexible foraging strategy with seasonal food preferences, and forages in the daytime. Brumation takes place in the soil from late March or April to September (O'Shea 2005).

Victoria's largest documented and best studied population (an estimated 600 individuals) is in the Iramoo Grassland Reserve, Cairnlea. O'Shea (1997) provided preliminary details of alternative detection and trapping techniques for the lizard. O'Shea (2005) found that the population at Iramoo was present in areas dominated by either *T. triandra* or *N. neesiana* and *N. trichotoma*, however the exotic habitat was contiguous with the native habitat. Small scale (0.5 ha) summer and autumn fires interspersed in larger areas of unburnt habitat appeared to have little effect on population size and structure or habitat quality.

Roofing tiles were found to be regularly used as artificial shelters and determined to be a useful survey and population monitoring tool. She also developed an objective pictorial method of identifying individual animals based on head scale patterns.

D. impar is listed as Vulnerable at the national level (Hadden 1995, Webster *et al.* 2003), Vulnerable in the ACT (Sharp 1997) and NSW and Endangered in South Australia and Victoria (O'Shea 2005).

Tympanocryptis pinguicolla (Mitchell) Grassland Earless Dragon (Agamidae)

Tympanocryptis Peters is an endemic Australian genus of small, terrestrial dragons distributed through most of mainland Australia (Cogger 1983). *T. pinguicolla* was originally described as *T. lineata pinguicolla* Mitchell in 1948 and raised to species status in 1999 with a change of common name from Eastern (ACT Government 2005) or Southern Lined Earless Dragon (Brereton and Backhouse 2003). The vernacular name refers to the absence of an external ear opening, and of a functional tympanum (ACT Government 2005) which is "hidden below the skin of the head" (Cogger 1983 p. 250). It was once abundant in the ACT and was recorded from near Cooma in the Southern Tablelands and Bathurst in NSW (ACT Government 2005). In Victoria, anecdotal evidence indicates it was once not uncommon in basalt plains grasslands north and west of Melbourne. All Victorian records with habitat data were from areas of rocky, open *T. triandra* grassland, including sites on the Jackson Creek at Holden Flora Reserve near Diggers Rest, the upper reaches of the Merri Creek, north of Donnybrook, and the Little River Gorge west of Werribee. All sites where it was observed between 1988 and 1990 were *T. triandra* grasslands with Red-leg Grass *Bothrichloa macra* and Silky Blue-grass *Dichanthium sericeum* (R.Br.) A. Camus in ungrazed or lightly grazed paddocks (Brereton and Backhouse 2003). In the ACT it is known from seven sites in natural temperate grassland and appears to prefer sites with little disturbance and grasslands that are short and open (ACT Government 2005). *T pinguicolla* is a diurnal, wholly terrestrial, insectivorous(Brereton and Backhouse 2003) and arachnivorous (ACT Government 2005)species which shelters in small burrows (Brereton and Backhouse 2003) including those of invertebrates, under rocks and within *Austrostipa* tussocks (ACT Government 2005). It is an oviparous species and females are believed in the main to breed only once, and to die after 1 year (ACT Government 2005). Loss and modification of habitat is probably largely responsible for its great decline (Brereton and Backhouse 2003).

Other species

The Pink Worm Lizard *Aprasia parapulchella* Kluge was known only from Coppins Crossing on the Molongo River, ACT and from near Tarcutta and Bathurst, NSW, the type specimens recorded under weathered granite rocks on a grazed, grassy riverside (Cogger 1983) and was listed as nationally endangered (Sharp and Shorthouse 1996). A recovery plan for the species in the ACT was published in 1995 (Sharp and Shorthouse 1996). The Corangamite Water Skink *Eulamprus tympanum marnieae* (Lvnnberg and Andersson) is endemic to the Victorian Volcanic Plain (DNRE 1997, Department of Sustainability and Environment 2007). Its inhabits rocky areas on the margins of wetlands in a limited area of the Victorian volcanic plains so exists on the margins of grasslands. "Weed invasion" is one threat to this species (Department of Sustainability and Environment 2007). The Pygmy Bluetongue, *Tiliqua ?adelaidensis* (Peters) is another grasslands species that may be threatened. Cogger (1983 p. 388) recorded that its distribution was "not known" with most recorded specimens from the Adelaide region. It was listed as 'Indeterminate' in the IUCN Red List of Threatened Vertebrates (IUCN 1988) with not enough information available to determine whether it was enadangered or rare. The Pygmy Bluetongue reportedly "depends on spider holes for shelter in the grasslands around Burra in South Australia's Mid North" (Lunt *et al.* 1998).

Invertebrates

Plant invasions have the potential to modify interactions amongst species at all trophic levels. Changes to the composition, structure and functioning of communities caused by alien plant invasions have a major impact on native insects (Samways 2005). These effects include alteration of species richness and the composition of the fauna. The mechanisms include displacement of indigenous food plants, alterations to solar insolation by shading, and to shelter characteristics of the vegetation (Samways 2005). The impacts are generally complex, with individualistic responses by the range of taxa.

On a world basis, ungulate mammals are the dominant herbivores in tropical grasslands whereas in temperate grassland this role is taken by insects (Tscharntke and Greiler 1995). Insects consume a greater proportion of the plant biomass compared to their own biomass than mammals (Tscharntke and Greiler 1995). Several features of grasses play a role in determining their insect fauna: lack of secondary thickening (woody tissue), simple architecture, protected buds, almost complete lack of secondary compounds with herbivore deterrence properties, but an abundance and great variety of silica bodies (phytoliths) in the epidermis that increases their resistance to invertebrate herbivory (Stebbins 1986, Tscharntke and Greiler 1995,Witt and McConnachie 2004).

Invertebrates are the major component of biodiversity in temperate native grasslands in Australia (Yen 1999, Gibson and New 2007). New South Wales grasslands "have abundant herbivorous insects" (Keith 2004 p. 104). But surveys of grassland invertebrates in Australia had barely begun by the mid-1990s when Driscoll (1994) stated that the invertebrates of south eastern Australian grasslands had "never been surveyed'. Keith (2004 p. 104) exaggerated the extent of knowledge when he stated that the "invertebrate fauna of the grasslands before their modification and use as pastures is poorly documented". Wapshere's (1993 p. 344) statement that "nothing" was known about the nematode, mite and insect faunas of *Austrostipa* spp., despite their economic importance in native pastures, while not strictly correct (see the section above on the curculionid predators of *Nassella* species in Australia), nicely reflects the general paucity of information. Gibson and New (2007) considered remnant lowland native grasslands to be "among the least investigated" ecosystems entomologically in south-eastern Australia. Nevertheless it is has been "presumed widely" that loss of native plants in these systems has been accompanied by similar loss of invertebrate diversity (New 2000 p. 154).

Invertebrate diversity appears to be particularly suitable for study and assessment of remnants because most of the vertebrate diversity has been lost from native grasslands, and because invertebrates are highly diverse, abundant and easy to collect (Yen 1995). It has been suggested that the suites of macroinvertebrates present are most appropriate for characterising grasslands for conservation, and can act as flagship taxa, and that microinvertebrates may be superior for monitoring ecological functioning (Yen 1995). However invertebrates hardly offer direct approaches to biodiversity assessment. Inventory studies are a primary requirement, but unlike plants and vertebrates, complete inventories are idealistic (Yen 1999). Basic studies are required to characterise the invertebrate communities present and identify threatened species, and long term monitoring of permanent sites is necessary to fully determine the biodiversity that exists and the ways that it fluctuates. Yet, studies of natural grassland invertebrate communities in Australia have until recently been totally lacking (Yen 1995) and the conservation significance of existing invertebrate populations is difficult to assess because of major anthropogenic alteration of the habitat and lack of baseline survey data (Yen 1995 1999).

Invertebrates have functional roles in most ecological processes including decomposition, nutrient cycling, soil aeration, seed dispersal, herbivory and pollination, and in food chains as prey, predators and parasites (Yen 1995 1999, Ens 2002a, Samways 2005, Stephens 2006).They therefore offer possibilities for exploring ecosystem structure and function, given an understanding of their biology.

Identification of the effects of biodiversity threats and management practices on invertebrates is difficult (Yen 1995 1999) and knowledge of the how insect diversity and conservation is affected by alien plant invasion is “very limited” (Samways 2005 p.115). Assessment of insect populations and communities is complicated by their high spatial (<1 cm^2 to regional) and temporal (inter-annual, seasonal, diurnal, etc.) variability, complex life cycles with discrete stages, large numbers of species, wide size range, taxonomic impediments, etc. (New 1984, Hill and Michaelis 1988, Driscoll 1994,Yen 1995, Yen 1999, Farrow 1999, Ens 2002a, Farrow 2006). Farrow (2006 p. 7) found large gains and losses of canopy-dwelling insect species in consecutive years of sampling in ACT grasslands, with 72-73% of species found consistently each year. He concluded that 30-40% of species populations were “relatively unpredictable” and “spatially and temporally dynamic”.

The taxonomic impediment exists because there are few specialists able to provide accurate identifications, many species are undescribed, some may not have been previously collected, and the lifecycles and specific requirements of only a very small proportion have been studied.

Driscoll (1994) evaluated the utility of the concepts of naturalness, representativeness, area, diversity, rarity, landscape type and threat of interference in regard to selection of areas for invertebrate conservation and significant taxa in ACT grasslands. Threat of interference to a particular grassland is more readily determined than all the other criteria (Driscoll 1994) and obviously should propel conservation action. Most of the other criteria are difficult to apply because of lack of fundamental and baseline data. Driscoll (op. cit.) considered that the constituents of a natural grassland invertebrate community were unknown, but could possibly be retrospectively derived by assessment of the impact of European land management practices on indicator taxa that have known responses to environmental variables. Palaeo-entomological techniques could be applied (Melbourne 1993) but this is a relatively new field of research and very little such work has been undertaken in Australia (Elias 1994). Some exotic components of the invertebrate flora can fairly easily be identified, but others are as difficult to determine as native species.

The concept of representativeness is intended to enable identification of the important ecological units of the ecosystem and the minimum viable area of each unit. However in the first Australian attempt to identify such native grassland units, Yen, Horne, Kay and Kobelt (1994a) were unable to characterise a grassland invertebrate assemblage. In practice, determination of such units has largely been based on physical environmental characteristics and vegetation associations. Enabling such a classification for invertebrates is considerably more complicated, but should involve consideration of vegetation structure and composition, plant nutritional qualities, ground litter, soil characteristics and topography (Driscoll 1994) as well as the disturbance regime (Yen, Horne, Kay and Kobelt 1994a) and the ecological history of the site. New (2000) noted that there was very little specific information on the effects of disturbances on native invertebrate fauna, and resorted to comparisons of the ant faunas of lawns and urban gardens to elucidate potential impacts. Invertebrate components of grasslands in general do not correlate well with botanical components and may be more sensitive to degradation factors (Yen 1995). Indeed Yen, Horne, Kay and Kobelt (1994a) found no relationship between invertebrate and botanical ranking criteria for remnant grasslands of the Victorian Volcanic Plains, with most sites having an inverse relationship, perhaps reflecting high contributions to the fauna from habitat generalists in the more degraded areas. Nevertheless it is widely agreed that much smaller reserves may be adequate for protection of invertebate diversity than for vertebrates (New 1984) and that representative areas based on non-invertebrate criteria must form the basis of further study.

Assessment of existing diversity requires surveys, and even the simplest surveys invariably produce large numbers of taxa, many of which prove to be difficult or impossible to identify, and very large numbers of individuals. In the context of poorly known faunas with little previous survey work, increasing the sampling effort at a single site, over wider areas and through time may just reveal more species (e.g. as found by Hinkley and New 1997 and Kuschel 1990) with no indication of approach to an asymptote. Since larvae and juvenile stages are often undescribed, they usually cannot be confidently linked with adults except by rearing and this creates a high potential to mis-estimate species diversity.

Indicator taxa

Efforts to circumvent these problem have focussed on indicator species – conspicuous abundant species that have well defined responses to environmental change, or indicator groups – supraspecific taxa that supposedly provide a broad indication of diversity of other taxa, and can act as biodiversity surrogate measures (Melbourne 1993, Yen, Horne, Kay and Kobelt 1994a, Churchill 1997, Yen 1999, Samways 2005, Wolters *et al.* 2006). An indicator taxon can be chosen to indicate diversity or conservation significance of other invertebrate groups, as an indicator of habitat quality and changing ecological conditions, or as a measure of degradation and state of restoration (Yen, Horne, Kay and Kobelt 1994a, Yen 1999, New 2000, Samways 2005). Diptera and Hymenoptera parasitoids for example have been argued to be good indicators of both habitat quality and diversity of other invertebrate taxa because they have high diversity in all vegetated areas, parasitise a diverse range of invertebrates in a wide variety of higher taxa across a range of trophic levels and most microhabitats, and can be sampled with relatively simple methods (Stephens 2006). Farrow (1999) argued similarly for micro-Hymenoptera, noting that in the ACT grasslands surveyed there were on average two individuals collected of each species, compared to 73 individuals for other taxa, but he acknowledged that taxonomic impediments and time constraints render the use of this group extremely difficult. Spiders as dominant invertebrate predators, have similarly been advocated (Churchill 1997). Mgobozi *et al.* (2008) considered them good ecological indicators of change because they are at the top of arthropod community food chains and “are expected to integrate the biotic and abiotic influences affecting lower trophic levels". However there has been very little comparable research into spider communities in any habitats in Australia (Churchill 1997), they interact with invasive plants only indirectly (Mgobozi *et al.* 2008) and their specialisation by prey type also appears to be relatively low, limiting their usefulness.

Correlations between the richness of taxa may be coincidental, a response to common environmental factors (e.g. climate) or to different factors that are spatially covariant, or the result of biological interactions between taxa (e.g. Hymenoptera parasitoids and their hosts) (Wolters *et al.* 2006). Unfortunately many studies have used groups for which there is no a priori reason to believe have good indicator value (Wolters *et al.* 2006).

Driscoll (1994) recommended beetles, ants and grasshoppers as suitable indicator groups for south-eastern Australian grasslands, based on the relatively large size of the constituent species, their functional significance, variablity in dispersal abilities and, possibly most importantly, the availability of taxonomic knowledge and expertise. But what studies of these groups might 'indicate' is unclear. New (2000) suggested that ants might be good indicators of habitat complexity, but lack of primary phytophagy in the group suggests they would show little response to simple floristic change. Gibson and New (2007) suveyed beetles and ants in a Victorian grassland, but found that nearly all were widespread regionally, and provided no correlative measures for environmental change. Farrow (1999) argued that the use of phytophagous Chrysomelidae and Curculionidae – the most diverse Coleoptera families he detected in ACT grasslands – as indicators was compromised by poor understanding of their life histories and larval and adult host plants. Grasshoppers were considered also to be not particularly useful because of their highly clumped distributions due to particular oviposition requirements, their need for solar insolation and inter-annual dependence on rainfall (Farrow 1999).

New (2000) assessed previous studies of ant diversity in temperate Australian grasslands and evaluated the suitability of ants as indicators of habitat conditions. Surveys that detected most of the surface active resident species commonly detected 20-30 morphospecies. He considered ants to be poor indicators in Victorian grasslands because the species present are relatively habitat tolerant and the habitat is relatively heterogeneous at the fine scale. Ant diversity of grasslands dominated by native or exotic grasses were similar, and species composition of the grasses was probably less influential than structural diversity in the vegetation and overall habitat complexity. Miller and New (1997) evaluated pitfall trapping of ants as an indicator of grassland disturbance as manifested by the invasion of the exotic grass *Holcus lanatus* L., in *Austrodanthonia* grasslands at Mount Piper, Victoria. They detected 36 morphospecies by fortnightly pitfall trapping over seven months and concluded that the rankings of generic diversity at each site "usually coincided" with ranking of sites on a scale from "most natural" to "most degraded". The grassland ant fauna appeared to be easier to define in terms of sampling effort than the much more diverse fauna of woodlands, but the grasslands sampled nevertheless indicated a mosaic of ant assemblages that differred between sites with apparent vegetational homogeneity. Native and exotic dominated sites had a similar number of species, while rare species and many more common species were not habitat specific. Only the subordinate *Camponotus* group appeared to be a good indicator of 'natural' sites (New 2000). Hinkley and New (1997) found that short term sampling using pitfall traps was inadeqate to assess ant species diversity and that sampling across seasons and extensive sampling in summer were required to enable reasonably complete inventories. Single trapping events (of c. 14 days) collected no more than half the species found by repeated trapping over fortnightly intervals for 7 months.

Despite Evans' (1966 p. 9) comment that the Australian cicadelloid (Hemiptera: Cicadellidae, Eurymelidae and Membracidae) fauna of "grasses, and of annuals and perennials generally, is very sparse", Farrow (1999) found that the diversity and distribution 32 species of Cicadellidae obtained in sampling at 11 grasslands in the ACT, provided a good approximation of the total number of canopy insect species at individual sites. He recommended the family as a relatively homogeneous grass-feeding group suitable for use as an indicator. However Yen *at al.* (1994a) found only five Cicadellidae spp. in Victorian basalt plains grasslands. It is not clear whether this contrast in regional diversity is real or a sampling artefact (Farrow 1999).

Ease of sampling, taxonomic accesibility, ecological (trophic and microhabitat) diversity and functional importance are generally agreed to be the most important criteria for indicator groups (Melbourne 1983, New 1984, Churchill 1997). Melbourne (1993) found that the diversity of genera of Formicidae and to a questionable degree Carabidae (Coleoptera) provided sufficient taxonomic resolution to assess differences in the species diversity of these groups in ACT grasslands, and that plant community was a reasonably good predictor of diversity of these taxa. However it is likely that no single invertebrate group could be be used as an adequate estimater for all the others (Melbourne 1993). Farrow (1999) for example found that ACT grassland sites ranked for biodiversity using the Collembola data of Greenslade (1994) did not correspond with his own rankings based on canopy-dwelling insects. A recent meta-analysis of over 200 studies found that no vertebrate, invertebrate or vascular plant taxon has been found to be a good predictor for the richness of other taxa; indeed supposed indicator taxa have often proved to be disappointingly inadeqate for the task, although invertebrates at the <1ha scale are among the best indicators (Wolters *et al.* 2006)..

Surrogate biodiversity measures

Surrogate measures of species diversity accept a level of taxonomic resolution below that of species and can be used to speed up biodiversity assessment (Melbourne 1993), in theory. 'Morphospecies' (species that the particular investigator can distinguish) or "recognisable taxonomic units" are frequently employed (e.g. Churchill 1997, Farrow 1999, Ens 2002a). They may be sound when used by specialists in the particular taxon (Melbourne 1993) but are potentially fraught with errors when used by the less experienced (personal observations). Genera, families and orders are often used as surrogates when the intention is to investigate broad patterns of ecological functioning and organisation (Melbourne 1993) and this approach has been particularly widely used with ants to assess land degradation and restoration processes (New 2000). Sharp (1997) quantified the abundance of individuals by order to investigate the relationships with grassland soil and litter characteristics, disturbance and mangement factors and floristic associations. Farrow (1999 2006) identified morphospecies at family level for the purposes of comparison of biodiversity in ACT grasslands.

Both 'indicator' and 'surrogate' approaches assume congruence between the actual diversity and the measured entities. Establishing such congruence is a major research goal in insect biodiversity research (Melbourne 1993). Diversity assessment is certainly fraught with complications if species are not identified: introduced pest species and widespread common species may be assigned the same biodiversity score as those that are rare and narrowly distributed (New 1984, Driscoll 1994) and links with other biological studies where species names are used can rarely be made except by later reference to preserved voucher specimens. Imprecise taxonomic information severely limits connections with the whole range of existing biological and ecological information about particular taxa (Churchill 1997).

Thus it is generally difficult to determine whether a particular grassland area contains a good representation of the invertebrate fauna. The criterion of rarity is also difficult to assess given the general low level of invertebrate knowledge. It requires examination over temporal and spatial scales largely beyond the reach of current resources. Endemism may be a better criterion (Driscoll 1993), but again often requires more knowledge than is available (Melbourne 1993), except for a very limited range of organisms, or at the biogeographical scale.

Landscape criteria and the biological attributes of species

Landscape criteria are intended to enable the integration of habitat patch attributes, dispersal characteristics and dispersal opportunities of the organism with population biology, conservation genetics and the features of the surrounding landscape to arrive at guidelines for conservation (Driscoll 1994). For example, small populations may frequently become extinct, but that is not a problem if recolonisation from surrounding habitat is inevitable. However knowledge of the dynamics of invertebrate metapopulations is very difficult to investigate in fragmented grassland remnants (Yen 1999). Consideration of these complications led Driscoll (1994) to conclude that until such time as a wide range of invertebrates with variable dispersal abilities and life strategies could be assessed, all native grassland remnants were potentially important for invertebrate conservation, and conservation approaches should attempt to ensure maximal connectivity between the remnants.

Consideration of the biological significance of grassland invertebrate faunas must include identification of taxa restricted to grasslands and determination of the presence of threatened species (Yen 1995). The most important criteria in determination of species at risk are low vagility (Hill and Michaelis 1988, Farrow 1999), low reproductive rate, long development period and degree of endemicity (Hill and Michaelis 1988). These criteria are clearly apparent for grassland invertebrate taxa known to be endangered (see below).

Knowledge of the distribution of invertebrate species is often too limited to determine whether a species is restricted to grasslands. Ants are amongst the better known groups and ants of native grasslands have been found to be largely a subset of those of neaby woodlands (New 2000), again paralleling the vascular plants. Most grassland plants are also found in other vegetation formations, particularly grassy woodlands, but if invertebrate foodplants or larval hosts are restricted to grasslands then breeding populations of the invertebrate must also be restricted to grasslands. Some species may be restricted to grasslands by multiple factors, e.g. microclimate and food plant distribution. The endangered Ptunurra Xenica *Oriexenica ptunarra* L.E. Couchman (Lepidoptera: Satyrinae), a Tasmanian endemic, has *Poa*-feeding larvae and occurs in “open plains and poorly drained areas bordering mountain lakes and swamps”, in open grassy woodlands and tussock grasslands, mainly in the Midlands (Braby 2000 pp. 495-496). Two other Xenica species *O. orichora* (Meyrick) and *O. latialis* Waterhouse and Lyell are mainly restricted to alpine grasslands in south-eastern Australia (Braby 2000). The thermal requirements of these species (including open sunny areas for the adults to bask) are probably important in determining the habitat occupied. Similarly, grasshopper diversity is impacted when trees reduce insolation in grasslands (Samways 2005).

Low vagility occurs when species are wingless or have reduced aptery, e.g. female grass anthelids, *Pterolocera* spp., (Lepidoptera: Anthelidae) are virtually wingless (Common 1990); the primitive, diverse, endemic Australian tribe Amycterini (Coleoptera: Curculionidae) with some species in grasslands, are wholly flightless (Zimmerman 1993), and morabine grasshoppers are very sluggish and sedentary. Poor dispersal abilities are particularly important in highly fragmented habitats where remnant habitat patches are small and vulnerable to severe disturbances. Farrow (1999) noted that three of four endangered ACT insects were flightless, but found that only seven species, about 2% of species sampled in canopies of ACT grasslands, had flightless adults: one cicadellid, four Orthoptera and two micro-Hymenoptera spp. A higher proportion, of course could be expected to occur in the ground- and soil-dwelling faunas.

Low reproductive rates probably occur in some large weevils and morabine grasshoppers. Species with long development periods probably include the Golden Sun Moth *Synemon plana* Walker (Edwards 1994). *Rhopaea* sp. (Coleoptera: Melolonthinae) may have a 2 or 3 year life cycle, making them more vulnerable to local extinction (Allsopp 2003). Local endemicity is exhibited for example by sun moths (Castniidae), anthelids, Amycterinae and Morabinae. These factors are considered in more detail below in relation to various grassland invertebrates identified as threatened or at risk in south-eastern Australia.

Management effects

Various effects of grassland management on invertebrate species have been studied. Intensification of use generally results in loss of specialist species and increases in the proportion and dominance of common generalist species and exotic species (Tscharntke and Greiler 1995). Driscoll (1994) provided a brief review of grazing, pasture improvement, chemical use and fire. Kirkpatrick *et al.* (1995 p. 87) claimed that herbicides “may badly affect native invertebrates”, but there appears to be little published evidence. Farrow (1999 2006) evaluated the effects of grazing, fire and mowing on sites he sampled in the ACT, but the small number of sites sampled provided largely inconclusive results. “There was no consistent evidence that burning had any long-term impact on diversity” and “limited evidence from one site ... that regular mowing did not appear to limit biodiversity” (Farrow 2006 p. 2). Natural variation due to drought had a more profound effect in reducing diversity than any of these management measures (Farrow 2006).

Maintenance of microhabitat and habitat variability and plant diversity are basic requirements for invertebrate conservation. Manipulation of patch dynamics, by promoting variation in plant diversity, plant age and successional stage can enhance species richness (Tscharntke and Greiler 1995) but the increased diversity may comprise widespread, abundant species with little habitat specificity. Farrow (1999 2006) found that the small, isolated urban grasslands with relatively uniform vegetation in the ACT had markedly fewer species of canopy-living insects than the larger, better-connected, more vegetatively diverse, peri-urban grasslands, but Farrow (2006 p. 11) concluded that the diversity was “not related to measurable or easily observable environmental variables including vegetation diversity”.

Insect diversity in diverse central European meadows is approximately 1500 species (Tscharntke and Greiler 1995). Comparable data is not available for Australia. Yen (1999) found what appeared to be lower invertebrate diversity at ordinal (Order) or higher levels in the fauna of Derrimut Grassland compared to other, non-grassland regions of Victoria, but cautioned that a range of methodological factors might be the cause. Farrow (1999) found 328 morphospecies by sweep net sampling of 11 native grasslands in the ACT, considered to be a good representation of the canopy fauna, but excluding Lepidoptera, almost all Diptera and some minor orders. Similarly, Farrow (2006) found an estimated 383 species at 15 grasslands sites. Yen, Horne, Kay and Kobelt (1994a) found a total of 210 spp. in Victorian Basalt Plains grasslands remnants, but surveyed only three orders as a whole (Coleoptera, Hemiptera and Orthoptera) and just a small part (Formicidae) of another (Hymenoptera). The rest of the Hymenoptera along with the unsurveyed orders Lepidoptera and Diptera are all highly speciose, with micro-Hymenoptera in particular being highly diverse (Farrow 1999 2006).

Increased insect diversity and biomass is generally correlated with increased floristic diversity, structural complexity (including vertical stratification) of the vegetation and plant biomass (Tscharntke and Greiler 1995, Ens 2002a). However if increased biomass results in reduced floristic diversity, invertebrate diversity is likely to decline (e.g. Hadden and Westbrooke 1999, McQuillan 1999, Ens 2002a) and increased biomass in temperate south-eastern Australian grasslands is generally associated with overdominance by a limited number of grasses which suppress smaller inter-tussock species.

Impact of invasive grasses

Data on the impact of invasive grasses on insects is very limited. Chown and Block (1997 cited by Samways 2005) found that the beetle *Hydromedion sparsutum* was smaller in areas of South Georgia Island where alien grasses were dominant. New (2000) found that ant diversity in grasslands dominated by native or exotic grasses was similar and species composition of the grasses was probably less influential than structural diversity in the vegetation. However Gibson and New (2007) pointed out that disturbance effects were confounded. Hagiwara *et al.* (2009) demonstrated the potential benefits to the endangered butterfly *Lycaeides argyrognmon praeterinsularis* of removing *Eragrostis curvula*, which increased flowering and seed production of the butterfly's host plant. Melbourne (1993) and Melbourne *et al.* (1997) investigated the variation in numbers of a range of invertebrate taxa in grasslands of the ACT dominated by exotic or native species. Miller and New (1997) compared the ant faunas of areas dominated by an exotic grass and by native grasses.

Grassland insects

Pasture pests have generally been the main focus of invertebrate research in Australian grasslands (e.g. Gregg 1997). The great majority are native species subject to occasional outbreaks and are valuable components of biodiversity in natural areas. Losses from insect attack in grasslands on a global basis are estimated to amount to 9-32% of plant biomass (Tscharntke and Greiler 1995). Insect herbivory can have significant impacts on rare and endangered plants. Archer (1984) recorded the depradations of unidentified grasshoppers on colonies of *Thesium australe*, a plant once widespread in temperate native grasslands, attributed to severe depletion of other vegetation by mammalian grazers (Archer 1984 1987). Important agricultural grassland pest taxa in Australia include grasshoppers and locusts (Acrididae), *Teleogryllus commodus* (Walker) (Orthoptera: Gryllidae), *Therioaphis trifolii* (Monell) and *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), weevils (Coleoptera: Curculionidae), larvae of Elateridae, Tenebrionidae and Scarabaeidae (particularly Melolonthinae, *Aphodius tasmaniae* (Hope) (Aphodiinae) and *Adoryphorus couloni* (Burmeister) (Dynastinae)(Coleoptera), underground grass grubs (Lepidoptera: Hepialidae), larvae of Noctuidae and Pyralidae (particularly *Hednota* spp.) (Lepidoptera) and ant seed predators (Hymenoptera: Formicidae) (Gregg 1997). Mites including *Balaustium* and *Penthaleus* spp. are important cereal pests (Anon. 2008b).

Many adult Melolonthinae species feed on trees, particularly *Eucalyptus* spp., or use them for mating, while others do not feed in the adult stage (Roberts *et al.* 1982). Larvae live in the soil, eating roots, probably often of grasses, and other organic matter. In pastures on the New England tablelands (NSW), smaller species in the tree-feeding group were significantly more abundant in areas with low tree densities than larger species (Roberts *et al.* 1982). Highest densities of the non-tree-feeding group, which included the largest species (e.g. *Rhopaea* spp.), occurred in areas with 0-10% tree cover. Ridsdill-Smith (1975) noted that several of the Northern Tablelands species were known to eat living grass roots and found that *Sericesthis nigrolineata* (Boisduval) preferred grass roots to dead organic matter. Hardy (1976b) found that *Scitala sericans* Erichson predominantly inhabits grasslands and dry sclerophyll forests, the native grasslands inhabited being dominated by*Poa* spp. and also the exotic *Agrostis capillaris* L. in some areas. Larvae of *Antitrogus* Burmeister (Melolonthini) "feed on the roots of grasses and other similar plants" (Allsopp 2003 p. 159).

Various Dynastinae are also common in pastures and lawns in south-eastern Australia, where many feed on grass roots. *Cyclocephala signaticollis* Burmeister, introduced to Australia from South America has larvae that damage pasture and turf in Australia (Carne 1956) and is now common in the ACT (Robin Bedding CSIRO pers. comm. via M. Malipatil). This species inhabits the core range of *N. neesiana* in Argentina and likely damages it. According to A. Martinez (reported in Carne 1956 p. 220) it is found in "the provinces of Buenos Aires, the eastern part of Córdoba, southern Santa Fé, in Entre Rios and the north-east of the Pampa territory [and] Uruguay ... the roots of native grasses are the natural food .. while they also attack ... wheat, maize ... and barley". The well-studied pasture pest *Adoryphorus couloni* was the most abundant beetle collected in pitfall traps at Craigieburn grassland by Gibson and New (2007).

Dramatic fluctuations of native insect populations in pastures are commonplace (e.g. Davidson 1982), as they are in natural grasslands (Yen 1999). Population irruptions of phytophagous species may play a role in the patch dynamics of the lowland grasslands. For example, the underground feeding damage to *Poa* snow grass by the Alpine Grassgrub *Oncopera alpina* Tindale in the Australian Alps, described as "extensive patch death" by McDougall and Walsh (2007) is "part of an important ecological cycle opening up overgrown grass swards to invasion by the numerous flowering herbs for which the Kosciuszko area is famous" (Edwards 2002 p. 61). Similarly Green and Osborne (1994) reported that the *Poa* snow grass feeding larvae of the casemoth '*Plutorectis*' *caespitosae* Oke (Psychidae, *Lomera caespitosae* in Common 1990) cause severe patch damage to large areas in the subalpine zone, especially below the treeline, when in large numbers, but recovery after winter is rapid.

Nematodes are mostly minute animals that can be extremely abundant in soils and on plants, particularly on the roots. Numerous species are associated with grasses in Australia and several have been recorded from native Stipeae. These are discussed in an Appendix to this literature review.

Exotic invertebrates are often widespread and common in native grasslands, particularly in urban fringe areas (personal observations). Collembola is one group with a substantial proportion of exotics, however many higher taxa including various Coleoptera families and Formicidae are largely or almost entirely dominated by native species (New 2000). Common exotics present in grasslands include molluscs (slugs and snails), red legged earth mites *Halotydeus destructor* (Tucker), insects such as the aforementioned aphids, the African black beetle *Heteronychus arator* (Scarabeidae: Dynastinae), the weevils *Graphognathus leucoloma* (Boheman) and *Sitona discoideus* (Gyllenhal) (Gregg 1997, Hill *et al.* 1997),the European honeybee *Apis mellifera*, and possibly earthworms (Annelida: Haplotaxida). Morgan (1995b) found that *H. destructor* grazed seedlings of the endangered *Rudidosis leptorrhynchoides* but did not significantly affect their survival, and that grazing by unidentified slugs occurred mostly on very young seedlings and caused little damage. Exotic *Chriothrips* spp. (Thysanoptera: Thripidae) are found on grasses in south-eastern Australia (Mound and Palmer 1972). The grassland daisy *Senecio macrocarupus* is subject to attack by red-legged earthmites *Halotydeus destructor* (Tucker) and aphids (Hills and Boekel 2003). *H. destructor* and blue oat mites *Penthaleus major* (Dugès) attack a wide range of native grassland forbs including species of *Craspedia*, *Podolepis* and *Senecio* (Robinson 2005). The Portuguese Black Millipede *Ommatoiulus moreletti* (Lucas) (Julidae) has spread into Victorian basalt plains grasslands, and although there is no evidence of competition with native millipedes, it may influence litter decay rates (Yen 1995). Many of the invasive insect species probably have significant effects on grassland plants and the ecological functioning of the system, but there appear to be no studies that have directly addressed particular impacts. The agricultural literature, although restricted to few species, contains some valuable data about invertebrate impact on ecosystem processes, particularly effects on plant biomass production (Gregg 1997) and soils.

A range of exotic molluscs are considered pests of pastures (Smith and Kershaw 1979, Kershaw 1991) and have been suggested to be important predators of sensitive native plants such as orchids (Sydes 1994, Daniell 1994). Exotic slugs "appear to be highly invasive of native grasslands" and were found to be equally abundant in grasslands dominated by exotic and native grasses in the ACT (Melbourne *et al.* 1997 p. 366). Daniell (1994) recorded no or few species of native molluscs at four Melbourne grasslands, and observed that exotic slugs can occur at very high densities in native grasslands. Holland *et al.* (2007) found only exotic molluscs, three snail and five slug species, in extensive surveys in the Victorian volcanic plains. A few mollusc species have been identified as threats to particular native taxa, e.g. unidentified slugs and snails are considered a threat to *Diuris fragrantissima* (Webster *et al.* 2004), the Black-keeled Slug *Milax gagates* (Draparnaud) defoliates *Rutidosis leptorrhynchoides* (Daniell 1994), slug predation has caused the loss of a *Pterostylis nutans* R.Br. (Orchidaceae) colony (Sydes 1994), while unidentified slugs and possibly Common Garden Snails *Helix aspersa* (Müller) caused mortality of *Thesium australe* planted at Lake Omeo (Scarlett et al. 2003). Lenz *et al.* (2003 p. 30) applied molluscide in a low-diversity, weedy native grassland with a high population of the white snail *Cernuella virgata* da Costa and found that snail exclusion had no effect on vascular plant species composition over 9 months. The dietary preferences of introduced herbivorous molluscs in regard to native plants do not appear to have been investigated (Lenz *et al.* 2003) except for *M. gagates* which was found by Holland *et al.* (2007) to prefer some native plants over others, with the two native grasses tested having relatively low palatability.

Grass-feeding insects

Various insect groups that avoid plants with toxic metabolites are restricted to Poaceae including some Acrididae (Orthoptera) and Auchenorrhyncha (Hemiptera). Theoretical considerations suggest that the general absence of toxic principles should result in a lower ratio of endophagous to ectophagous feeders in grasses than in dicotyledons, and that appears to be the case, with external feeders being much more common than gall-makers, borers and miners. Ratios of c.30:10 and 30:1 have been recorded in six grass species (Tscharntke and Greiler 1995). Dominance of ectophages is also apparent in *Sporobolus* spp. (Witt and McConnachie 2004). Veldtman and McGeoch (2003) found five grass species with insect galls, caused by five gall-forming insect species, in a broad survey in South Africa. Poaceae had one of the highest number of galled species compared with other plant families. However, herbaceous plants generally have fewer gall-forming species than woody plants, possibly in part because lignified material is more long-lasting, and is thus 'safer' for gall formation (Veldtman and McGeoch 2003). Most of the chewing ectophages on grasses are oligophagous, whereas amongst the main 'sucking' groups (Hemiptera) Delphacidae are monophagous while Cicadellidae has a higher proportion of oligophages (Tscharntke and Greiler 1995).

As with vertebrates, the nutritional quality of grass foliage, particularly silicate and lignin content, are important determinants of palatability for invertebrates. Juvenile foliage has a reduced content of these structural polymers but has better chemical defenses against herbivores. C_3 species have higher protein contents than C_4 species, so may be preferred by herbivores. Large abundant grasses generally have larger faunas (5-12x) than rare, small species. Two variables, shoot length and life-cycle dichotomy (annual or perennial) explain a high proportion of variance in the species richness of a particular grass. Unpredictably in the spatial and temporal distribution of annuals, rather than any difference in the number of possible niches they offer appears to explain this (Tscharntke and Greiler 1995).

Data on the grass food plants of insects in Australia, as elsewhere in the world, is very fragmentory. The literature appears to be devoid of studies of whole faunas associated with Australian native grass species. According to Wapshere (1993) no arthropods had been recorded from *Nassella trichotoma* in Australia, despite its long presence in the country, and nothing was known of the invertebrate faunas of *Austrostipa* species (although this is no longer correct for these grasses). At attempt has been made to draw together some of the scattered information sources on grass invertbrates in an Appendix to this Literature Review. Taxa of Gondwanan origin such as *Austrodanthonia* may harbour a larger range of endemic coevolved invertebrates than species such as *T. triandra* which have colonised Australia more recently from the north (E.D. Edwards cited by Driscoll 1994).

Lawton and Schroder (1977 p.137) compiled data on the insects associated with species of British plants but excluded Poaceae "because the insect data appeared to be particularly unreliable", the entomological literature frequently recording "grass", rather than particular grass species as food plants. However they found that the monocots studied had the fewest insect species associated with them compared with shrub, perennial herb, 'weeds and annuals', and aquatic dicot herb groups investigated.

Nevertheless, based largely on Northern Hemisphere knowledge, the basic insect phytophage assemblage, for the smallest grasses, consists of one species each of Eurytomidae (Hymenoptera), Cecidomyiidae (Diptera) and Pseudococcidae (Hemiptera) (Tscharntke and Greiler 1995). The large, cosmopolitan Common Reed, *Phragmites australis* (Cav.) Trin. ex Steud., is the most speciose host known, attacked by c. 100 insect species (Tscharntke and Greiler 1995) and has a total of over 160 associated arthropods, approximately half of which are endophages (Witt and McConnachie 2004). Its diverse flora may be largely a result of a long evolutionary history, it being a "Palaeogenic relict" belonging to the"most ancient of modern grasses" the Arundineae (Tsvelev 1984 p. 59) and its broad geographical distribution. The phytophage complement is dependent on many factors, but larger faunas are associated with wider geographical range, large size, predictable occurrence and perenniality (Lawton and Schroder 1977). More than 24 arthropod species have been identified as potential biological control agents for the intertidal grass *Spartina alternifolia* Lois. in the USA, while *Calamagrostis epigejos* (L.) has 10 endophagous arthropod species (Witt and McConnachie 2004).

Isoptera (Termites)

Drepanotermes grass-harvesting termites are a conspicuous feature of arid Australia but are not found in the grasslands of temperate south-eastern Australia (Watson 1982), where most grasses appear to escape termite attack.

Coleoptera

Unlike on dicotyledonous groups, beetles (Coleoptera) are generally relatively depauperate on grasses. Only 8 spp. are known from *Phragmites australis* and only 2 of 24 apparent specialists on *Spartina alternifolia* are beetles (Witt and McConnachie 2004). Coleoptera are "relatively abundant" on smaller grasses including *Sporobolus* spp. and *Nassella trichotoma*, but are mostly pollen feeders (Witt and McConnachie 2004).

Thysanoptera

Thrips (Thysanoptera) are common inhabitants of grasses. *Chirothrips* species breed only in the flowers of grasses and can reduce seed production and limit grass regeneration (Mound and Palmer 1972). Six species are recorded in Australia, all introductions. Native thrips of grass flowers are species of *Odontothripella*. Other species associated with Poaceae flowers include *Caliothrips striatopterus* (Kobus), common in grass flowers in Queensland, *Haplothrips froggatti* Hood common in subtropical Australia, *Desmothrips reedi* Mound and *D. tenicornis* (Bagnall). Many other species are associated with grasses including *Phibalothripis longiceps* (Karny), leaf tissue-feeding species related to *Anaphothrips*, usually found in leaf funnels, *Podothrips* species predatory on coccoids at the base of grasses in the tropics, and species found in the bases of grass tussocks that feed on fungi (Mound and Palmer 1972). *Desmothrips reedi* (Aelothripidae)lives at the base of grasses, *Moundothrips* and *Phibalothrips* (Thripidae) live on grasses and *Odontothripella* are found on grass flowers (Mound and Heming 1991) including *O. compta* Pitkin, *O. reedi* Pitkin and *O. unidentata* Pitkin (Pitkin 1972). Introduced *Limothrips* is common on grasses in cooler areas of southern Australia often living on leaves, the introduced *Aptinothrips rufus* is abundant on grasses and *Haplothrips* (Phlaeothripidae) live in grass flowers (Mound and Heming 1991), five species (*H. anceps* Hood, *H. angustus* Hood, *H. gowdeyi* (Franklin), *H. froggatti* Hood and *H. pallescens* (Hood)) apparently breeding there, one species living in the base of tussocks, and other species including *Antillothrips cingulatus* (Hood), *Apterygothrips australis* Pitkin and *Podothrips xanthopus* Hood living on or amongst grasses, the latter probably predatory on small arthropods such as coccids, mites or other thrips (Pitkin 1973).

Diptera

True flies are relatively more common on Poaceae than on dicotyledons, notably gall midges Cecidomyiidae, leafminer flies Agromyzidae and grass flies Chloropidae. On a world basis, many stem-boring and stem-galling Diptera on grasses have narrow host ranges (Witt and McConnachie 2004).

Many cecidomyiid species appear to be monophagous at species level (Witt and McConnachie 2004). The Australian cecidomyiid fauna is extremely poorly known (Harris 1979, Gagné 2007, R. Adair and R. Gagné pers. comms.) but several species belonging to three genera, *Contarinia*, *Lasioptera* and *Geromyia* have been recorded from grasses, largely in northern Australia (Harris 1979). Larval Cecidomyiidae feed in the inflorescence, inside the culms, or under leaf sheaths often near the base of the plant. The *Contarinia* spp. inhabit inflorescences and seed heads, and include *C. brevipalpis* Harris which attacks *Eragrostis brownii* (Nees) Kunth, *C. dichanthii* Harris which attacks *Dichanthium* spp. including *D. sericeum* (R.Br.) A. Camus, and undescribed species on *Heteropogon contortus* (L.) P. Beauv. ex Roem.and Schult. and *Themeda triandra* (Harris 1979). There are "probably hundreds" of undescribed Australian species (Harris 1979 p. 168). *Lasioptera* species are found on inflorescences of grasses including *Panicum*, *Setaria*, *Bothriochloa* and *Heteropogon*, while the single *Geromyia* species is "probably restricted to *Setaria*" (Harris 1979 p. 164). No Cecidomyiidae species are known from *Austrostipa* or *Austrodanthonia* spp. It is highly likely that exploration of the temperate Australian fauna will reveal many species that inhabit native grasslands and attack grasses (Adair and Gagné pers. comms.). The biology of a New Zealand species that feeds on developing seeds of New Zealand 'snow-tussocks' *Chionochloa* spp. has been described by Kolesik *et al.* (2007). The larvae do not form galls but overwinter in the floret after feeding on developing seeds. The species appears to be the main seed predator driving mast seeding of these grasses, destroying up to 60% of florets (Kolesik *et al.* 2007, Kelly *et al.* 2008).

Agromyzidae has relatively high host plant specificity with most species specific to a single plant genus or family, Asteraceae hosting the greatest number of species, and polyphagy (across plant families) being rare (Spencer 1977). Larvae may be leaf miners, internal feeders throughout the plant or selective feeders in roots, stems or flowers (Ferrar 1987, Spencer 1989). Adults feed on plant sap via punctures in the tissue made by the female (Ferrar 1987). No Australian Agromyzidae are known from Stipeae (Spencer 1977), but members of the family are recorded from other grasses in Australia. Spencer (1977) listed *Pseudonapomyza ?spinosa* Spencer from *Urochloa subquadripara* (Trin.) R.D. Webster at Darwin, NT (as *Agromyza* sp. on *Brachiaria miliformis* (Presl.) Chase in Kleinschmidt 1965), *P. spinosa* from the introduced *Eleusine indica* (L.) Gaertn. and *Agromyza* sp. from *Oplismenus compositus* (L.) Beauv., while Kleinschmidt (1965) also listed *Cerodontha australis* Malloch from *Poa annua* L. and *Pseudonapomyza spicata* (Malloch), a "common grass-mining species", probably of exotic origin, from *Eleusine indica*. Elsewhere in the world *P. spinosa* attacks wheat and barley and "other wild grasses certainly serve as hosts" (Spencer 1977). *U. subquadripara* is widespread in NSW, but not in areas of temperate grassland, the common weed *E. indica* is found in all mainland states, *O. compositus* is not known from Victoria or NSW. Other *Pseudonampomyza* spp. with angulate third antennal segments have host plants restricted to Poaceae, but no known Australian hosts: *P. probata* Spencer, *P. rara* Spencer, *P. salubris* Spencer and *P. pudica* Spencer. *Agromyza mellita* Spencer and *A. venusta*, both known from northern Queensland have male genitalia with "the characteristic form of grass-feeders" (Spencer 1977 p. 122).

Some Anthomyiidae (Diptera) also attack grasses including the wheat bulb fly *Delia coarctata* (Fallén), *D. extreminata* (Malloch) in *Bromus* in the USA, and *Phorbia* spp. mining stems and shoots (Ferrar 1987). Others are known to breed on *Epichloe* fungi on grasses (Ferrar 1987).

Larvae of numerous Chloropidae species live in young shoots and stems of grasses and may feed largely on bacteria (Colless and McAlpine 1991) or be saprophagous rather than phytophagous (Ferrar 1987), however little is known of the biology of Australian species (Sabrosky 1989). Ferrar (1987) provided summary information on some pests of cereals and pasture grasses elsewhere in the world, plus a tabulation of the genera known from Poaceae. Most Chloropinae attack Poaceae or Cyperaceae, as do some Oscinellinae (Ferrar 1987). Some *Oscinella* species appear to be monophagous on particular grass species, while others have multiple known grass hosts (Ferrar 1987). Thirty-two Chloropidae spp., mostly endophages, have been collected from *Phragmites*, over 20 of which are monophagous (Witt and McConnachie 2004). *Diplotaxa similis* Spencer has been commonly found in the florets of *Chionochloa* spp. in New Zealand and has been viewed as the major seed predator, although they may actually often destroy the flower before seed formation, and there has been considerable confusion about whether the damage is caused by the chlropopid or Cecidomyiidae (Kelly *et al.* 1992). The wingless *D. moorei* (Salmon) Spencer is a predator of *Festuca novae-zelandiae* author (Kelly *et al.* 1992).

Some Ephydridae, mostly Hydrellini, attack grasses, and some are cereal pests, but most breed in aquatic situations or wet areas and feed on decaying matter, algae etc. (Ferrar 1987). *Hydrellia* spp. are recorded from Lolium, Poa, Pennisetum, Holcus, Panicum, Echinochloa and other grasses outside Australia (Ferrar 1987)

Hemiptera

Hemiptera also appear to have good representation on grasses. Specialist insects on *Spartina alternifolia* are mainly Hemiptera (Witt and McConnachie 2004). Among the Heteroptera, the Leptocorisini (Alydidae: Leptocorisinae) is closely associated with grasses and includes a number of rice pests, while the Stenodernini (Miridae) and Blissinae (Lygaeidae) are also grass inhabitants (Ahmad 1965). Lygaeids are mostly seed eaters but the Blissinae (Chinch Bugs) feed on grass sap (Slater 1991). Subfamily Cyminae of Lygaeidae contains "small, brown bugs that live in seed heads and resemble seeds of various sedges and rushes" (Slater 1991 p. 502) and possibly includes some grass feeders. The pachygronthine *Stenophyella macreta* Horváth "is often common in seed heads of grasses" (Slater 1991 p. 502) and "appears to feed on a number of grasses even when they are completely dry" (Slater 1976 p. 135). Nabidae are predacious but oviposit in grass stems (Gross and Cassis 1991). Many grass-feeding Homoptera have a narrow host range, but mealybugs Pseudococcidae and soft scales Coccidae are generally polyphagous (Witt and McConnachie 2004).

Farrow (1999) found that Cicadellidae (leafhoppers) were very numerous in grasslands in the Australian Capital Territory and this family along with other planthoppers (Delphacidae, Eurymelidae, Flatidae, Membracidae, Ricanidae), froghoppers (Cercopidae), cicadas (Cicadidae) and allies, collectively classified in the suborder Auchenorryhncha, has been identified as a highly appropriate higher taxon for evaluation of the conservation significance of grasslands and monitoring environmental and habitat change, at least in Europe (Biedermann *et al.* 2005). They are diverse, with many rare species, wholy herbivorous, their numerical abundance supports higher trophic levels, and perhaps most importantly, rhey have high and rapid sensitivity to a range of disturbances (Biedermann *et al.* 2005). The European grassland fauna however is much better described than that of Australia, baseline studies of whole faunas have been undertaken and some effects of grassland management on the faunas have been determined.

Poaceae probably supports a higher diversity of Australian cicadas (Cicadidae) than any other plant family, but few species inhabit the grasslands of the south-east (Moulds 1990). Nymphs of the grass-feeding species feed on grass roots, and the adults of some species oviposit in grass stems or leaves (Moulds 1990). Evans (1966) considered the cicadelloid fauna of Australian grasses and herbs to be depauperate and Australian grasslands to carry "a very small leafhopper population and ... even fewer cercopids" (p. 20) in comparison with other parts of the world. However Day and Fletcher (1994 p. 1119) noted that there had been "little systematic collecting" of Cicadelloidea in Australia and that distribution data was "very inadequate". According to Evans (1966 p. 21) both Cicadelloidea and Cercopoidea were "not usually abundant on grasses" in Australia, and most grass-frequenting species were introduced, but he acknowledged that records of food plants were very scanty. However Evans (1966 p. 133) thought it "probable" that all species of Hecalini (Cicadellidae) are grass-feeders. *Hecaleus arcuatus* (Motschulsky) known from Queensland and outside Australia is recorded from *T. triandra* and *Heteropogon* (Day and Fletcher 1994). Day and Fletcher (1994) listed numerous species with known grass hosts in Australia but their designation of "host" is not rigorous; e.g. Evans (1966) stated that *Mircrolopa minuta* Evans was collected on grasses, which became in Day and Fletcher (1994 p. 1123): "Known hosts: Poaceae (Evans 1966: 87)". Their host information "frequently reflects the plant species on which specimens were colleced and do not necessarily reflect the true hosts" (Day and Fletcher 1994 p. 1121).

Hymenoptera

Many 'seed chalcids' Eurytomidae (Hymenoptera) are host specific and different species develop in different positions within the culm (Witt and McConnachie 2004). They can cause major reductions in forage yield and seed weight, including a reduction of 60% in *Heterostipa comata* (Trin. and Rupr.) Barkworth, with consequent reduction in germinability (Witt and McConnachie 2004). A *Tetramesa* sp. in Africa that bores in the stems of *Sporobolus* spp. was found to infest 33% of culms at one site. Infested culms were significantly shorter than uninfested and 60% had deformed infloresences (Witt and McConnachie 2004).

The tribe Cephini of the sawfly family Cephidae consists of grass-mining specialists, a number of which are cereal pests, but is restricted to the Nearctic and Holarctic (Ivie 2001).

Lepidoptera

Amongst the Lepidoptera that attack Poaceae, the Noctuidae are generally polyphagous (Witt and McConnachie 2004). A high proportion of Satyrinae (Nymphalidae) and Hesperiidae are grass feeders (Braby 2000). A study of 13 satyrines and 3 hesperines showed that they all stored the grass secondary metabolite flavonoid tricin, while one species stored glycosylflavones, with the flavone stored in the wings and body and constituting 1-2% of their dry weight.(Harborne and Williams 1986). One important role of flavonoids in grasses is probably as grazing deterrents (Harborne and Williams 1986) and these butterflies have therefore to some extent overcome those defences. A species of Gelechiidae has been found rarely attacking the florets of *Chionochloa* spp. in New Zealand (Kelly *et al.* 1992).

Australian Grassland Invertebrate Faunas

A few studies of the faunas of particular natural grassland associations have been undertaken in Australia including Sharp (1997), Melbourne (1993), Farrow (1999 2006), New (2000), Gibson and New (2007) and the studies of Yen and colleagues in Victoria. The study of Farrow (1999) was a pioneering quantification of the biodiversity of a major part of the insect fauna of ACT grasslands.

Victoria

Terrestrial invertebrates of western Victorian Basalt Plains Grasslands have been surveyed and discussed by Yen (1999) and assessed by Yen, Horne, Kay and Kobelt (1994) and Yen *et al.* (1995), and in the western region of Melbourne by Yen, Kobelt, Lillywhite and Van Praagh (1994). These were the first baseline invertebrate surveys of native temperate grasslands in south-eastern Australia (Farrow 1999), however these are long unpublished reports containing little analysis. Previous studies covered only a very limited number of individual taxa (e.g. Key 1978, Horne 1992, McDougall 1989), or were a part of dietary studies of endangered vertebrates including *Delma impar* (Coulson 1990, Wainer 1992) and *Perameles gunnii* (Yen 1995) or related to agricultural pest species (e.g. Schroder 1983). Approximately 50 taxa were identified from pitfall trap specimens taken at Derrimut Grassland Reserve by Kathy Ebert (Coulson 1990) but only ants and some spiders were identified, and only to genus.

Initial pitfall trap sampling suggested that basalt plains grasslands have lower invertebrate divesity than other habitats in Victoria (Yen 1999), paralleling Willis's (1964) view of the vascular plant and bryophyte diversity.

Hadden (1997, 1998) investigated invertebrates in both the Northern and Western Plains, but did not provide specific identifications. Hadden and Westbrooke (1999) detected 160 arthropod morphospecies using pitfall traps, sweep net and hand searching in a grazed *T. triandra* pasture near Ballarat: 26 Formicidae, 90 Coleoptera and 44 Araneae. The Coleoptera and Araneae were identified to family level and the Formicidae to genus. Various features of the fauna were identified including the low number of aerial web-building spiders, the dominance of *Iridiomyrmex* spp. ants and the small size of those Coleoptera spp. that were abundant. Gibson and New (2007) detected 24 morphospecies of Formicidae and 27 Coleoptera species by pitfall trapping in spring and summer at Craigieburn grassland, Victoria. Both major taxa appeared to be representative of regional diversity and included no rare or apparently grassland-specific species.

Collecting techniques used in the surveys of Yen *et al.* were pitfall trapping, weeping, suction sampling, canopy fogging and direct searching. Yen, Horne, Kay and Kobelt (1994) reported on 1992-3 seasonal surveys of 12 remant grassland sites representative of the range of site types, management practices and conservation ranking of all sites previously listed McDougall and Kirkpatrick (1994): 5 roadside reserves (4 burnt annually), 3 railway reserves (2 burnt annually), 2 privately owned pastures, 1 conservation reserve and 1 cemetry; and an additional 5 sites were surveyed once: 2 rail, 1 roadside, 2 private, along with 6 areas adjacent to seasonally sampled sites. Yen, Kobelt, Lillywhite and Van Praagh (1994) surveyed a variety of vegetation types during 1991-93 that included 2 *Poa* grasslands (Point Cook and Werribee) and 5 *T. triandra* grasslands (Truganina, Derrimut, St Albans rail reserve, Manor rail reserve, Evan St rail reserve). Yen *et al.* (1995) surveyed 29 additional grassland sites during 1994, completing their coverage of all the remnant grasslands listed by McDougall and Kirkpatrick (1994) that were still in existence. 5 of these sites were in the Melbourne region and the remainder between Ballarat and Hamilton.

Yen, Kobelt, Lillywhite and Van Praagh (1994) quantified the numbers of individuals collected by order, and by genus or species (where possible) for Coleoptera (beetles), Formicidae (ants) and Araneae (spiders). Yen, Horne, Kay and Kobelt (1994) and Yen *et al.* (1995) duplicated this analysis but also included species or genus level data for Orthoptera (grasshoppers and crickets) and Hemiptera (true bugs) and reported on spiders only at family level.

A reference collection of grassland invertebrates has been established at the Museum of Victoria under the supervision of Peter Lillywhite, and identification of included taxa is proceeding gradually (Yen pers. comm. 2006, Kobelt pers. comm. 2007).

Miller and New (1997) determined the ant fauna of (?derived) *Austrodanthonia* grasslands at Mount Piper, Victoria. The fauna was a far less diverse subset of that found in nearbye woodland and only one species was restricted to grassland. They found that sites invaded by *Holcus lanatus* supported an average of c. 16 and a total of 28 morphospecies while the more natural grasslands supported an average of c. 21 and a total of 33 morphospecies. However matched invaded and uninvaded sites"only a few tens of metres apart, did not differ significantly from each other in diversity" (p. 378) and "many species" showed "little apparent discrimination in relation to dominant grass species" (p. 381). Four morphospecies were trapped only at *H. lanatus* sites, while seven were trapped only at the *Austrodanthonia* sites. "Overall disturbance may be more significant to ants than simple replacement of native by exotic grass species" (Miller and New 1997 p. 381).

Few unique features have been noted about Victorian grassland invertebrate assemblages. One such example is the presence of ants that make use of rocks as a habitat. These ants are absent from ACT grasslands (Melbourne 1993).

Australian Capital Territory

Little is known about the distribution and ecological requirements of most invertebrate species in ACT grasslands (Sharp 1997 p. 4), although the fauna is much better studied that most other grassland areas, partly due to the presence of CSIRO Entomology and its predecessors in the national capital since 1928. Driscoll (1994) integrated knowledge then available to develop an invertebrate conservation and research strategy for the ACT. Numerous localised studies of selected grassland groups or species have been undertaken, including Edwards (1994) on the Golden Sun Moth, Rowell and Russell (1995) on the grasshopper

Keyacris scurra, Melbourne (1993) on ants and carabid beetles, Greenslade (1994) on Collembola, Melbourne *et al.* (1997) on native crickets (Gryllidae) and exotic slugs (Arionidae, Limacidae and Milacidae), Sharp (1997) on all orders and their relationship to grassland composition, structure and functioning and Farrow (1999, 2006) on canopy-living insects and their relationships to management factors, season of sampling and vegetation type.

Melbourne (1993) sampled three types of native grassland, dominated respectively by *T. triandra*, *Austrostipa* (typically *A. bigeniculata*) and *Austrodanthonia* and two types of exotic grassland dominated by *Phalaris aquatica* (improved pasture) and *Avena fatua* (an enriched grassland) maily using pitfall traps. A total of 37 ant species in 18 genera and 24 carabid species in 22 genera were detected. The pitfall trap catch size of ants was significantly larger in plots where vegetation was experimentally cleared and plots where litter was removed. Some species were more commonly trapped in cleared areas, some in uncleared, with one species showing no response to vegetation density. Slug (Limacidae and Milacidae) catches were approximately equal across treatments. However analysis suggested that structural differences in the grassland vegetation effected the efficiency of the traps, and that the trap catches in different vegetation types did not reflect actual abundance. Further analysis indicated that ant catches in the relatively open *Austrodanthonia* grasslands were approximately twice those in the more dense *T. triandra* and *Austrostipa* associations, and were by far the lowest in *Phalaris* pasture. Grassland type also affected carabid abundance (almost all being *Notiobia edwardsii*), with *T. triandra* having the lowest numbers and *Austrostipa* the highest. Catches of crickets were also lowest in *T. triandra*, while slugs were most abundant in the two most highly modified grassland types and next in *T. triandra*. The number of ant species trapped also varied significantly between grassland types, *Austrostipa* and *Austrodanthonia* being highest, but the number of carabid species was not signifcantly different between types. Other sampling methods yielded only very low numbers of individuals.

Melbourne *et al.* (1997) further reported on the crickets and slugs, the real abundances of which were determined to be properly reflected in the pitfall trap catches. Slug numbers increased with increasing density of the grasslands, possibly because slugs moved less on the drier substrates associated with more open habitat. The cricket *Bobilla victoriae* Otte and Alexander was several times more abundant in *Phalaris aquatica* grassland than the other grassland types, while *T. commodus* was also more common in *P. aquatica*.

Greenslade (1994) sampled springtails (Collembola) at 29 grassland and grassy woodland sites in the ACT and compared numbers and abundances of native, exotic and rare species. One new species of in the Tomoceridae was found at an ungrazed *T. triandra* site. Results showed a high degree of congruence with assessments of biodiversity based on vascular plants but not with ants and only partially with carabid beetles. Sites with high disturbance and weed invasion consistently had low Collembola diversity. *T. triandra* and *Austrostipa* sites had distinct faunas. Abundance of exotic species correlated with the amount of bare ground, as did the abundance of the rare native species *Australotomurus* sp., probably corresponding with their high temperature threshold for activity.

Sharp (1997) analysed invertebates collected from soil samples at grassland sites. Species representing 22 orders were found, dominated numerically by Acarina (mites), Collembola (springtails) and Coleoptera (beetles). Abundance and order richness of soil invertebrates were highest at sites dominated by*T. triandra* (rather than *Austrodanthonia*), at sites with darker wet-soil colour and at sites managed by mowing, and lowest in grazed sites, and was not significantly related to floristic association.

Farrow (1999) sampled canopy-living insects by sweep netting in 11 of the most important ACT grasslands in January and November 1998 and February 1999. He found representatives of 8 orders and 48 families and 'super groupings', and approximately 328 morphospecies including approximately 150 micro-Hymenoptera but excluding Lepidoptera, all Diptera except Tephritidae and some minor orders. Apart from micro-Hymenoptera, four families each were represented by >10 morphospecies: Chrysomelidae and Curculionidae (Coleoptera), Cicadellidae (Hemiptera) and Acrididae (Orthoptera), and Hemiptera were most speciose with 73 spp., followed by Coleoptera with 58 spp. and Orthoptera with 18 spp. Cicadellidae spp. were by far the most abundant family comprising 77% of the total individuals in summer1998 and 37% in summer 1999. Next in abundance was Acrididae, followed by micro-Hymenoptera, Lathrididae (Coleoptera), Tephritidae (Diptera) and Alydidae (Hemiptera). 34-40% of species were detected at only one location, and further 16-21% at two locations, confirming that most species are rare. There was no evidence of a total biodiveristy difference between habitats dominated by forbs and grasses. Insect predators were relatively uncommon. Spiders outnumbered insects in summer 1999. Farrow (2006) resurveyed the same sites and four additional ones in 1999, 2000 and 2001. He found representatives of 57 families and 'super groupings' and an estimated 383 species, with similar family representation to the previous study.

Conservation of grassland invertebrates

A 1984 survey of Australian entomologists identifed *Austrostipa*, *Austrodanthonia* and *T. triandra* grasslands among the broad habitat types that were poorly conserved from the invertebrate viewpoint (Hill and Michaelis 1988). Indentified taxa of conservation significance with many species associated with these grasses included *Synemon* (Lepidoptera: Castniidae), *Pterolocera* (Lepidoptera: Anthelidae), Hesperiidae (Lepidoptera) and Acridoidea (Orthoptera) (Hill and Michaelis 1988).

Small reserves can be sufficient for the conservation of grassland invertebrates (Key 1978, Hill and Michaelis 1988). In alpine grasslands, management regimes are a threat to dayfling Geometridae (Lepidoptera) (Hill and Michaelis 1988, McQuillan 1999). Trends apparent from sampling of mown vs. unmown grasslands in the ACT indicate that mown areas have fewer individual insects and that insects may aggrergrate in unmown areas (Farrow 1999).

Five relatively well known invertebrate taxa of conservation significance found in grasslands are discussed in more detail below: the xanthorhoinine geometrid moths (Lepidoptera), the sun moths, *Synemon* spp. (Lepidoptera: Castniidae), the morabine grasshoppers (Orthoptera) , the cricket *Cooraboorаama canberrae* Rentz (Orthoptera) and the Perunga grasshopper *Perunga ochracea* (Sjöstedt). Two grassland invertebrate species are officially declared threatened species in the ACT, *Synemon plana* (endangered) and *P. ochracea* (vulnerable) (ACT Government 2005). Other species with notable conservation significance in the ACT include Lewis's laxabilla *Laxabilla smaragdina* Sjöstedt (Orthoptera) and Whisker's Springtail Tomocereridae new genus undescribed sp. (Yen 1995, Anonymous 1997).

Other grassland insects of conservation significance include *Tropiderus childreni* Gray (Phasmatodea: Bacteriidae), SA, Vic, NSW, savannah, mallee, grass, reportedly threatened by urbanisation in the Adelaide Hills (Hill and Michaelis 1988); *Anisynta albovenata* Waterhouse (Lepidoptera: Hesperiidae), SA, WA, NSW, associated with *Austrostipa*, reportedly threatened by roadworks, clearing and overgrazing (Hill and Michaelis 1988); *Oriexenica kershawi kanunda* Tindale (Lepidoptera: Satyriinae) of SA and Vic , associated with open grassland, reportedly threatened by fire at Canunda National Park (Hill and Michaelis 1988); *Trapezites lutea* (Tepper) (Lepidoptera: Hesperiidae) of SA and Vic found on *Lomandra dura* threatened by fire and drought in SA (Hill and Michaelis 1988).

Xathorhoini, Larentiinae, Geometridae

McQuillan (1999) reported on studies on the Xanthorhoini, a tribe of small, colourful, largely diurnal Geometridae (Lepidoptera) with high diversity and endemicity in Australian grasslands. Members of the subfamily Larentiinae are "numerous of the tablelands and mountains of sout-eastern Australia and Tasmania" (Common 1990 p. 375). The tribe is represented in Australia by about 20 spp. of *Xanthorhoe* Hűbner, mostly found in the south (Common 1990, but only 13 spp. listed by Nielsen *et al.* 1996), many species of *Chrysolarentia* Butler, three species of *Acodia* Rosenstock, one of *Austrocidaria* Dugdale, eight of *Epyaxa* Meyrick and two of *Visiana* Swinhoe (Nielsen *et al.* 1996). Adults of many *Chrysolarentia* spp. are "common in summer at the higher altitudes on the tablelands and mountains" of southern NSW, Victoria and Tasmania (Common 1990, as *Euphyia* Hűbner). Larval Xanthorhoini are sluggish and nocturnal and most species appear to be stenophagous on a small number of low-growing annual native herbs, including species of *Hydrocotyle*, *Geranium* and *Acaena* (McQuillan 1999). McFarland (1988) recorded details of the habitats and diets of *X. actinipha* (Lower) and *X. vicissata* (Guenée) which both consumed *Medicago polymorpha* L. in captivity. No Australian Geometridae are known to consume grasses or any other monocots (McFarland 1988).

The studies of McQuillan (1999), in Tasmanian grasslands mainly dominated by *Poa labillardieri* or other *Poa* spp., *Themeda triandra*, exotic grasses, *Gymnoschoenus sphaerocephalus* (R.Br.) (Cyperaceae) or other Cyperaceae and Restionaceae, found that species richness increased with altitude, rainfall and greater sedge-content, and declined in areas with greater grass dominance, livestock grazing and weediness. Site species richness was lowest in highly modified grasslands and reached a maximum of 15 in unmodified grasslands and sedgelands, and 25 spp. were detected overall. Many species survived in small remnant grassland patches. Some species required grass tussocks for shelter in the adult stage and used tussocks as pheromonal 'calling' and mating sites.

Synemon spp., Sun Moths (Lepidoptera: Castniidae)

The Australian Castniidae or sun-moths consist of 20 (Douglas 2003b), 22 (Douglas and Marriott 2003) or 24 (Douglas 2000, Edwards 1996 1997a) named species and 22 (Douglas 2003b) or possibly 21 or more unnamed species of the endemic genus *Synemon* Doubleday (Edwards 1997a, Douglas and Marriott 2003). Douglas (2003a) provided a brief bibliography for the family. Adults normally fly only in bright sunshine (Edwards 1997a, Douglas 2003b), hence the common name, and resemble butterflies, having broad wings, clubbed antennae and usually bright colours (Douglas 2000). Females have very long, retractable ovipositors and deposit eggs underground between foodplant and soil or on the base of the tillers of the foodplant (Common and Edwards 1981, Edwards 1994, Dunn 1996, Douglas 2000). There is pronounced sexual dimorphism of adults, e.g. the the sexes of *S. plana* Walker were described as separate species in 1854 and 1874 and their identity was not recognised until 1926 (Edwards 1994).

The larvae of different species feed inside the rhizomes of *Lomandra* spp. (Xanthorrhoaeaceae), *Ecdeiocolea* sp. (Ecdeiocoleaceae), in the tillers and then against the rhizomes of *Lepidosperma viscidum* R.Br. (Cyperaceae) or in tunnels entirely undergound, on the roots of grasses (Poaceae) or other sedges (Cyperaceae) (Common and Edwards 1981, Edwards 1994, Dunn 1996, Douglas 2000, Douglas and Marriott 2003). Douglas (1999) also mentions unnamed Juncaceae as larval food plants. Most species are found in areas with sandy or light textured soils (Edwards 1994). Final instar larvae pupate in their feeding gallery and the pupa works its way upwards to protrude from the ground or the foodplant to enable adult emergence (Edwards 1994, Douglas 2000). The whole life cycle occupies 1-3 years (Common and Edwards 1981, Edwards 1994, Douglas 2000, Endersby and Koehler 2006) so the adults present in any one year may represent only a small proportion of the population (Edwards 1994). All species are localised in their occurrence and the adult flight period is brief (Dunn 1996), "as short as a fortnight" (Edwards 1997b). Adults are usually present in only small areas (hundreds of square metres) (Dear 1996).

Determination of what plant is actually eaten is a vexed question for some species. Edwards (1994) stated that digging the roots to find pupae "is the surest method … Finding protruding pupal shells within and between tussocks is the next most reliable", female oviposition probing is unreliable as a foodplant indicator, although local distribution of adults, particularly females, is indicative. None of these methods establish actual feeding relationships. Nevertheless the appear to be the basis for the food plant relationships recorded, until recently with little criticism, in the literature. Determination of the actual food of the larvae is difficult and requires a clear protocol to indicate the various levels of uncertainty inolved (Edwards 1997a)

The literature records species of *Austrodanthonia* as known or probable foodplants for five species found in Victoria including *A. setacea* (R.Br.) H.P. Linder and *A. laevis* (Vickery) H.P. Linder (Marriott 2004), while *A. carphoides* and *A. auriculata* are also probable food plants (Dear 1996) as well as *Austrostipa* sp. (Marriott 2004). Food plants of Queensland *Synemon* spp. include the grasses *Chrysopogon* sp. and *Thellungia advena* (Edwards 1997a).

Recently Braby and Dunford (2006) identified *N. neesiana* and red-leg grass *Bothrichloa macra* as probable larval food plants for the Golden Sun Moth *S. plana* on the basis of the location and distribution of empty pupal cases (protruding from or beside tussocks) in ACT grasslands. Despite Edwards' reliance on this method himself (e.g. Edwards 1994) he disputes this attribution (pers. comm. October 2006) believing it more likely that the moth has bred on undetected *Austrodanthonia* or in plants no longer visible above ground at the site, the juvenile stages being prolonged. More recently Gilmore *et al.* (2008) reported female oviposition on *N. neesiana* and pupal cases amongst a dense *N. neesiana* sward at Greenvale, Victoria. Gilmore et al. (2008) also reported oviposition on *Austrostipa* spp. and *Microlaena stipoides*. Edwards (1994) suggested that *S. plana* larvae may consume a mixture of roots, rhizomes and culm bases.

S. plana is one of the few invertebrate taxa that have been used as flagship taxa for grassland invertebrate conservation in Australia (New 2000) and is ranked as critically endangered in Australia (Endersby and Koehler 2006, Gilmore *et al.* 2008). It was once widespread in south- eastern Australia but in 1993 there were only three known populations recorded since 1950, one in the ACT and two in Victoria (Edwards 1994). Edwards (1994) investigated eight additional likely sites in Canberra and one in NSW and found populations at all except one in central Canberra. Recent surveys have found it at 43 sites in NSW and 12 in the ACT (Endersby and Koehler 2006). The South Australian distribution is based on a single individual from Bordertown (Edwards 1994) and it has not been found recently in that State (O'Dwyer 2004). Endersby and Koehler (2006 citing C. O'Dwyer pers. comm.) stated that: "Prior to 2003, the species had been reported from just six areas in Victoria – Broadford, Tallarook, Flowerdale, Dunkeld, Hamilton and near Nhill-Salisbury". However that is a highly misleading statement that should have been qualified, perhaps as 'probably extant populations'. Edwards' (1994 pp. 32-33) map and list of historical records showed many more localities with much wider distribution. The map provided by O'Dwyer(1999) apparently leaves out historical records noted by Edwards (1994) including Ararat, Bendigo, Castlemaine, Gisbourne, Maryborough, Monbulk, Nagambie and Woodend. The map provided by O'Dwyer (2004) is more complete, showing c. 24 distribution localities prior to 1970 and c. 7 sites after that time. Gilmore et al. (2008) stated that there were only four records in the Melbourne area prior to 2003, near Keilor, Broadmeadows and Laverton. Recent records in Victoria include grasslands in the Deer Park, Craigieburn and Epping areas (Endersby and Koehler 2006, Gilmore *et al.* 2008), at Greenvale and Woodlands Historic Park (personal observations, Gilmore *et al.* 2008) and Moyhu (personal observations).

Edwards (1994) considered *S. plana* to be restricted to *Austrodanthonia* patches in native grasslands, mostly on low hills or rises, sometimes in grazed and mown areas. He stated (p.34): "The foodplant is known to be *Danthonia*". Driscoll (1994) stated that the moth requires *Austrodanthonia carphoides* and *A. auriculata* grassland for survival. According to O'Dwyer (1999) and O'Dwyer and Attiwill (1999) *S. plana* inhabits native grasslands and grassy woodlands with >40% *Austrodanthonia* cover with some sites having up to 75% cover, on soils ranging from sands, through loams to clays, with available P below 14μg/g. O'Dwyer (2004) states that its habitat is native grasslands dominated by *Austrodanthonia* spp. particularly including also *A. eriantha* and *A. setacea*. She noted that oviposition by *S. plana* has not been observed. At Craigieburn and Epping, Victoria, it has recently been found in habitat previously considered atypical, dominated by *T. triandra* (Endersby and Koehler 2006).

The flight period of *S. plana* is variable from place to place and year to year (Driscoll 1994), possibly late October peaking in mid November and early December and through to at least the end of January in ACT (Edwards 1994), mainly 11 am – 2 pm (Edwards 1994). According to Driscoll (1994) the likely duration of the larval stage is 21-22 months. O'Dwyer (2004 p. 3) suggests "about 11 months". Edwards (1994) mentioned the absence of parasite records, and recorded some bird predators of adults. O'Dwyer (2004) mentioned Willie Wagtail *Rhipidura leucophrys* and robber fly (Asilidae) predation of adults.

Much of the literature on *S. plana* repeats unproved suppositions or speculation as facts, usually including *Austrodanthonia* spp. being food plants and native grassland habitat specificity, and fails even to provide full lists of known sites of occurrence. A large number of research projects on the species have failed to establish its most basic life history, including hosts plants and the duration of the larval stage. The most recent information (e.g. Braby and Dunford 2006, Endersby and Koehler 2006, Gilmore *et al.* 2008) indicate it is a widespread and common species that thrives in degraded pastures, including areas dominated by *N. neesiana*. The development of knowledge of this species is instructive. It has never been, as claimed by New (2000) a species "appraised reasonably fully" and its use as a flagship taxon has been of little value even for its own preservation, since so much of its basic life cycle remains poorly understood.

S. selene has been considered a particularly significant taxon because it exists in five distinct parthenogenetic forms (Douglas 2000); however it has not been listed under Victoria's Flora and Fauna Guarantee Act (Department of Sustainability and Environment 2009a) (Table 18).

The Cryptic Sun Moth *S. theresa* Doubleday is morphologically similar to other *Synemon* species in the grass-feeding group and it has been suggested that it too feeds on *Austrodanthonia* (Douglas 2003b). No existing populations are known but locality data on old specimen labels indicate it was an inhabitant of open grassy woodland with *Austrodanthonia* and *Austrostipa* in the understorey (Douglas 2003b). It is listed as a threatened species under the Victorian *Flora and Fauna Guarantee Act* (Department of Sustainability and Environment 2009a).

The Orange Sun Moth *S. nais* Klug occurs in the Mallee in Victoria and in South Australia and Western Australia. In the Mallee it is known from "a floristically diverse combination of open grassy areas interspersed with stands of trees and shrubs", the grassy areas dominated by *Austrodanthonia setacea* and *Austrostipa* spp. (Douglas 2003b p. 7). Oviposition behaviour suggests that *A. setacea* and an unidentified *Austrostipa* sp. may be larval hosts (Douglas 2003b). It is listed as a threatened species under the Victorian *Flora and Fauna Guarantee Act* (Department of Sustainability and Environment 2009a).

Only a single population of the Striated Sun Moth *Synemon* sp. aff. *collecta* is known in Victoria, from near Shelley. Its habitat may have originally been open grassy woodland and grassland dominated by *Austrodanthonia* spp. (Douglas 2003b).

Edwards (1996) noted that the "grass feeding species in particular have sufferred drastic reductions in distribution from the use of grasslands for agriculture"; urban development threatens populations of some species and invasion by introduced weeds has been identified as a threat to *S. plana*: "Without grazing or mowing the low-growing natives can become shaded and eventually choked out by taller exotic plants" (Edwards 1993 p. 17, Edwards 1994). In western Victoria this species survives in sheep-grazed *Austrodanthonia* pastures in which fertilisers and pesticides are not used (Dear 1996). According to Douglas and Marriott (2003 p. 90): "Any disturbance, through ploughing and other types of cultivation and/or excessive invasion of exotic grasses and forbs" leads to the disappearance of *Synemon* spp. Exotic perennial and annual grasses, not including *Nassella* spp., are listed as threats by O'Dwyer (2004). Cultivation in Two Wells area of South Australia was blamed for the extinction of *S. selene* in South Australia (Douglas 2000). These opinions should be viewed with some scepticism since they are based almost solely on observational correlations. *S. plana* continues to exist in areas of the ACT subject to light grazing or mowing, and the underground larval stage probably confers resistance to fire (Driscoll 1994). Douglas (2000) suggested that moderate disturbance from grazing, slashing or possibly fire appears to be necessary for *S. selene* to flourish (Douglas 2000). Douglas and Marriott (2003) advocated weed control and regular mowing, burning or grazing to remove accumulated dead grass "that provides cover for predators and reduces the extent of acceptable sites for oviposition".

Table 18. Conservation status of south eastern Australian *Synemon* taxa. Status: CE = critically endangered, E = endangered, S = secure, V = vulnerable, X = extinct; Other symbols: – = not present. References: 1. Marriott 2003; 2. Douglas and Marriott 2003; 3. Endersby and Koehler 2006; 4. O'Dwyer 1999; 5. Edwards 1994, 6. Sharp 1997; 7. O'Dwyer 2004; 8. Douglas 2003b; 9. Dept. of Sustainability and Environment 2009a.

Species and form	**Status Aust**	**Status ACT**	**Status NSW**	**Status SA**	**Status Vic**	**Habitat**	**Grass-land sp.?**	**Refs.**
selene Klug		–	–	E	E/CE	native perennial grassland	y	1 2
selene Klug pale morph		–	–		E	native perennial grassland	y	1
selene Klug dark morph		–	–		E	native perennial grassland	y	1
selene Klug Nhill morph		–	–		CE	native perennial grassland	y	1
selene Klug narrow-winged morph		–	–		CE	native perennial grassland	y	1
selene Klug Terrick Terrick morph		–	–		E	native perennial grassland	y	1
plana Walker	CE	E	E	X?	T/E	grassland	y	1 3 4 5 6 7 9
nais Klug		–	–	possibly widespread	T/E	Belah/Callitris wodland and grassland; Walpeup, Sealake	y	1 3 8 9
collecta Swinhoe (=? near *collecta* and sp. aff. *collecta*)		–	prob S	–	CE	open grassy woodland and grassland?; 1 site Vic: Shelley nr Corryong, many New England	y?	1 3 8
theresa Doubleday		–	–	E	T/X	grassy woodland?; Castlemaine, no extant populations know	n?	1 2 3 8 9
jcaria R. Felder		–	?	?	T/V	woodland, mallee heathland; Kiata, Big Desert	n	1 8
parthenoides R. Felder					S	heathland	n	1
discalis Strand		–	–	?	CE	mallee, heathland. Big Desert, Hattah	n	1 8
undescribed sp.		–	V?	–	–	1 site Kosciusko National Park	?	3

Driscoll (1994) listed elucidation of the lifecycle and food plants as a research priority for *S. plana*. This remains to be achieved. Recent data (Braby and Dunford 2006) suggest it could be polyphagous on suitable Poaceae, or may be a narrow oligophage that has evolved new preferences. In grazed situations, eggs, larvae and perching adults of *S. plana* may selectively survive on or near tussocks of *N. neesiana* because they are taller and bulkier than *Austrodanthonia* tussocks, so are less liable to trampling damage, and because they are not grazed by livestock in the reproductive phase, which corresponds in time with flight and oviposition periods of the moth. Possibly increased survival rates of all life stages on *N. neesiana* under grazing and declining abundance of *Austrodanthonia* spp. may have combined to create selection pressure for host shifting. Any genetic change could persist more readily *S. plana*, with its very localised populations with restricted gene flow, than in more mobile insects. The several forms of *S. selene* suggest that *S. plana* may have adequate genetic variation on which selection could act. A similar host shift from native to exotic plant, demonstrated to be genetically based, occurred in the butterfly *Euphydryas editha* in pastures in Nevada USA. Larval survival was much greater on the alien plant (Cox 2004). Many other Lepidoptera species have adapted to use exotic plants (e.g. Shapiro 2002).

In summary, the literature on *S. plana* contains many incorrect statements, assumptions taken to be facts etc. *S. plana* appears to be much more widespread, with less specific habitat requirements than previously assumed (Endersby and Koehler 2006). Larval feeding has never been observed and foodplant information is based on surmise.

Morabine grasshoppers

Morabinae (Orthoptera: Eumastacidae), known as matchstick grasshoppers (Rentz 1996), are a primitive, endemic Australian subfamily of about 250-260 species and 40 genera, of extraordinary biological interest as subjects for studies of genetic drift, cytology, chromosomal polymorphism, karyotype evolution and parapatric speciation (Key 1973 1976 1978 1981, Rentz 1996). Key (1976) provided a bibliography of this literature. They are wingless, mostly very small, slender, fragile, inconspicuous grasshoppers resembling matchsticks, with subtle colouration, mainly active at night (Rentz 1996). External morphology within the subfamily shows very little variation except for male cerci (Key 1981). Morabinae had probably evolved by the Cretaceous, preceding the appearance of Poaceae and a few species are known to consume ferns, assumably a primitive character, although diversification in a number of groups is associated with widespread grass genera (Key 1976). Genitalia dissection of males or examination of the karyotype is the best means of identification (Key 1981, Rentz 1996). 39 chromosomal fusions due to translocations and 22 dissociations due to chromosome breakage have been identified in the subfamily, making most species chromosomally unique (Hartl and Clark 1989 presumably from White 1968 1968). Congeneric species and races of morabines frequently exhibit parapatric distributions with no obvious mechanisms of pre-mating isolation. Detailed studies have demonstrated the extreme difficulty of determining whether these populations consist of races or species and have resulted in reappraisal and clarification of these taxonomic concepts (Key 1981).The species and races appear to be able to mate freely but produce no viable offspring, because of chromosomal incompatibility, so effectively "each population prevents the other from invading its territory by breeding with it" (Key 1981 p. 432).; or the offspring have (often little) reduced fertility; or interbreed occurs despite radical chromosome differences (Key 1981).

Many morabines live on trees or shrubs but some on grasses and forbs, and many are monophagous (Rentz 1996) and dependent on specific features of plants for shelter (Key 1978). Like other groups that exhibit parapatric speciation they have low vagility, being sluggish and wingless, and exist, or once existed, in numerous small sub-populations (Key 1978). Conservation of many of the remnant populations as possible is desirable because of their large genetic and chromosomal variation.

Three species of Morabinae are known from areas of grassland in south-eastern Australia. *Vandiemenella viatica* (Erichson), the first morabine grasshopper described, occurs from south-eastern Tasmania and King Island through south and west Gippsland and western Victoria to Kangaroo Island, and has 19 and 17 chromosome races, the former present in Victoria and Tasmania (Key 1976 1981). *Vandiemenella* species are dicotyledon feeders (Key 1976). The genus has been the subject of the most comprehensive studies of parapatry in the Morabinae. Twelve species or races have been distinguished based on karyotype, male cercus and genitalia characters, and size relationships (Key 1981 p. 433). Natural hybrids between the chromosome race of *V. viatica* with an estimated fertility depression of only c. 10%, occur in the contact zone in South Australia. Hybridisation experiments with the various *Vandiemenella* races and species have found no evidence that offspring males are completely sterile (Key 1981).

Keyacris Rehn contains c. 10 species that occur on forbs and low shrubs in south-eastern Australia through southern South Australia to south-east coastal Western Australia (Key 1976). *Keyacris scurra* (Rehn), Key's matchstick, is found on the tablelands of southern NSW and the ACT (Key 1981, Rowell and Crawford 1995) in grassland and grassy woodland (Driscoll 1994), and was considered by Key (1978) to be the second most threatened morabine. New (2000) listed it as one of few flagship invertebrate taxa for Australian temperate grassland. It was previously found over a large area of south-eastern NSW, the ACT and Victoria but its range has severely contracted due to destruction of habitat, including grazing and other disturbances (Rowell and Crawford 1995). It is a small species about 25 mm long with form and colouring that makes it difficult to distinguish from dry grass and litter (Driscoll 1994). It is "dependent for its survival" upon stands of *T. triandra* and associated forbs, is eliminated, "along with its habitat", under intensive sheep grazing, and is now largely restricted to country cemetry reserves (Key 1978 p. 7), fenced areas along railway lines, and some paddocks only ever grazed by cattle or horses (Key 1981). Rowell and Crawford (1995) surveyed 700 ha of potentially suitable habitat in the northern ACT in 1994 and found populations at 7 sites with widely varying management histories, with a total area of 25 ha, and along the Queanbeyan to Williamsdale rail easement in adjacent areas of NSW. Colonies occupied areas from 0.1 ha to 20 ha. They also reported on an unconfirmed site in Namadgi National Park in the southern ACT. Three populations were new records, and two previously known populations were found to be extinct. Its presence was correlated with that of 14 uncommon to endangered plants, also threatened by grazing and with *Delma impar*. Sharp and Shorthouse (1996) mentioned a then current study to determine the effects of vegetation composition and past management on populations. Farrow (1999) recorded its presence at one ACT grassland.

K. scurra is a winter grasshopper with a single generation per year, hatching in February and reaching maturity by May (males) or in spring. It has very low fecundity: a maximum of 21 eggs was produced by a female in a laboratory colony. The eggs are deposited shallowly in surface soil (Rowell and Crawford 1995).

T. triandra is used for shelter and perennial Asteraceae "usually a species of *Helichrysum*" are eaten (Key 1981 p. 432). "*Helichrysum*" is an old portmanteau name, subsequently split into numerous genera. Driscoll (1994) stated that the preferred food plants are *Chrysocephalum semipapposum* and *C. apiculatum*, the former also being used for shelter. The actual diet may be much more diverse, since individuals ate a wide range of native and exotic herbs and shrubs when offerred no other food (Rowell andCrawford 1995, citing Blackith and Blackith 1966). Rowell and Crawford (1995) distinguished three inhabited plant assemblages: *Chrysocephalum semipapposum* woodland and wet and dry *T. triandra* grasslands sometimes with derived origins. Dense *T. triandra* was not suitable habitat. Other native daisies in the tribe Inulae were suspected to be the food plant in areas where *Chrysocephalum* was absent.

K. scurra has two races, with 15 and 17 chromosomes respectively, which are believed to have once been in contact over a distance ofabout 200 km, but by the late 1950s were much depleted, although a 16 chromosome hybid individual, with an estimated reduction in fertility of 10% was detected in a relict of the contact zone. An artificial field population consisting of males of one race and females of the other survived for at least four generations (Key 1981). Rowell and Crawford (1995) provided additional details of populations, colouration, behaviour and habitat of *K. scurra* and discussed threatening factors. These include exotic grass invasion (namely *Nassella trichotoma*, *Anthoxanthum odoratum*, *Eragrostis curvula* and *Holcus lanatus*), increased cover of *T. triandra*, grazing and changed fire regimes.

Achurimima Key contains 17 species found in the herbaceous stratum or on low shrubs, very irregularly in the southern two thirds of inland Australia (Key 1976). *Achurimima* sp. P42, appears to be the most threatened morabine, recorded from only 6 localities in south-eastern NSW "where small populations survive on lightly grazed native pastures including the composite *Helichrysum semipapposum*" (Key 1978 p. 18) (now *Chrysocephalum semipapposum*). Driscoll (1994) noted that efforts by the NSW National Parks and Wildlife Service to reserve an area where this species was present along with *K. scurra* were frustrated by an uncooperative landholder.

Replacement of forb-rich *T. triandra* grassland by *Austrostipa-Austrodanthonia* pasture due to sheep grazing on the southern tablelands of NSW produced "a complete change in the grasshopper fauna", including the loss of two species which became restricted to cemetries (Key 1978).

Canberra raspy cricket *Coorabooraama canberrae* Rentz

C. canberrae (Orthoptera: Gryllacrididae) is a very large cricket, with a body about 40 mm long and antennae of twice this length, recorded only from urban areas in Canberra. The genus is monospecific (Rentz 1996). No populations were known in 1994 (Driscoll 1994). It probably lives under bark and litter and is found in suburban gardens (Driscoll 1994). Rentz (1996) considered it likely to be a grassland species. Virtually nothing is known about its biology. Farrow (1999) collected an unidentifed first instar gryllacridid at the Majura grassland in the ACT and noted that adults are known to occur there. Rentz (1996) provided a colour photograph of a male. Gryllacridids are predatory and often have highly specific food preferences. They all stridulate and are nocturnal, spending the day in burrows or leaf shelters they construct using silk from the mouthparts (Rentz 1996).

Perunga grasshopper *Perunga ochracea* (Sjöstedt)

The Perunga grasshopper *Perunga ochracea* (Sjöstedt) (Acrididae: Catantopinae) is a medium sized, flightless (Farrow 1999), almost wingless grasshopper with a narrow distribution in the ACT and neighbouring areas of NSW (Rentz *et al.* 2003). Farrow (1999) found the species at 6 of 11 grasslands surveyed by sweep netting in the ACT, but only in spring, and considered it to be unusual amongst the grassland Orthoptera in being winter-spring active. It occurs in *T. triandra* (Farrow 1999), *Austrostipa* and *Austrodanthonia* grasslands, feeds on forbs, overwinters as a nymph and is present as adults during spring and summer (Rentz *et al.* 2003). In the ACT it has disappeared from areas where it was once common, possibly as a result of "encroachment of dense cover of introduced grasses" (Rentz *et al.* 2003). *P. ochracea* is officially declared vulnerable in the ACT (ACT Government 2005).

Lewis's Laxabilla, *Laxabilla smaragdina* Sjöstedt

Lewis's Laxabilla, *Laxabilla smaragdina* Sjöstedt (Acrididae: Oxyinae) is a small grasshopper with wingless females and fully winged or brachypterous males, found in grasslands and "open savannah" from southern NSW to Mackay, Queensland (Rentz *et al.* 2003). Farrow (1999) noted that it had not been recorded in the ACT for 20 years.

Impact of *N. neesiana* on invertebrates

Weed invasion can eliminate native host plants and may enhance the spread of exotic invertebrates (Yen 1995).

Ens (2002a) conducted the only study to date of the effects of *N. neesiana* on invertebrates. She studied two endangered ecological communities in New South Wales: the edge of remnant Cumberland Plain Woodland (grassy woodland) at St Clair and much altered Sydney Coastal River-flat Forest (a coastal swamp forest) at Mt Annan. Pitfall trap and vacuum sampling were undertaken to enable comparison of areas dominated by *N. neesiana* and relatively devoid of native ground cover species, and native areas relatively free of *N. neesiana*. Sites had similar distrubance history, geology, topography and proximity to water. Point quadrats were assessed to quantify basal cover of *N. neesiana*, other exotic plants, native plants, bare ground, *Eucalyptus* litter, grass litter and sticks. Tree canopy cover was estimated using charts. Vegetation community structure was assessed by a point-height method with 4 height classes. Temperature and light were also measured above and below foliage, as well as distance to the nearest tree. Ens (*op. cit.*) reported significant quantitative impact, with a negative effect of *N. neesiana* on Formicidae and 3 Formicidae spp., reportedly "by altering the ground cover composition", and on mean abundance of Thysanoptera and Cicadidae moults, but a beneficial effect ("significant habitat") on Blattodea and two unidentified Coleoptera spp. Abundance of Collembola, Hemiptera, Gastropoda, Lepidoptera larvae and Araneae was significantly reduced in invaded areas. These results were attributed to the altered habitat structure and "change in plant architecture" i.e. the scale, complexity and heterogeneity of plants in the invaded community, and "indirect effects on the trophic heirarchy". Ens (2005) summarised her results as reduced ant abundance and alteration of "the entire invertebrate community composition".

However the higher proportion of bare ground in the native vegetation explained the effects on Formicidae at one site and an increased cover of *Eucalyptus* bark at the other, neither necessarily related to *N. neesiana* effects. The effects on one ant species was best explained by the higher weed richness in the native vegetation. Multiple regression analysis failed to reveal a sensible cause for decreased Thysanoptera or inreased Blattodea. The abundance of cicada moults was explained by *Eucalyptus* bark cover, suggesting the native plots were closer to trees, the roots of which some Cicadidae nymphs feed upon, however the reduction in bark cover was attributed as an effect of *N. neesiana* (Ens 2002a p. 67) and there was no correlation with the variable 'distance to nearest tree'. Some cicadas are grass feeders, so this may be a host plant influence. Identification of the species would have helped resolve this question. A number of correlations between environmental variables or higher taxa and other taxa with significantly different abundance in the *N. neesiana* areas do not make much biological sense e.g. Hemiptera were more abundant in greater litter depths of the native areas (?protection from predation), gastropods were more abundant in areas with more sticks (?protected from predation), Araneae with abundance of larvae (which they don't consume) but not larvae with abundance of Araneae, but these perhaps await fuller explanation. No trophic cascades or indirect effects on the trophic heirarchy are clear. No attempt was made to distinguish exotic and native invertebrates, pest or beneficial species, or widespread versus rare taxa and no trophic links to *N. neesiana* were identified.

The main effects were attributed to "changes in habitat parameters, cascade effects to higher trophic levels, changes to invertebrate community structure … decreases [in] ground temperature and ground incident light ... [and a] thick layer of foliage 10-20 cm above ground when a thick monoculture" (Ens 2005). These however were correlations and may not represent true causative relationships. Dense growth of *T. triandra* appears likely to produce a very similar set of effects and alter community structure in a similar way.

Grassland restoration

Restoration of degraded, weed-invaded grasslands is difficult. Corbin *et al.* (2004) advocated an integrated approach utilising all available tools, including traditional weed management techniques, fire, grazing, and reduction of soil N availability, along with measures that increase the abundance of native seeds and seedlings. Reintroduction of the disturbance regimes to which the systems are adapted is usually the first step in restoration (MacDougall and Turkington 2007). But the original functioning of the system may not be properly understood, the disturbances may function in different ways because the degraded systems differ from the original ones and there may be substantial risks, especially related to small species populations, and costs (MacDougall and Turkington 2007). "The more degraded the site, the less likely the recovery by native species other than those already present. Supplemental measures targeting dispersal and the survival of juveniles are needed in conjunction with treatments that reduce the disturbance-sensitive competitive dominants" (MacDougall andTurkington 2007 p. 270).

Preservation of native grassland remnants has been both politically and ecologically challenging. Simultaneous limited understanding of ecology. A critical turning point where most of the saveable remnants have been saved or their value appreciated and are being managed conservatively to preserve or enhance their biodiveristy. Future challenge of widespread restoration and, if Australia follows the European path, of extensifying agricultural land back to native grassland to achieve biodiversity and ecosystem services goals.

Biomass reduction techniques – fire, grazing, cutting and raking, manual removal – shown to have similar effects in removal of exotic grasses (MacDougall and Turkington 2007).

Nutrient reduction technqiues There is good evidence that the ability of perennial C_4 (such as *T. triandra*) grasses to outcompete C_3 grasses (including *Nassella* spp.) is enhanced under low soil N conditions (Badgery *et al.* 2002).

Reintroduction of species

MacDougall and Turkington (2007) compared the effects of annual cutting and raking, fire and hand weeding of the dominant invasive exotics *Poa pratensis* and *Dactylis glomerata*, in the restoration of invaded Garry Oak (*Quercus garryana*) savannah in British Columbia, unburnt for decades. All treatments significantly increased light levels at the ground surface and the amount of bare ground, reduced the growth and reproduction of the invasive grasses, and increased native plant cover and flowering. After four years of summer treatments the cover of *P. pratensis* and *D. glomerata* was reduced on average to <2.5%, from c. 70% in the former and 15-20% in the latter. One native grass, *Bromus carinatus* Hook. and Arn., showed similar declines and one perennial forb disappeared from some plots but the growth and reproduction of many native species increased significantly. Recruitment of natives into plots in which they were not already present did not occur.

Inadquate seed rain of native forbs and much reduced availability of suitable microsites for seedling establishment due to impoverishment of the burrowing and digging vertebrate fauna (Reynolds 2006).

Evidence of a threshold level of about 50% (pasture composition biomass) above which perennial C_4 species are able to reduce the content of *N. trichotoma* in pasture (Badgery *et al.* 2002). To maximise the competitive abilities of C_4 species in pastures Badgery *et al.* (2002 p. 97) proposed removal of grazing in late spring and summer, to enable their maximal growth, and "a focus on keeping [soil] fertility low".

Restoration of othe components of grasslands has had mixed success. McDougall and Morgan (2005) reported on the fate of seed, sod and individual species planting on former agricultural land at Organ Pipes National Park between 1986 and 1993 and found between 1991 and 1999 that more than half the species had persisted in low numbers, and only a few had expanded their range. Scarlett (1994) briefly reported techniques and some experimental results for re-establishing bryophyte soil crusts, namely salvage operations involving pieces of intact crust and spreading a slurry of small crust pieces. He had not then developed a technique for efficiently harvesting spores to enable testing of re-establishment by spore broadcast.

CONCLUSIONS

The geographic and temporal scales of the *N. neesiana* invasion is relatively well understood. The impact of *N. neesiana* on biodiversity in Australian native grasslands has a historical dimension (the impact to date) and a future dimension (potential damage), and the historical impact needs to be appreciated in the context of long sequence of invasions by a large number of serious exotic pests, both plant and animal, and of major disturbance and radical land use changes. The biodiversity impacts of these historical changes are partially known, but particular causes and effects are difficult to disentangle. The future prospects are dependent on the extent and type of management that is undertaken.

The theory of fluctuating resource availability posits a positive correlation between invasibility of an ecosystem or plant community and availability of 'unused' resources in the system, and provides a mechanistic, quantitative framework in which *N. neesiana* invasion of native grasslands can be understood. The enemy release and biotic resistance theories enable predictions to be made about the impact of its invasion on grassland animals.

Large proportions of the remaining grasslands have low native plant species diversity, so probably have very limited biotic resistance to further invasions. The current distribution and size of grasslands increases their invasibility. Their habitat quality and plant biodiversity is largely dependent on their ecological histories, proximity to urban areas and ongoing management regimes. Many can be characterised as "abandoned grasslands", which for some period in the past or currently have been neither grazed nor burned and consequently have "high dominance of usually few tussock grass species and low diversity of hebaceous species" (Overbeck *et al.* 2007 p. 107). The grassland network is fragmentory, most remnants are small, and mostly located in areas that have been intensively urbanised and developed for agriculture. Theory predicts that high perimeter to area ratios increase vulnerability to invasion (Byers *et al.* 2002). Native grasslands are subject to a variety of threatening processes including invasion by perennial grasses and other weeds, continued fragmentation, altered fire and grazing regimes, nutrient enrichment, climate change and invasions by animals. Simple reservation has proved to be insufficient for their conservation: and appropriate, usually intensive, management is generally required, the precise nature of which has been and remains difficult to determine. Temperate native grasslands have lost most of their orginal vertebrate diversity and consequently lack the structuring effects of large herbivores and the disturbance regimes upon which major elements of diversity are dependent. Aboriginal management, which maintained many elements of biodiversity, has disappeared. The origin of grasslands and the ecological and evolutionary processes that resulted in the assemblage of their flora and fauna are very incompletely understood, and this makes the development of remedial approaches even more difficult.

Determining cause and effect in relation to *N.neesiana* invasion is complicated by this range of compounded factors. Changes in community composition and biodiversity coinciding with invasion by an alien grass may be the result of the anthropogenic disturbances, rather than the invader. This situation is exemplified by the natural grasslands and subsequent 'invaded' pastures of Australian and North America (see Mack 1989), where it is not possible in the historical context to separate the effects of introduced grazing animals from that of the invasive plants (Woods 1997). Distinguishing between direct effects of disturbance on native plants and the competitive effects of invasive species has generally been difficult, as has determination of the interaction between disturbance and the invader (McIntyre 1993). Morgan (1998c p. 153) stressed that "conservation of many perennial native plants of species-rich grasslands would appear to be critically dependent on the conditions that maintain the standing [native] flora (i.e. low levels of canopy shading by the dominant grasses); that maintain flowering ... and that maintain opportunities for occasional successful recruitment, i.e. large canopy gaps". The extent to which N. neesiana invasions prejudice these objectives are a critical issue in restricting its biodiversity impact.

N. neesiana responds positively to anthropogenic disturbance. It appears to invade when there is nutrient enrichment with N and P, particularly the former, a condition that occurs when the major nutrient pool of the grassland system, contained in the roots and crowns of the dominant grasses, is mobilised by the death of these grasses. Exogenous nutrient inputs of diverse kinds, including water enrichment, may also be driving invasions. Although the dominant native Poaceae generally survive fire, burning appears to promote exotic annual weeds, and possibly releases smaller labile nutrient pools which *N. neesiana* may utilise in initial colonisation. Burning, grazing and herbicide application can all create bare ground which *N. neesiana* seedlings require to establish. Best practice mangement of *T. triandra* grasslands in Victoria generally includes regular burning to reduce *T. triandra* cover. Areas that are not burned rapidly loose their vascular plant diversity through loss of forbs, which generally have very small short-lived soil seed banks. *N. neesiana* invades *T. triandra* grasslands that are not burnt regularly or otherwise managed to reduce their biomass. *T. triandra* becomes senescent and dies under such conditions, resulting in liberation of the major nutrient stores in the crowns and roots. Other types of native grassland in south-eastern Australia are usually managed by low intensity livestock grazing to reduce grass biomass and maintain plant diversity. Periodical harvest of the livestock removes nutrients from the system and is probably a significant factor in protecting them from invasion.

Native vascular plant diversity, overwhelmingly comprised of species that grow in the inter-tussocks spaces, also responds positively to disturbance. Regular biomass reduction is required to maintain open areas in *T. triandra* grasslands. The germination requirements of inter-tussock forbs are poorly understood and current poor recruitment levels are probably linked to the loss of vertebrate biodiversity. It is not clear whether the disturbances that facilititate invasion of *N. neesiana* and other weeds are of the same magnitude and type that are required to maintain existing native plant diversity,and it is not clear whether *N. neesiana* invasion is a cause of plant biodiversity loss, or a consequence of it.

N. neesiana seed appears to be widely and commonly dispersed by human agencies. Propagule pressure is a pre-requisite for any plant invasion. Seed dispersal processes and rates are difficult to significantly reduce in the highly developed landscapes in which most remnant grasslands exist. All remnants are located in the cultural steppe or urban contexts and most have high perimeter : area ratios, allowing propagule pressure to be more or less relentless while the grass remains uncontrolled on roadsides, in pastures and in neglected areas. Protection of native grassland therefore requires greater emphasis on post-dispersal processes and minimisation of significant disturbance.

Occupation of a site by an exotic perennial grass can effectively be permanent if there is no managment intervention. Heavily invaded, high nutrient grasslands constitute a metastable state that is very difficult to shift. Extensification of native pasture and more highly developed grassland tracts, and the restoration of native grasslands from degraded enriched grasslands require a similar set of techniques to reduce their nutrient levels and establish a large range of native plants. These techniques are poorly developed in Australia and have limited effectiveness.

Given the trajectories of these factors, what is the prognosis for the impact of *N. neesiana* on biodiversity? Previous studies of invasive grass impacts on biodiversity in Australia have correlated presence of the grass with reduced native vascular plant diversity (e.g. McArdle *et al.* 2004) and alterations in invertebrate communities (Ens 2002a), but have generally failed to demonstrate cause and effect relatioships: 'matched' invaded and uninvaded areas are selected, compared, found to be similar, and the grass is ultimately assumed to be the cause of the impacts detected. Prediction of impact requires an understanding of the causes and mechanisms of invasion, many of which are undoubtedly disturbance-related, and require historical ecological understanding of the area invaded. The prognosis is continued invasion, as management failures accumulate across the grassland realm, to the climatic limit. New biiotic constraints on *N. neesiana* will develop as predators, parasites and competing plants evolve. There is some evidence that *N.neesiana* is used by native organisms and has begun to accumulate predators. General considerations suggest that whatever native invertebrates utilise *Austrostipa* spp. may have some preadaptations that enable them to exploit *N. neesiana* or to host shift on to it, because of the close generic relationship of the hosts.

N. neesiana is expected to support a small fauna of generalist phytophagous insects and may according to biotic resistance theory be favoured over a native grasses by some of the polyphagous generalist invertebrate herbivores. Native herbivores mammals should favour *N. neesiana* over native grasses. Where it displaces native grasses, specialist grass feeders with a narrow host range can be expected to be displaced. What this fauna might be is largely unknown. Detritovores dependent on grass litter may be little affected unless there are major differences in the nutrient content or indigestible components. *N. neesiana* has a different seasonal growth pattern which may restrict its utilisation by grass-feeding insects that have lifecycles synchronised with the native grasses. Little specificity is expected for insects with larvae that feed on grass roots, and a number of these probably exploit *N. neesiana*. Post dispersal seed feeders may be little affected or advantaged due to the similarilty of *N. neesiana* and *Austrostipa* seeds and seeding patterns. Some specialist *Austrostipa* feeders may be able to shift hosts to *N. neesiana* given the close relationship between the genera. The balance of evolved and adaptive changes might be expected to reduce the dominance of *N. neesiana*, but it too will evolve. Some evolved changes may happen rapidly and reduce the significance of *N. neesiana* as a weed, but predicting outcomes is far beyond our capabilities.

There are many similarities in the biology and ecology of *N. neesiana* and dominant native caespitose grasses it displaces, and some differences. Both *N. neesiana* and *T. triandra* resprout post-fire and retain dead leaf material that promotes fire frequency. Both have large, awned seeds, probably adapted for dispersal over longer distances mainly by animals, but which usually fall close to the plant are able to bury themselves in the ground. Both are drought adapted. *T. triandra* has a C_4 photosynthetic pathway, while the subdominant native grasses and *N. neesiana* are C_3 species. *N. neesiana* can form dense closed swards, with high tussock densities, as does *T. triandra*.

One factor that may contribute to the superior competitive abilities of *N. neesiana* is its early-mid spring growth peak, which coincides better with periods of high soil moisture than the late-spring-early summer *T. triandra*. In years when rainfall is limiting to native grassland growth, and that may be most years, established *N. neesiana* presumably depletes soil moisture pools that would otherwise be available for use by native forbs and by the later growing *T. triandra*. A similar process has been demonstated in competition between seedlings of *Bromus tectorum* and native perennial grasses in the USA (Evans and Young 1972). Earlier growth may also enable preemption of any soil nutrient pools that form during autumn and winter. These two impacts on the physical environment reinforce the benefits for *N. neesiana*: lower success of the dominant native grass means more resources for *N. neesiana* in the next growing season. Cool season native grasses may thereby be advantaged.

N. neesiana reportedly excludes all other species (Kirkpatrick *et al.* 1995), but any long-lived grass may be able to exclude other plants from the areas it occupies, i.e. effectively hold its ground under metastable management regimes, unless its competitors have large advantages. Distel *et al.* (2008) suggested that dominance of unpalatable grasses under livestock grazing is a stable vegetation state in central Argentine grasslands, caused by continual grazing pressure against palatable species, low seed banks of palatable species and low availability of safe germination sites for the palatable species. There, successful establishment of native perennial grasses requires adequate soil moisture in autumn and winter, and the replacement of dominant unpalatable casespitose species by palatable species requires their destruction, e.g. by disc ploughing, otherwise they are “impervious to invasion” (Distel *et al.* 2008).

Native grassland at any density and cover of the dominant native grass is resistant to *N. neesiana* invasion because *N. neesiana* seed germination requires more sunlight than is present in dense swards and seedling survival requires a soil nutrient pool not available unless existing vegetation is killed. Similarly, Barger *et al.* (2003) found that native *Trachypogon plumosus* Nees grassland in Brazil, in the absence of soil disturbance and external fertiliser addition, was resistant to invasion of *Melinis minutiflora*.

Reducing the impact of *N. neesiana* on biodiversity in grasslands can be achieved by:

1. Maintaining cover of the dominant grass *Themeda triandra* which is able to resistant invasion (Lunt and Morgan 2002, Hocking 2005b).

2. Eliminating disturbance that kills native grassland plants, especially the dominant grasses. (e.g. better off not to spray weeds) including vehicle traffic

3. Creation of larger buffer zones around native grassland, whether or not weed invaded and managing the weeds within that zone so as to minimise propagule pressure on the grassland.

3. Burning *T. triandra* grasslands in late spring-early summer (after most forbs have flowered and fruited and before the main growing period of *T. triandra*) so that bare ground is not created at a time when it can best be occupied by *N. neesiana* seedlings.

Hypotheses

1. Soil disturbance that kills dominant native grasses enables *N. neesiana* invasion.

2. *N. neesiana* reduces angiosperm diversity

3. *N. neesiana* supports a greater abundance and diversity of polyphagous native invertebrate phytophages than *Themeda triandra* and other dominant native grasses.

N. neesiana may passively occupy voids created by disturbance.

Literature Review Appendix

Appendix L1. Grass-feeding invertebrates of south-eastern Australian temperate grasslands

This is a partial compendium of published records of invertebrates occurring or thought likely to occur in south-eastern Australian lowland grasslands that are known to feed on grasses or particular grass species found in these grasslands, plus a limited number of extra-Australian records of invertebrates known to feed on such grasses. Such taxa , except for Nematoda are listed in Table A2.1. Nematodes of grasses are recorded in Table A2.2 and are discussed in more detail below. When an invertebrate taxon (other than nematodes) with recorded grass host is known not to be present in south-eastern Australia the invertebrate is not included. Taxa where the recorded hosts are not known from temperate south-eastern Australia are also excluded (e.g. sugarcane). In many instances these distributions could not be determined, so many taxa are probably listed that may not occur in temperate grasslands. The vast literature has been incompletely surveyed and there are certainly major gaps. The tabulation provides the name of the invertebrate taxon, the life stage which feeds on grass, the known host plants, the host tissue eaten, the reference source, and miscellaneous notes for various entries. An entry is included if both the plant and the invertebrate are recorded from south-eastern Australia, unless otherwise stated (in the 'Notes' column). Records for *Nassella* spp. are highlighted in bold. * = introduced sp.

Table A2.1. Literature records of invertebrates and their grass hosts recorded in south-eastern Australia, excluding Nematoda.

Species	**Life stage**	**Family**	**Order**	**Host**	**Host tissue**	**References**	**Notes**
Halotydeus destructor (Tucker)	all	Penthaleidae	Acarina	grasses		Gregg 1997	seedlings most vulnerable
Penthaleus major (Dugès)	all	Penthaleidae	Acarina	grasses		Gregg 1997	readily damages grasses, seedling most vulnerable
Nala lividipes (Dufour)	nymphs, adults	Labiduridae	Dermaptera	*maize, *sorghum, *winter cereals	seed, roots, stubble	Allsopp & Hitchcock 1987	"usually feeds on decaying stubble but also eats newly-sown and germinating seed and the roots of crops" (Allsopp & Hitchcock 1987 p. 86)
grasshoppers	all		Orthoptera	alpine grasses	foliage	Carr & Turner 1959	"extremely abundant in some years and in severaly infested areas they shorten the sward considerably"(Carr & Turner 1959 p. 19)
	all	Acrididae	Orthoptera	grasses	foliage	Rentz *et al.* 2003	most species "can be raised on grass": see Rentz et al. (2003) for details of individual acridid spp.
Teleogryllus commodus (Walker)	nymphs, adults	Gryllidae	Orthoptera	grasses and forbs, mainly damages grass foliage	seeds, leaves, crowns	Browning 1954, Heath 1968, Allsopp & Hitchcock 1987, Panetta *et al*. 1993, Gregg 1997	"pasture seed loss – the most serious effect" (Allsopp & Hitchcock 1987 p. 81). Feeds on the crowns of grasses (Heath 1968, New Zealand). "The main source of food ... is green grass" (Browning 1954). Seedling predator.
				Nassella neesiana	seeds	Slay 2001	hollows out fallen seed in New Zealand (Slay 2001)
Gryllotalpa spp.	nymphs, adults	Gryllotalpidae	Orthoptera	*cereals, *sugarcane, lawns	roots	Allsopp & Hitchcock 1987	
**Chirothrips ah* Girault	larva, adult	Thripidae	Thysanoptera	grasses, *Austrostipa aristiglumis*	flowers	Mound & Palmer 1972	breed only in the flowers of grasses
**Chirothrips atricorpus* Girault	larva, adult	Thripidae	Thysanoptera	**Sorghum*, **Melinis repens*	flowers	Mound & Palmer 1972	breed only in the flowers of grasses
**Chirothrips frontalis* Williams	larva, adult	Thripidae	Thysanoptera	grasses	flowers	Mound & Palmer 1972	breed only in the flowers of grasses
**Chirothrips manicatus* Haliday	larva, adult	Thripidae	Thysanoptera	grass	flowers	Mound & Palmer 1972	breed only in the flowers of grasses

Table A2.1 (continued)

Species	Life stage	Family	Order	Host	Host tissue	References	Notes
**Chirothrips mexicanus* Crawford	larva, adult	Thripidae	Thysanoptera	grasses, **Avena barbata*, *Leptochloa fusca*	flowers	Mound & Palmer 1972	breed only in the flowers of grasses
Odontothripiella	larva, adult	Thripidae	Thysanoptera	grasses	flowers	Pitkin 1972, Mound & Palmer 1972, Mound & Heming 1991	
Odontothripiella aloba Pitkin	larva, adult	Thripidae	Thysanoptera	grasses?		Pitkin 1972	
Odontothripiella buloba Pitkin	larva, adult	Thripidae	Thysanoptera	grasses		Pitkin 1972	
Odontothripiella compta Pitkin	larva, adult	Thripidae	Thysanoptera	grasses, *Austrostipa aristiglumis*. *A. stuposa*, *Themeda triandra*	flowers	Pitkin 1972	"lives in grass flowers"
Odontothripiella reedi Pitkin	larva, adult	Thripidae	Thysanoptera	grasses, *Themeda triandra*.		Pitkin 1972	
Odontothripiella unidentata Pitkin	larva, adult	Thripidae	Thysanoptera	grasses, reeds, *barley grass, *Themeda triandra*, **Hordeum leporinum*, **Hordeum vulgare*	flowers	Pitkin 1972	"feeds in the flowers of grasses"
Caliothrips striatopterus (Kobus)	larva, adult	Thripidae	Thysanoptera	grasses	flowers	Mound & Palmer 1972	"common in grass flowers in Queensland"
Haplothrips	larva, adult	Phlaeothripidae	Thysanoptera	grasses	flowers	Mound & Heming 1991	"particularly on grasses" (Mound & Heming 1991)
Haplothrips anceps Hood	larva, adult	Phlaeothripidae	Thysanoptera	grasses, *Themeda triandra*	flowers	Pitkin 1973	"grass-flower living ... apparently confined to Queensland"
Haplothrips angustus Hood	larva, adult	Phlaeothripidae	Thysanoptera	grasses, **Pennisetum clandestinum*, *Paspalidium* sp., **Secale cereale*, "*Danthonia linkii*", *Themeda triandra*, **Hordeum leporinum*	flowers	Pitkin 1973	"grass-flower living ... apparently widespread" (Pitkin 1973)
Haplothrips gowdeyi (Franklin)	larva, adult	Phlaeothripidae	Thysanoptera	grasses, *Melinis repens*	flowers	Pitkin 1973	"apparently breeds on grasses"
Haplothrips froggatti Hood	larva, adult	Phlaeothripidae	Thysanoptera	grasses, *Leptochloa digitata*, *Leptochloa fusca*, *Sorghum* sp., *Paspalidium* sp., **Triticum aestivum*, **Zea mays*	flowers	Mound & Palmer 1972, Pitkin 1973	"common in flowers of Gramineae" (Mound & Palmer 1972); "grass-flower living ... apparently widespread" (Pitkin 1973)
Haplothrips pallescens (Hood)		Phlaeothripidae	Thysanoptera	grasses, *Themeda triandra*, *Melinis repens*		Pitkin 1973	found on grasses, possibly predatory
Antillothrips cingulatus (Hood)		Phlaeothripidae	Thysanoptera	grasses, **Oryza sativa*.		Pitkin 1973	found on grasses, possibly predatory
Podothrips xanthopus Hood		Phlaeothripidae	Thysanoptera	grasses, *Themeda triandra*		Pitkin 1973	found on grasses, probably predatory
Apterygothrips australis Pitkin		Phlaeothripidae	Thysanoptera	grasses, "*Danthonia linkii*", "*Stipa*" sp., *Paspalidium* sp., *Sporobolus virginicus*		Pitkin 1973	"apparently widespread in southern Australia", possibly predatory
Desmothrips reedi Mound	larva, adult	Aeolothripidae	Thysanoptera	grasses	flowers	Mound & Palmer 1972	"associated with grass flowers"
Desmothrips tenuicornis (Bagnall)	larva, adult	Aeolothripidae	Thysanoptera	grasses	flowers	Mound & Palmer 1972	"associated with grass flowers"
**Limothrips*	larva, adult	Thripidae	Thysanoptera	grasses	leaves	Mound & Heming 1991	"in cooler southern areas ... common on grasses ... often on leaves"
Phibalothrips spp.	larva, adult	Thripidae	Thysanoptera	grasses		Mound & Heming 1991	

Table A2.1 (continued)

Species	**Life stage**	**Family**	**Order**	**Host**	**Host tissue**	**References**	**Notes**
Stenchaetothrips biformis (Bagnall)	larva, adult	Thripidae	Thysanoptera	**Oryza sativa*		Mound & Heming 1991	"found on grasses in moist habitats in Queensland"
Aptinothrips rufus (Haliday)	larva, adult	Thripidae	Thysanoptera			Mound & Heming 1991	"common on grasses"
Phibalothrips longiceps (Karny)	larva, adult	Thripidae	Thysanoptera	grasses	leaves	Mound & Palmer 1972	"feed on leaf tissue"
Species related to *Anapothrips* Uzel		Thripidae	Thysanoptera	grasses	leaves	Mound & Palmer 1972	"feed on leaf tissue"
Leptocorisa acuta Thunberg, *L. oratorius* (Fabricius)		Alydidae	Hemiptera	grass	-	Gross 1991b	"common on grasses"
Pemphiginae		Aphididae	Hemiptera	grasses	roots	Gair *et al.* 1983, Carver 1991	
**Metopolophium dirhodum*	all	Aphididae	Hemiptera	*cereals, grasses		Carver 1991	
**Rhopalosiphon insertum* (Walk.)	all	Aphididae	Hemiptera	*oat,*wheat, *barley, *rye; grasses	roots	Gair *et al.* 1983, Carver 1991	anholocyclic on grass roots (Carver 1991)
**Rhopalosiphum maidis* (Fitch)	all	Aphididae	Hemiptera	*oat,*wheat, *barley, *rye, *maize, *cereals, grasses	leaves	Gair *et al.* 1983, Carver 1991	
**Rhopalosiphum padi* (L.)	all	Aphididae	Hemiptera	*oat,*wheat, *barley, *rye, *cereals, grasses	leaves	Gair *et al.* 1983, Carver 1991	
**Rhopalosiphum rufiabdominalis* (Sasaki)		Aphididae	Hemiptera	grasses, *rice	roots	Carver 1991	anholocyclic on grass roots
**Sitobion* spp.		Aphididae	Hemiptera	*cereals, grasses		Carver 1991	
Arawa pulchra Knight	-	Cicadellidae	Hemiptera	grass		Day & Fletcher 1994	
*(?) *Arawa taedius* (Kirkaldy)	-	Cicadellidae	Hemiptera	collected on grasses		Evans 1966	probably synonymous with *A. pulchra* (Day & Fletcher 1994)
Balclutha incisa (Matsumura)	-	Cicadellidae	Hemiptera	Poaceae		Day & Fletcher 1994	plus hosts in several other families
Balclutha punctata (Fabricius)	-	Cicadellidae	Hemiptera	mainly Poaceae		Day & Fletcher 1994	
Balclutha rosea (Scott)	-	Cicadellidae	Hemiptera	mainly Poaceae		Day & Fletcher 1994	
Chiasmus varicolor (Kirkaldy)	-	Cicadellidae	Hemiptera	collected on grass		Evans 1966	
Deltocephalinae	-	Cicadellidae	Hemiptera	grasses		Fletcher & Semeraro 2001	
Deltocephalinae: Macrostelini	-	Cicadellidae	Hemiptera	grasses		Evans 1966	"many species feed on grasses"
Exitianus spp.	-	Cicadellidae	Hemiptera	grasses		Evans 1966	
Hecalinae: Hecalini	-	Cicadellidae	Hemiptera	grasses		Evans 1966 Day & Fletcher 1994	"probably that all species are grass-feeders" no Hecalini spp. known from NSW, Vic, SA, Tas
**Nephotettix apicalis* Motschulsky	-	Cicadellidae	Hemiptera	collected on grasses		Evans 1966	not listed as an Australian sp. by Day & Fletcher 1994
Mircrolopa minuta Evans	-	Cicadellidae	Hemiptera	collected on grasses		Evans 1966	
Nesoclutha pallida (Evans)	-	Cicadellidae	Hemiptera	collected on grasses		Evans 1966	
	-			*cereals, *maize, *Chloris*, **Paspalum*		Day & Fletcher 1994	vector of viruses that attack these plants
Pardorydium menalus Kirkaldy	-	Cicadellidae	Hemiptera	collected on grasses		Evans 1966	
Recilia hospes (Kirkaldy)	-	Cicadellidae	Hemiptera	**Cynodon dactylon*, *Digitaria henryi*		Day & Fletcher 1994	other hosts: sedges, low shrubs
* *Stirellus fatigandus* (Kirkaldy)	-	Cicadellidae	Hemiptera	collected on grass		Evans 1966	
Togacephala vetus (Knight)	-	Cicadellidae	Hemiptera	grass		Day & Fletcher 1994	plus other monocots and dicots

Table A2.1 (continued)

Species	Life stage	Family	Order	Host	Host tissue	References	Notes
Cicadetta waterhousei (Distant)	nymph	Cicadidae	Hemiptera	grass	roots	Moulds 1990	habitat: "grasses of several species; usually long and partly or completely browned ... In South Australia ... often found on on dried-out seed-bearing ..._Avena_ spp."
Diemeniana euronotiana (Kirkaldy)	nymph	Cicadidae	Hemiptera	grasses	roots	Moulds 1990	habitat: "at low altitudes on grass ..."
Diemeniana frenchi (Distant)	nymph	Cicadidae	Hemiptera	grasses	roots	Moulds 1990	habitat: "Grass, usually growing along river and creek flats"
Oliarius	nymph	Cixiidae	Hemiptera	grass	roots	Gross 1983	
Eriococcus		Coccidae	Hemiptera	_"Danthonia"_		Boucek 1988	New Zealand record; ?both plant and insect in SE Aust.
Symonicoccus		Coccidae	Hemiptera	grasses		Williams1991	?both plant and insect in SE Aust.
Phaenacantha australiae Kirkaldy		Colbathristidae	Hemiptera	?grasses, *sugar cane		Gross 1991a	"occurs in large numbers on grasses in coastal Qld and may be a pest of sugar cane" ; ?both plant and insect in SE Aust.
Cyminae?	-	Lygaeidae	Hemiptera	?grasses	seeds?	Slater 1991	as _Kosmioplex varicolor_ Kirkaldy
Blissinae?	-	Lygaeidae	Hemiptera	grasses	sap	Slater 1991	subfamily occurs "most commonly on grasses"
Opistholepis spp.	-	Lygaeidae	Hemiptera	grasses		Slater 1976	? in SE Australia
Stenophlegyas spp.	-	Lygaeidae	Hemiptera	grasses		Slater 1976	? in SE Australia
Stenophyella macreta Horváth	-	Lygaeidae	Hemiptera	grasses		Slater 1976 1991	"often common in seed heads" (Slater 1991); "appears to feed on a number of grasses even when they are completely dry" (Slater 1976 p. 135)
Anzac bipunctatus (Fabricius)	-	Membracidae	Hemiptera	collected on grasses		Evans 1966	
Euciodes suturalis Pascoe	larva	Anthribidae	Coleoptera	*_Arrhenatherum elatius_, *_Bromus_ sp., *_Dactylis glomarata_, *_Festuca arundinacea_,*_Holcus lanatus_	stems	Penman 1978, May 1994, Kuschel 1972, Holloway 1982	New Zealand host records, no published Australian data (Zimmerman 1994a)
Hispellinus	larva adult	Chrysomelidae	Coleoptera	_Themeda_	leaves	Jolivet & Hawkeswood 1995	
Hispellinus australicus (Motschulsky)	larva	Chrysomelidae	Coleoptera	grasses	leaves	Matthews &Reid 2002	larva is a leafminer
Oulemma spp.	larva	Chrysomelidae	Coleoptera	native and introduced grasses	leaves	Matthews &Reid 2002	
Rupilia spp. ?	larva	Chrysomelidae	Coleoptera	grasses	prob leaves	Matthews &Reid 2002	hosts unclear. _Eulali_a in Central Australia
Steriphus caudata (Pascoe)	larva	Curculionidae	Coleoptera	*cereals and pastures	seeds, seedling stems, tiller bases	Allsopp & Hitchcock 1987	in cereals "larvae eat out the swelling seeds .. bore into the underground part of the stem ... tillers may be affected without the plant dying" (Allsopp & Hitchcock 1987 p. 60). Wide host range outside Poaceae.
*_Graphognathus leucoloma_ (Boheman)	larva, adult	Curculionidae	Coleoptera	wild grasses, *maize		Allsopp & Hitchcock 1987	"Adult weevils chew the foliage of most plants but rarely cause economic damage" (Allsopp & Hitchcock 1987 p. 51); wide host range outside Poaceae
*_Listronotus bonariensis_ (Kuschel)	larva	Curculionidae	Coleoptera	*_Zea mays_, *_Lolium_	stem-miner	May 1994	New Zealand
Cubicorhynchus spp.	larva adult	Curculionidae	Coleoptera	native and introduced grasses	roots, stems	Zimmerman 1993	
Cubicorhynchus calcaratus Macleay	larva adult	Curculionidae	Coleoptera	?_Austrostipa_		Zimmerman 1993	found in a clump of "_Stipa_"
Cubicorhynchus crenicollis Waterhouse	larva	Curculionidae	Coleoptera	unidentifed grass		May 1994	

Table A2.1 (continued)

Species	**Life stage**	**Family**	**Order**	**Host**	**Host tissue**	**References**	**Notes**
Cubicorhynchus sordidus Ferguson		Curculionidae	Coleoptera	***Nassella trichotoma*** and “some other grasses”	roots, stems	Zimmerman 1993	
Cubicorhynchus taurus Blackburn	larva	Curculionidae	Coleoptera	*Austrostipa nitida*, *A. nodosa*, *Enneapogon nigricans*, *Eragrostis eriopoda*, unidentified grasses		Zimmerman 1993, May 1994	possibly restricted to semiarid grasslands
*_Floresianus sordidus_ Hustache		Curculionidae	Coleoptera	Poaceae		May 1994	?insect found in SE Aust.
*_Linogeraeus urbanus_ (Boheman)	larva adult	Curculionidae	Coleoptera	*_Paspalum distichum_	roots, stolons	May 1994	as *Paspalum paspaloides* (sic); ?insect found in SE Aust.
Maleuterpes spinipes Blackburn	larva	Curculionidae	Coleoptera	grass	roots	May 1994	main hosts Rutaceae; ?insect found in SE Aust.
Phalidura abnormis (Macleay)	larva adult	Curculionidae	Coleoptera	***Nassella trichotoma***		Zimmerman 1993, May 1994	
Phalidura elongata (Macleay)	larva	Curculionidae	Coleoptera	***Nassella trichotoma*** and “other grasses”	underground parts	Zimmerman 1993, May 1994	
Sclerorinus sp.		Curculionidae	Coleoptera	“*Stipa* sp.”		May 1994	
*_Sphenophorus brunnipennis_ (Germar)		Curculionidae	Coleoptera	*_Pennisetum clandestinum_ and *“bent grass”	basal nodes, crowns, stolons	May 1994	?insect found in SE Aust.
-	larva	Elateridae	Coleoptera	grasses etc.		Gregg 1997	damage seedlings
Agrypnus and *Hapatesus* spp., wireworms	larva	Elateridae	Coleoptera	*wheat, *arley, *oats, *sugar cane, *maize, *sweet corn, *sorghum		Allsopp & Hitchcock 1987, Calder 1996	“Grasslands and pasture are the natural habitat ... sporadic ... pests of newly-sown cereals” (Allsopp & Hitchcock 1987 p. 44)
Arachnodima bribbarensis (Calder) & *A. xenikon* (Calder)	larva	Elateridae	Coleoptera	*_Triticum aestivum_	seeds, seedlings	Calder1996	larvae “attack germinating wheat seeds and seedlings” (Calder 1996 p. 139)
Arachnodima ourapilla (Calder)	larva	Elateridae	Coleoptera	*_Triticum aestivum_		Calder1996	“attacks wheat crops” (Calder 1996 p. 139)
Arachnodima opaca Candèze	larva	Elateridae	Coleoptera	**_Hordeum vulgare_.		Calder1996	“attacks barley crops” (Calder 1996 p. 139)
Dicranolaius bellulus (Guérin-Méneville)/*D. cinctus* (Redtenbacher)	adult	Melyridae	Coleoptera	aquatic grasses, *rice	flowers, seeds	Hely 1958, Booth *et al.* 1990	normal foods of adults are flowers of sedges, rushes, and aquatic grasses “of the millet type” (Hely 1958 p. 30)
Mordellistena spp.	larva	Mordellidae	Coleoptera	grasses	stems	Booth *et al.* 1990	no Australian grass host records located
Melolonthinae - various	larva	Scarabaeidae	Coleoptera	pasture grasses	roots	Allsopp & Hitchcock 1987	
Melolonthinae: Scitalini - various	larva	Scarabaeidae	Coleoptera	probably grasses	roots	Britton 1987	
Adoryphorus couloni (Burmeister)	larva	Scarabaeidae	Coleoptera	grasses	roots	Blackburn 1983, Hill *et al*. 1993, McQuillan & Webb 1994Gregg 1997	“Pasture species that form a shallow-rooted turf (for example Yorkshire fog, barley grass and perennial ryegrass) are more susceptible to attack” (Blackburn 1983 p. 3); “reduce the productivity and persistence of perennial pastures” (McQuillan & Webb 1994 p. 49)
Antitrogus spp.	larva	Scarabeidae	Coleoptera	grasses and other plants	roots	Allsopp 2003	
Aphodius tasmaniae Hope	larva	Scarabaeidae	Coleoptera	grasses	foliage	Allsopp & Hitchcock 1987, Panetta *et al*. 1993, Gregg 1997	
Chlorochiton sp.	larva	Scarabaeidae	Coleoptera	***Nassella trichotoma***	roots	Lowe 1954	New Zealand sp., large patches killed in NZ
*_Cyclocephala signaticollis_ Burmeister	larva	Scarabaeidae	Coleoptera	pasture and lawn grasses	roots	Carne 1956	most abundant in *Cynodon dactylon* and *Paspalum dilatatum* swards (Carne 1956)

Table A2.1 (continued)

Species	Life stage	Family	Order	Host	Host tissue	References	Notes
**Heteronychus arator* (Fabricius),	larva adult	Scarabaeidae	Coleoptera	mainly damages grasses, larvae on matt-forming grasses incl. *kikuyu, *paspalum; *maize, *sweet corn, lawns, pastures	roots, rhizomes, shoots, felled heads	Allsopp & Hitchcock 1987, Panetta *et al.*1993, Gregg 1997	larvae on roots, adults on shoots or chew holes in stems of young plants
Saulostomus villosus Waterhouse	larva	Scarabaeidae	Coleoptera	damages pastures and turf	roots	Hardy 1976a	the soil-dwelling larvae "feed on plant material including roots" (Hardy 1976a p. 282)
Scitala sericans Erichson	larva	Scarabaeidae	Coleoptera	damages pastures	roots	Hardy 1976b, Allsopp & Hitchcock 1987	
Sericesthis consanguinea (Blackburn)	larva	Scarabaeidae	Coleoptera	*wheat, *oats	roots	Allsopp & Hitchcock 1987	
Sericesthis geminata Boisduval	larva	Scarabaeidae	Coleoptera	grasses, including **Lolium perenne*	roots	Carne & Chinnick 1957, Wensler 1971, Allsopp & Hitchcok 1987, Panetta *et al.*1993, Gregg 1997	"after entering the third instar ... the larvae confine their feeding to the roots of grasses" (Carne & Chinnick 1957 p. 608); "prefer grasses over broad-leaf plants" (Allsopp & Hitchcock 1987 p. 20); "feed upon young roots" (Britton 1987 p.687).
Sericesthis harti Sharp	larva	Scarabaeidae	Coleoptera	*cereals	roots	Allsopp & Hitchcock 1987	
Sericesthis nigrolineata (Boisd.)	larva	Scarabaeidae	Coleoptera	grasses, incl. **Lolium perenne*	roots	Ridsdill-Smith 1975, Hardy 1976b, Allsopp & Hitchcock 1987, Britton 1987, Gregg 1997	"larvae preferentially select and feed on living roots" (Ridsdill-Smith 1975 p. 75); "feed upon young roots of grasses" (Britton 1987 p.687)
-	larva	Tenebrionidae	Coleoptera	grasses etc.		Gregg 1997	damage seedlings
Helea, Pterohelaeus, *Gonocephalum*, *Isopteron* and *Saragus* spp.	larvae, adults	Tenebrionidae	Coleoptera	*cereals, incl. **Triticum aestivum*	seeds, seedlings	Allsopp & Hitchcock 1987, Matthews & Bouchard 2008	larvae damage seed and seedlings before emergence, adults usually eat the seedling at ground level; *Pterohelaeus* are "major root and seedling pests", *Isopteron* "recorded feeding on geminating wheat" (Matthews & Bouchard 2008)
-	larva	Agromyzidae	Diptera	grasses, *rice	leaves, stems	Wapshere 1990, Colless & McAlpine 1991, Hely 1958	Europe (Wapshere 1990). Rice leaf miner (Hely 1958). Leaf and stem miners, gall makers
Asphondylini sp.	larva	Cecidomyiidae	Diptera	*Themeda triandra*	spikelets	McDougall 1989	undescribed sp., prob a new genus (Robin Adair, pers. comm. 2006)
	larva	Cecidomyiidae	Diptera	*Austrostipa* spp.	spikelets	Yen 1999	"may ... be the same species" as on *T. triandra* (Yen 1999)
-	larva	Cecidomyiidae	Diptera	*Andropogon*		Boucek 1988 p. 561	gall former
-	larva	Cecidomyiidae	Diptera	grasses	stems	Boucek 1988, Wapshere 1990	Europe (Wapshere 1990)
bloodworms, ?*Chironomus tepperi* Skuse	larva	Chironomidae	Diptera	*rice	?roots	Hely 1958, Colless & McAlpine 1991	"failure of seedling development" (Hely 1958 p. 31), mainly physical disturbance to roots (Colless & McAlpine); may similarly effect other grasses in submerged situations
-	larva	Chloropidae	Diptera	grasses	shoots and stems	Colless & McAlpine 1991	inside young growth; may be largely bacteria-feeders
Hydrellia spp.	larva	Ephydridae	Diptera	*rice, *barley, *irrigated cereals	leaves, stems	Mathis 1989	

Table A2.1 (continued)

Species	Life stage	Family	Order	Host	Host tissue	References	Notes
Atherigona spp., shoot flies	larva	Muscidae	Diptera	grasses, *cereals	shoots	Pont 1989	"primary pests"
-	larva	microlepidoptera	Lepidoptera	grasses		Wapshere 1990	Europe
Anthela basigera (Walker)	larva	Anthelidae	Leidoptera	grasses	foligage	Marriott 2008	
Anthela denticulata (Newman)	larva	Anthelidae	Leidoptera	grasses,*cereals; *_Triticum aestivum_	foliage	French 1911, Common 1990, Edwards & Fairey 1996 , Marriott 2008	
Anthela euryphrica Turner	larva	Anthelidae	Leidoptera	grasses; causes periodic damage to crops	foliage	Common 1990; Edwards & Fairey 1996	
Anthela ferruginosa Walker	larva	Anthelidae	Lepidoptera	grasses, *cereals	foliage	Common 1990	
Anthela ocellata (Walker)	larva	Anthelidae	Lepidoptera	grasses, *cereals	foliage	French 1911, Common 1990, Marriott 2008	"frequently found feeding on grasses in gardens" (Common 1990)
				various introduced grasses, *_Ehrharta erecta_	foliage	Coupar & Coupar 1992	
Anthela oressarcha Turner	larva	Anthelidae	Leidoptera	grass	foliage	Common 1990	
Anthela ostra Swinhoe	larva	Anthelidae	Leidoptera	causes periodic damage to crops	foliage	Edwards & Fairey 1996	? grass feeder; ?insect found in SE Aust.
Pterolocera spp.	larva	Anthelidae	Lepidoptera	grasses; periodic damage to native pastures	foliage	Common 1990, Edwards & Fairey 1996, Marriott 2008	larvae "accept _Poa_ spp. and many introduced grasses" (Marriott 2008); also "clover and low growing shrubs" (Common 1990)
Synemon plana Walker	larva	Castniidae	Lepidoptera	_Austrodanthonia laevis_	roots	Common 1990	See general discussion on _Synemon_ spp.
-	larva	Elachistidae	Lepidoptera	grasses	leaf and stem miners	Wapshere 1990, Nielsen & Common 1991	Europe, Australia
Cosmiotes synethes (Meyrick)	larva	Elachistidae	Lepidoptera	grasses, *_Bromus catharticus_, *_Triticum aestivum_	leaf miner	Common 1990, Nielsen & Common 1991	"larva produces an elongate blotch mine" (Common 1990)
Fraus simulans Walker	larva	Hepialidae	Lepidoptera	grasses		Allsopp & Hitchcock 1987	feeds "mostly on grasses"
Oncopera spp.	larva	Hepialidae	Lepidoptera	grasses	roots, stems, leaves	Chadwick 1966, Allsopp & Hitchcock 1987, Common 1990, Gregg 1997, Edwards 2002	"prefer grasses, especially reyegrass" (Gregg 1997); "Young larvae ... feed on the roots and leaves of young grasses" (Allsopp & Hitchcock 1987 p. 74). Larve "feed on the bases of snow grass tussocks" (Edwards 2002 p. 61). Stem and blade-base most damaging (Chadwick 1966)
Oncopera alboguttata Tindale	larva	Hepialidae	Lepidoptera	**_*Nassella trichotoma_**	foliage	Campbell 1998	killed small areas
Oncopera alpina Tindale	larva	Hepialidae	Lepidoptera	_Poa_ "_australis_", _Poa_ spp. snowgrasses	tussock bases and roots?	Carr & Turner 1959, Chadwick 1966, Allsopp & Hitchcock 1987, Common 1990,	"extensive patch death" in Australian Alps (McDougall &Walsh 2007); "damage to the aerial parts of the tussocks is slight" (Carr & Turner 1959 p. 20).
Oncopera fasciculatus (Walker)	larva	Hepialidae	Lepidoptera	grasses and other pasture plants, annual grasses, *_Phalaris_, *_Dactylis glomerata_	foliage	Madge 1954, Erlich 1980, Allsopp & Hitchcock 1987	"eat new green pasture as it appears ... larger numbers ... eat both new green feed and old dry pasture", mature _Phalaris_ tussocks little damaged, _D. glomerata_ tussocks killed (Madge 1954 p. 193)

Table A2.1 (continued)

Species	Life stage	Family	Order	Host	Host tissue	References	Notes
Oncopera intricata Walker	larva	Hepialidae	Lepidoptera	grasses	foliage	French 1909, Allsopp & Hitchcock 1987	"the most destructive of all grass-eating grubs known to myself" French (1909 p. 103)
Oncopera rufobrunnea Tindale	larva	Hepialidae	Lepidoptera	***Nassella trichotoma***, grasses	foliage, stems	Campbell 1998, Gregg 1997, Common 1990, Allsopp & Hitchcock 1987, Hill *et al.* 1993	killed small areas of *N. trichotoma* (Campbell 1998); "widely distributed in native and sown pastures in Tasmania" (Common 1990)
Oncopera tindalei Common	larva	Hepialidae	Lepidoptera	grasses	foliage	Allsopp & Hitchcock 1987	
Oxycanus antipoda (Herrich-Schäffer)	larva	Hepialidae	Lepidoptera	grasses	foliage	Erlich 1980, Common 1990	
Oxycanus fuscomaculatus Walker	larva	Hepialidae	Lepidoptera	grasses	foliage	Allsopp & Hitchcock 1987	"Grasses are the favoured food" (Allsopp & Hitchcock 1987 p. 76)
Dispar compacta (Butler)	larva	Hesperiidae	Lepidoptera	*Poa tenera*, *Poa* sp.	foliage	Braby 2000	
Herimosa albovenata (Waterh.)	larva	Hesperiidae	Lepidoptera	*Austrostipa scabra*, *A. semibarbata,* ?*Austrodanthonia setacea*	foliage	Braby 2000	
Ocybadistes flavovitta (Latreille)	larva	Hesperiidae	Lepidoptera	Poaceae	foliage	Braby 2000	
Ocybadistes walkeri Heron	larva	Hesperiidae	Lepidoptera	**Cynodon dactylon*, **Ehrharta erecta*, **Lolium* sp, **Pennisetum clandestinum*	foliage	Braby 2000	
Taractrocera papyria (Boisduval)	larva	Hesperiidae	Lepidoptera	*Austrodanthonia* sp., *Austrostipa scabra*, **Cynodon dactylon*, *Microlaena stipoides*, *Poa* sp., **Ehrharta* spp., **Paspalum dilatatum*, **Pennisestum clandestinum*	foliage	Braby 2000	
-	larva	Noctuidae	Lepidoptera	*Themeda triandra*	leaves	Wainer 1992	larval gut contents in *Delma impar* faecal pellets, Derrimut, Vic.
Agrotis infusa (Boisduval)	larva	Noctuidae	Lepidoptera	grasses, **Hordeum vulgare*, **Triticum aestivum*		Common 1990, Gregg 1997	cut through stems;"omnivorous ... all kinds of ... crops, fodder, and grass" (Froggatt 1910)
				**Hordeum vulgare*, **Triticum aestivum*		Coupar & Coupar 1992	
Agrotis munda Walker,	larva	Noctuidae	Lepidoptera	grasses, *cereals, **Hordeum vulgare*, **Zea mays*		Common 1990, Gregg 1997	cut through stems (Gregg 1997)
Agrotis ypsilon (Hufnagel)	larva	Noctuidae	Lepidoptera	**Zea mays*.		Common 1990, Gregg 1997	cut through stems
Bathytricha truncata (Walker)	larva	Noctuidae	Lepidoptera	grasses incl. **Oryza sativa*, **Zea mays*, **Paspalum dilatatum,* **Triticum aestivum*	stems	Common 1990	usually grass stem borers
Dasygaster padockina (Le Guillou)	larva	Noctuidae	Lepidoptera	native and introduced grasses, *cereals, **Triticum aestivum*		Common 1990	
Helicoverpa armigera (Hűbner)	larva	Noctuidae	Lepidoptera	**Sorghum*, **Zea mays* L.	heads	Common 1990	
Helicoverpa punctigera (Walleng.)	larva	Noctuidae	Lepidoptera	**Sorghum*, **Zea mays* L.	heads	Common 1990	
Heliocheilus cramboides Guenée	larva	Noctuidae	Lepidoptera	*Sorghum intrans*	seedhead	Matthews 1999	
Heliocheilus eodora Meyrick	larva	Noctuidae	Lepidoptera	*Eulalia aurea*	seedhead	Matthews 1999	
Heliocheilus pallida Butler	larva	Noctuidae	Lepidoptera	*Dichanthium tenuiculum*	seedhead	Matthews 1999	

Table A2.1 (continued)

Species	**Life stage**	**Family**	**Order**	**Host**	**Host tissue**	**References**	**Notes**
Metopiora sanguinata (Luc.)	larva	Noctuidae	Lepidoptera	grasses		Common 1990	
Mocis frugalis (Fabricius)	larva	Noctuideae	Lepidoptera	grasses, *_Avena sativa_		Common 1990	
Mythimna convecta (Walker)	larva	Noctuidae	Lepidoptera	_Astrebla pectinata_	leaves	McDonald 1991	
				grasses, *cereals, *graminaceous forage crops, *_Avena_, *_Hordeum_ (barley), *_Oryza sativa_, *_Setaria_, *_Triticum aestivum_, *_Zea mays_	seed heads, foliage, stems	Common 1990, Goodyer 1983, Gregg 1997	eat or sever flower heads (Goodyer 1983)
Mythimna separata (Walker)	larva	Noctuidae	Lepidoptera	grasses, *cereals, *_Saccharum officinarum_, pastures and crops		Common 1990, Goodyer 1983	
Neocleptria punctifera (Walker)	larva	Noctuidae	Lepidoptera	*_Triticum aestivum_, *_Zea mays_		Common 1990	highly polyphagous, many families
Numichtis nigerrima (Guen.)	larva	Noctuidae	Lepidoptera	*_Zea mays_		Common 1990	highly polyphagous
Persectania dyscrita Common	larva	Noctuidae	Lepidoptera	pastures and crops, *_Triticum aestivum_		Goodyer 1983, Common 1990	
Persectania ewingii (Westwood)	larva	Noctuidae	Lepidoptera	pasture grasses, primarily grasses; *cereals and *graminaceous forage crops, *_Avena_, *_Hordeum_ (barley), *_Triticum aestivum_	seed heads, foliage, stems	Schroder 1983, Goodyer 1983, Common 1990, Gregg 1997	eat or sever flower heads (Goodyer 1983)
Proteuxoa spp.	larva	Noctuidae	Lepidoptera	native and introduced grasses	foliage	Common 1990	
Proteuxoa sanguinipuncta (Guen.)	larva	Noctuidae	Lepidoptera	native and introduced grasses	foliage	Common 1980	
Spodoptera exempta (Walker)	larva	Noctuidae	Lepidoptera	grasses, grass pastures, *cereals, _Urochloa mutica,_ *_Sorghum_, *_Paspalum dilatatum_, *_Pennisetum clandestinum_		Goodyer 1983, Common 1990	_U. mutica_ is present in NC NSW
Spodoptera exigua (Hubner)	larva	Noctuidae	Lepidoptera	pastures and crops, *_Oryza sativa_, *_Sorghum_, *_Zea mays_		Goodyer 1983, Common 1990	found in NSW (Goodyer 1983)
Spodoptera litura (Fabricius),	larva	Noctuidae	Lepidoptera	_Urochloa mutica_		Common 1990	_Brachiaria_ the old name? Plant on NC NSW
Spodoptera mauritia (Boisduval)	larva	Noctuidae	Lepidoptera	grasses, *cereals, pastures, lawns, *_Cynodon dactylon_, *_Pennisetum clandestinum_, *_Sorghum_	leaves	Goodyer 1983, Common 1990, Gregg 1997	found north from N NSW (Common 1990)
Argynnina hobartia (Westwood)	larva	Nymphaliidae	Lepidoptera	*_Lolium perenne_	foliage	Braby 2000	"probably ... native grasses such as _Poa labillardieri_ and _Austrodanthonia_" (Braby 2000 p. 491)
Geitoneura acantha (Donovan)	larva	Nymphalidae	Lepidoptera	native grasses, _Themeda triandra_, _Poa_ spp., _Microlaena stipoides_	foliage	Coupar & Coupar 1992	
Geitoneura klugii (Guérin-Méneville)	larva	Nymphalidae	Lepidoptera	native grasses, _Microlaena stipoides, Austrostipa flavescens_, _Joycea pallida_, _Poa labillardieri_, _P. morrisii_, _P.tenera_, _T. triandra_, *_Brachypodium distachyon_, *_Ehrharta calycina_, *_Vulpia_ sp.	foliage	Coupar & Coupar 1992, Braby 2000	
Heteronympha merope (Fabricius)	larva	Nymphalidae	Lepidoptera	native and introduced grasses, *_Lolium perenne_, *_Cynodon dactylon_, _Microlaena stipoides_, _Poa poiformis_, _P. tenera_, _Themeda triandra_, *_Brachpodium distachyon_, *_Bromus catharticus_, *_Ehrharta erecta_	foliage	Coupar & Coupar 1992, Braby 2000	

Table A2.1 (continued)

Species	**Life stage**	**Family**	**Order**	**Host**	**Host tissue**	**References**	**Notes**
Heteronympha penelope Waterh.	larva	Nymphalidae	Lepidoptera	_Austrodanthonia penicillata_, _Austrodanthonia pilosa_, _Poa_ sp., _Poa_ snowgrass, _Themeda triandra_	leaves	Braby 2000	butterfly not a grassland sp. Sources: Jarvis 1908, Tindale 1952a, Common & Waterhouse 1981
Hypocysta metirius Butler	larva	Nymphalidae	Lepidoptera	_Alexfloydia repens_, *_Cynodon dactylon_,	leaves	Braby 2000	source for _C. dactylon_ E.O. Edwards 1948
Oriexenica ptunarra L.E. Couchman	larva	Nymphaliidae	Lepidoptera	_Poa gunnii_, _P. labillardieri_, _P. rodwayi_	foliage	Braby 2000	
Philobota productella (Walker), _P. chionoptera_ Meyrick, _P. diaereta_ Turner, _P. physaula_ Meyrick	larva	Oecophoridae	Lepidoptera	grasses	foliage, litter	Allsopp & Hitchcock 1987, Hill _et al._ 1993, Common 1990	plus "other herbaceous plants ... at times damage pastures" (Common 1990); "Foliage is cut and often left uneaten on the ground" (Allsopp & Hitchcock 1987 p. 80)
'Lomera' caespitosae Oke ("_Plutorectis_" _caespitosae_)	larva	Psychidae	Lepidoptera	_Poa_ Snow Grass, "_Poa australis_"	leaves, leaf lamina just above the sheath	Carr & Turner 1959, Chadwick 1966, Common 1990, Green & Osborne 1994, Edwards 2002	"feeds exclusively on snow grass", "heavily infested ... tussocks are completely cut through at the base and do not recover" (Carr & Turner 1959 p. 19). "Extensive patch death" in Australian Alps (McDougall &Walsh 2007). But damage confused with _Oncopera alpina_, which does most of the damage.
'Lomera' boisduvalii (Westwood)	larva	Psychidae	Lepidoptera	probably grasses		Common 1990	
'Lomera' spp.	larva	Psychidae	Lepidoptera	probably grasses		Common 1990	most other spp. probably feed on grasses.
Achyra affinitalis (Led.)	larva	Pyralidae	Lepidoptera	*_Sorghum_, *_Zea mays_		Common 1990	highly polyphagou – many families
Callamatropha leptogramella (Meyrick)	larva	Pyralidae	Lepidoptera	grasses, cereals, *_Paspalum_		Common 1990	"minor pasture pest"
Conogethes punctiferalis (Guen.)	larva	Pyralidae	Lepidoptera	*_Sorghum_, *_Zea mays_	heads	Common 1990	occurs S to N. NSW
Cnaphalocrocis medinalis (Guen.)	larva	Pyralidae	Lepidoptera	*_Oryza sativa_			
Culladia cuneiferellus (Walker)	larva	Pyralidae	Lepidoptera	grasses, *cereals, *_Cynodon dactylon_	leaves	Common 1990	grass both exotic and native, sometimes damages lawns
Hednota spp.	larva	Pyralidae	Lepidoptera	grasses, *cereals incl. wheat, barley and rye, *_Hordeum_ spp., *_Bromus_ spp., *_Vulpia_ spp.	foliage	Allsopp & Hitchcock 1987, Panetta _et al._ 1993, Gregg 1997	"minor pests of native grasses" (Gregg 1997); damage evident from "chopped off shoots" (Allsopp & Hitchcock 1987 p. 78)
Hednota bivitella (Don.), _H. crypsichroa_ Lower, _H. longipalpella_ (Meyrick), _H. panteucha_ (Meyrick), _H. pedionoma_ (Meyrick), _H. pleniferellus_ (Walker)	larva	Pyralidae	Lepidoptera	grasses		Allsopp & Hitchcock 1987, Common 1990	larvae in silk galleries in crowns or surface soil
Herpetogramma licarsisalis (Walk.)	larva	Pyralidae	Lepidoptera	grasses, *cereals, *_Paspalum_, *_Pennisetum clandestinum_	leaves	Common 1990	lawn and pasture pest, S to N NSW
Mampava rhodoneura (Turn.)	larva	Pyralidae	Lepidoptera	*_Cenchrus ciliaris_	seed	Common 1990	insect in C Qld (Common 1990 p. 348) ; ?both plant and insect in SE Aust.
Marasmia venilialis (Walker)	larva	Pyralidae	Lepidoptera	grass		Common 1990	larva in rolled leaf shelter
Sclerobia trialis (Walker)	larva	Pyralidae	Lepidoptera	*_Cynodon dactylon_	leaves	Common 1990	_C. dactylon_ is both exotic and native; "minor pasture pest ...also damages lawns"
Eretmocera dioctis (Meyr.)	larva	Scythrididae	Lepidoptera	*_Chloris gayana_, _Enteropogon acicularis_		Common 1990	insect at least in N NSW (Common 1990 p. 266)
-	larva	Tineidae	Lepidoptera	grasses		Common 1990	larvae of some spp. "tunnel in the soil and feed on grass" (Common 1990 p. 183); however true phytophagy is "very rare" and generally facultative (Robinson & Nielsen 1993 p. 25)

Table A2.1 (continued)

Species	**Life stage**	**Family**	**Order**	**Host**	**Host tissue**	**References**	**Notes**
Nemapogon granella (L.)	larva	Tineidae	Lepidoptera	**Triticum aestivum*, **Hordeum vulgare*	seed	French 1900	
Crocidosema plegejana Zell.	larva	Tortricidae	Lepidoptera	**Triticum aestivum*.		Common 1990	highly polyphagous; "sometimes damage ears of wheat" in NSW and SA
Aprostocetus asperulus (Graham)	larva	Eulophidae	Hymenoptera	**Hyparrhenia hirta*		Boucek 1988	extralimital host record (Madiera), insect known from Brisbane, may be a parasite/ inquiline of another insect
Eurytoma spp.	larva	Eurytomidae	Hymenoptera	grasses	stems	Boucek 1988	normally develop with & consume *Tetramesa* spp.
Tetramesa spp.	larva	Eurytomidae	Hymenoptera	grasses	seeds, internodes	Boucek 1988, Wapshere 1990, Naumann 1991	3 Australian spp. associated with grasses (Naumann 1991); Wapshere: Europe, USA; pests of cereals elsewhere in the world
-	adult	Formicidae	Hymenoptera	grasses	seed	Gregg 1997	small, light seed readily taken, larger seeds are not
Pheidole spp.	adult	Formicidae	Hymenoptera	pasture grasses, *cereals, *sorghum	seed	Allsopp & Hitchcock 1987	"occasional pest sof newly-sown grass ... pastures and cereal crops, especially sorghum ... stands of annual grasses can also be severely reduced" (Allsopp & Hitchcock 1987 p. 91)
Ormocerinae	larva	Pteromalidae	Hymenoptera	Poaceae		Naumann 1991	"associated with galls especially on ... Poaceae"
Systasis	larva	Pteromalidae	Hymenoptera	grasses	seeds	Naumann 1991	"associated with grass seeds"
Systasis graminis (Cameron)	larva	Pteromalidae	Hymenoptera	*Panicum* sp.	seeds	Boucek 1988	

Nematodes of grasses and grasslands

Nematodes (Phylum Nematoda) constitute a vast, poorly explored taxon and are "the most abundant multicellular animals on earth" (Baldwin *et al.* 2004 p. 84). As many as 500,000 species have been predicted to exist, of which only 10,000 were known in 1951 (Meglitsch 1972). Most are entirely free-living in soil, water, etc. and a comparitively small proportion are plant parasites (Baldwin *et al.* 2004). Many of the parasitic groups have free-living stages and there is a full suite of intermediate lifestyles from fully sedentary ecto- or endoparasitism to migratory endoparasitism (Siddiqi 1986, Baldwin *et al.* 2004). Many of the plant parasitic nematodes are ecto- or endo-parastites of grasses. Secretion products from plant parasistic species promote plant pathologies including nurse cells, root-knots and cysts specific to particular taxa, while some groups transmit viruses to their hosts (Baldwin *et al.* 2004). The order Tylenchida, commonly called plant nematodes, is the largest and most economically important group of plant parasites, and its members damage all plant organs including seeds, flowers and especially roots (Siddiqi 1986). However the orders Dorylaimida and Triplonchida also include plant parasites (Baldwin *et al.* 2004).

Johnston (1938) recorded numerous species from unidentified grasses in Australia, along with species that attack sugar cane and cereals, but no records from native grasses. McLeod *et al.* (1994) recorded 42 taxa from unspecified grass or grasses in Australia and listed the nematode species found on a wide range of other grasses in Australia.

In the Stipeae, *Anguina* sp. is recorded from *Austrostipa drummondii* (Steud.) Jacobs & Everett and *A. nitida* (Summerh. & C.E. Hubb.) Jacobs & Everett in Victoria, *A. trichophylla* (Benth.) Jacobs & Everett in Western Australia and from "*Stipa*" sp. in NSW, *Neodolichodorus adelaidensis* and *Xiphinema monhystereum* are recorded from "*Stipa*" sp. in South Australia, and *Pratylenchus neglectus* is recorded from *Austrostipa trichophylla* (Benth.) Jacobs & Everett in Queensland (McLeod *et al.* 1994).

No species were known from *Themeda triandra* in south-eastern Australia, but 19 species have been found associated with the plant in Queensland (McLeod *et al.* 1994). *Radopholus intermedius* Colbran was described from material taken from around the roots of *Allocasuarina torulosa* (Aiton) L. Johnson and *T. triandra*, and *R. laevis* Colbran has also been found in this situation (Colbran 1971). The genus *Radopholus* Thorne contains 22 root endoparasitic species all but one of which are indigenous to Australia (Siddiqi 1986).

Table A2.2. Literature records of the hosts of grass-inhabiting Nematoda recorded in south-eastern Australia. Grasses included are inhabitants or probably occur in temperate south eastern Australian grasslands. South-eastern Australia excludes Queensland. Nematodes recorded from unspecified grass or grasses are not included. The list is indicative only, since a large proportion of the distribution records are not from grasslands. All data from McLeod *et al.* (1994). Nematode family assignment from Siddiqi (1986).

Grass	Nematode	Family	Distribution
**Agrostis capillaris*	*Belonolaimus* sp.	Dolichodoridae	NSW
	Helicotylenchus dihystera	Tylenchidae	NSW
**Agrostis stoloniferea*	*Paratrichodorus lobatus*	?	NSW
	Paratylenchus nanus	Paratylenchidae	NSW
**Avena fatua*	*Paratylenchus* sp.	Paratylenchidae	Vic
**Avena sativa*	*Ditylenchus dipsaci*	Anguinidae	SA
	Heterodera avenae	Heteroderidae	NSW, SA, Vic
	Meloidogyne javanica	Meloidogynidae	NSW
	Paratylenchus neglectus	Paratylenchidae	SA, Vic
	Pratylenchus thornei	Pratylenchidae	SA
	Pratylenchus sp.	Pratylenchidae	Vic
	Scutellonema brachyurum	Hoplolaimidae	NSW
Austrodanthonia caespitosa	*Paralongidorus sacchari*	?	SA
	Xiphinema monohysterum	Neotylenchidae	SA
Austrodanthonia setacea	*Paratylenchus* sp.	Paratylenchidae	SA
Austrostipa nitida	*Anguina* sp.	Anguinidae	Vic
**Bromus catharticus*	*Ditylenchus dipsaci*	Anguinidae	NSW
**Bromus* sp.	*Meloidogyne* sp.	Meloidogynidae	SA
**Chloris gayana*	*Meloidogyne incognita*	Meloidogynidae	NSW
**Cynodon dactylon*	*Belonolaimus lolii*	Dolichodoridae	NSW
	Criconema mutabilie	Criconematidae	SA
	Ditylenchus intermedius	Anguinidae	NSW
	Helicotylenchus dihystera	Tylenchidae	NSW
	Hemicriconemoides minor	Criconematidae	Vic
	Hemicycliophora labiata	Hemicycliophoridae	NSW, SA
	Hemicycliophora saueri	Hemicycliophoridae	Vic
	Hemicyliophora truncata	Hemicycliophoridae	NSW
	Heterodera graminis	Heteroderidae	NSW
	Heterodera sp.	Heteroderidae	NSW
	Macroposthonis sp.	Criocnematidae	Vic
	Morulaimus whitei	Dolichodoridae	Vic
	Paralongidorus eucalypti	?	Vic
	Paratrichodorus lobatus	?	NSW, SA
	Paratrichodorus minor	?	NSW
	Rotylenchus brevicaudatus	Hoplolaimidae	NSW
	Scutellonema brachyurum	Hoplolaimidae	NSW, SA

	Tylenchorhynchus annulatus	Dolichodoridae	Vic
	Tylenchorhynchus clarus	Dolichodoridae	SA
	Xiphinema americanum	Neotylenchidae	SA
	Xiphinema monohysterum	Neotylenchidae	Vic
**Digitaria sanguinalis*	*Scutellonema clariceps*	Hoplolaimidae	NSW
**Eragrostis cilianensis*	*Paratrichodorus lobatus*	?	SA
**Holcus lanatus*	*Anguina* sp.	Anguinidae	SA, Vic
	Pratylenchus penetrans	Pratylenchidae	Vic
**Hordeum leporinum*	*Heterodera avenae*	Heteroderidae	NSW, Vic
	Pratylenchus neglectus	Pratylenchidae	Vic
**Hordeum marinum*	*Pratylenchus neglectus*	Pratylenchidae	SA
Lachnagrostis filiformis	*Anguina* sp.	Anguinidae	NSW
**Lolium perenne*	*Heteodera avenae*	Heteroderidae	NSW, Vic
	Pratylenchus crenatus	Pratylenchidae	NSW
	Pratylenchus penetrans	Pratylenchidae	Vic
	Subanguina radicola	Anguinidae	Tas
	Xiphinema italiae	Neotylenchidae	NSW
	Xiphinema radicicola	Neotylenchidae	NSW
**Lolium rigidum*	*Anguina funesta*	Anguinidae	SA
	Heterodera avenae	Heteroderidae	SA, Vic
	Merlinus brevidens	Dolichodoridae	SA
	Pratylenchus neglectus	Pratylenchidae	SA
	Tylenchorhynchus clarus	Dolichodoridae	SA
**Lolium* sp.	*Longidorus elongatus*	?	SA
	Pratylenchus neglectus	Pratylenchidae	SA
	Pratylenchus thornei	Pratylenchidae	SA
Microlaena stipoides	*Anguina microlaenae*	Anguinidae	NSW, Vic
**Paspalum dilatatum*	*Heterodera graminis*	Heteroderidae	NSW
**Pennisetum clandestinum*	*Helicotylenchus dihytera*	Tylenchidae	NSW
	Paratrichodorus lobatus	?	NSW, SA
	Pratylenchoides leiocauda	Pratylenchidae	NSW
	Radopholus similis	Pratylenchidae	NSW
	Xiphinema americanum	Neotylenchidae	NSW
	Xiphinema ensicliferum	Neotylenchidae	NSW
	Xiphinema insigne	Neotylenchidae	NSW
**Poa annua*	*Belonolaimus lolii*	Dolichodoridae	NSW
	Subanguina radicicola	Anguinidae	Tas
Poa labillardieri	*Scutellonema* sp.	Hoplolaimidae	Vic
Poa sieberiana	*Hemicriconemoides minor*	Criconematidae	Tas
	Hemicylciophora truncata	Hemicycliophoridae	Tas
Poa sp.	*Criconema pasticum*	Criconematidae	Tas
	Pratylenchus coffeae	Pratylenchidae	NSW
**Polypogon monspeliensis*	*Anguina* sp.	Anguinidae	NSW, SA
"*Stipa*" sp.	*Anguina* sp.	Anguinidae	NSW
	Neodolichodorus adelaidensis	Dolichodoridae	SA
	Xiphinema monhystereum	Neotylenchidae	SA

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