The potential for classical biological control of invasive grass species with special reference to invasive *Sporobolus* spp. (Poaceae) in Australia

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Summary

Sporobolus africanus, *S. natalensis* and *S. pyramidalis* were accidentally introduced to Australia from Africa and have the potential to invade approximately 223 million hectares. Mechanical and chemical controls are largely ineffective and expensive, hence the search for potential biological control agents in southern Africa. Mycoherbicides are being used more widely today for the control of some invasive grass species in agricultural situations although no pathogen has been released as a classical biocontrol agent. Arthropods have been largely ignored as potential agents until very recently because it was assumed that the simple architecture of grasses and the lack of secondary compounds would militate against the evolution of monophagy. However, in recent surveys of *Phragmites australis* and *Calamagrostis epigejos* in Europe, some monophagous insect species have been found, and *Prokelisia marginata* (Delphacidae) has been released for the control of *Spartina alternifolia* on the west coast of the United States. Many *Tetramesa* spp. (Eurytomidae) are apparently monophagous and a species that has been reared from *S. pyramidalis* in South Africa is extremely damaging. A number of other damaging insects have been collected on these *Sporobolus* spp. but can only be considered as potential agents once they have undergone further trials. Many pathogens have also been collected, including a leaf rust (*Uromyces tenuicutis*), but a smut (*Ustilago sporoboli-indici*) appears to have the most potential. The biggest obstacle to the biological control of invasive *Sporobolus* spp. in Australia is the fact that there are 13 native *Sporobolus* spp., which will largely govern which agents can be selected for biocontrol. This paper considers the various factors which make grasses amenable to biological control and criteria used in the selection of agents, with particular reference to invasive *Sporobolus* species in Australia.

Keywords: grasses, pathogens, rust, smut, *Sporobolus.*

Introduction

Grasses cover more of the world's land surface than any other vegetation type. Grasses are the most important food crops in the world and are also utilized extensively for building materials, essential oils, ornamental plants, lawns and pastures. As a result, grass species have been introduced, either accidentally or intentionally, to many regions worldwide.

Species in the *Sporobolus indicus* complex, like *S. africanus* (Poir) Robyns & Tournay, *S. pyramidalis* P. Beauv. and *S. natalensis* (Steud.) Dur. & Schinz., were accidentally introduced to Australia from Africa and have subsequently become invasive, posing a major threat to the environment and livestock production. All of the introduced species are unpalatable to livestock and the carrying capacity of invaded pastures can be reduced by 10–80%, resulting in a potential loss of A$60 million per annum to the livestock industry in northern Australia (Department of Natural Resources and Mines 2001). It has been estimated that this complex of invasive species could invade approximately 223 million hectares (Department of Natural Resources and Mines 2001). Chemical and mechanical

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control measures have proved to be either ineffective, impractical or expensive, hence the search for potential biological control agents in southern Africa.

A number of potential agents have been found in surveys of *S. africanus*, *S. pyramidalis* and *S. natalensis* in South Africa, Swaziland and Botswana. In this paper, we report on progress towards the selection of control agents for this complex of *Sporobolus* spp. and comment more broadly on the selection of grasses as targets for biological control.

Sporobolus spp. taxonomy and biology

There are approximately 160 *Sporobolus* spp. in tropical and subtropical areas (Clayton & Renvoize 1986). Of the 21 *Sporobolus* species in Australasia, 13 are endemic (Simon & Jacobs 1999). However, the recognition of many of these species, especially those in the *S. indicus* complex, is difficult because of the morphological intergradation in the genus (Simon & Jacobs 1999). *Sporobolus pyramidalis*, *S. africanus* and *S. natalensis* are all known to hybridize, making field identification very difficult (Van Wyk & Van Oudtshoorn 1999).

Species in the *S. indicus* complex occur on all soil types and generally in areas with high rainfall (Van Wyk & van Oudtshoorn 1999). *Sporobolus pyramidalis* occurs throughout tropical Africa as well as Madagascar, Mauritius and Yemen while *S. africanus* and *S. natalensis* are found from southern Africa to East Africa as far north as Ethiopia (Van Wyk & van Oudtshoorn 1999). Weedy *Sporobolus* spp. can mature in as little as three months under favourable conditions (Department of Natural Resources & Mines 2001). Seed viability is 90–100%, with as many as 150,000 seeds/m^2 in infested pastures and a seed bank which may remain viable for as long as 10 years (Department of Natural Resources & Mines 2001).

Grasses as targets for biological control

According to Randall (2002), 18,146 plants species have become invasive worldwide. However, Randall (2002) has included 20,081 names which includes synonyms for various species. Of these 15,605 are dicotyledons, and 4476 are monocotyledons, of which 2176 are species in the family Poaceae. The exact figures are therefore smaller than those indicated but the ratio between monocotyledons and dicotyledons should remain fairly constant. The family with the greatest number of invasive species is the Asteraceae followed by the Poaceae and Fabaceae (Table 1) (Randall 2002). The top five species of weed worldwide, based primarily on the impact they have in agriculture in control costs and yield reduction (Holms *et al*. 1977), are in the Cyperaceae or Poaceae, with *Cyperus rotundus* L. being the worst weed worldwide (Holm *et al*. 1977).

To date, species in 40 plant families have been selected as targets for biological control (Julien & Griffiths 1998). Most are in the families Asteraceae (31 spp.), Cactaceae (23 spp.), Fabaceae (Mimosoideae, Caesalpinioideae, Papilionoideae) (19 spp.) and Rosaceae (4 spp.) (Julien & Griffiths 1998). Control programs have never been initiated against any species in the Poaceae until very recently and only two species in the Cyperaceae have had agents released for their control, despite the abundance of weedy species in these two families. This is possibly because grasses are perceived as lacking specific herbivores, and as being too similar in morphology, physiology and ecology to crop species (Gill & Blacklow 1984, Evans 1991). The apparent absence of host-specific arthropods has been ascribed to their simple structure and lack of secondary compounds, which reduces the evolution of monophagy (Evans 1991). This view was entrenched by surveys on *Imperata cylindrica* and *Cyperus rotundus* in the early 1970s (Simmonds 1972) and *Sorghum halepense* in northern Italy in the 1980s (Domenichini *et al*. 1989) which found that arthropods on these species were not sufficiently host specific and/or damaging. As a result, arthropods were widely discounted as potential control agents for grasses, with most attention focusing on the use of mycoherbicides (Evans 1991).

Table 1. The number of genera and species in each family classified as weeds by Randall (2002) together with the total number of species in each family (Mabberley 1997) and the percentage of weed species in each family.

Family	Genera	Species	Total species	% weeds
Asteraceae	1528	2373	22,750	10.4
Poaceae	668	2176	9,500	22.9
Fabaceae	643	2147	18,000	11.9
Cyperaceae	98	627	4,350	14.4
Rosaceae	95	550	2,825	19.5
Lamiaceae	251	497	6700	7.4

However, recent evidence would appear to suggest that even simple plants like grasses support large numbers of arthropods. A recent literature survey by Tewksbury *et al*. (2002) found more than 160 arthropod species associated with *Phragmites australis* (Cav.) Trin ex Steud. *Spartina alternifolia* Lois. has more than 24 arthropod species which have potential as biological control agents (F.S. Grevstad, University of Washington, pers. comm.) while *Calamagrostis epigejos* (L.) has 10 endophagous arthropod species (Dubbert *et al*. 1998). In any case, the number of species associated with a plant should not necessarily deter from its selection as a target species. Many simple plants like

Opuntia spp. and water weeds have been successfully controlled despite the fact that they have few arthropod species associated with them in their native ranges (Moran 1980, Julien & Griffiths 1998).

The fact that alkaloids are only present in less than 0.2% of grasses while other noxious terpenoids and chemical compounds are completely absent (McNaughton *et al*. 1985) should also not deter from their selection as target species. Recent evidence suggests that the role of plant toxicity in fostering monophagy has been overemphasized and that other explanations may be preferable (Futuyma & Keese 1992). Structural defences like trichomes, silica bodies and others may also play a role in driving monophagy in insects (Djamin & Pathak 1967).

Weed species with no closely related native species or crops are seen as better targets than weeds with native congeners (Pemberton 2000). Oligophagous species like *Cactoblastis cactorum* (Bergroth) and *Dactylopius opuntiae* (Cockerell) could be released against *Opuntia* spp. in South Africa because there are no native species in the Cactaceae and no closely related major crop species (Moran 1980). The family with the most species targeted for biological control, the Asteraceae (Julien & Griffiths 1998), contains no major crop species other than sunflower (Simmonds 1976). In contrast, the Poaceae which has no species targeted for biocontrol, has the highest percentage of weedy species and has more than 20 species of major crops, more than any other family (Simmonds 1976). Nevertheless, weed species have been selected as targets despite being closely related to major crops (Julien & Griffiths 1998). *Solanum elaeagnifolium* was selected as a target weed in South Africa despite there being many major crops in the same genus (Olckers *et al*. 1999). However, agents released for the control of invasive *Sporobolus* spp. in Australia will need to be extremely host specific to appease environmentalists because there are 13 (62%) endemic *Sporobolus* spp. in Australasia and two of these species are listed as rare and one as vulnerable in Queensland (Simon & Jacobs 1999).

Introduced invasive grass species may also be overlooked as biocontrol targets because they are not noticed in native grasslands, especially if they have many native congeners, and their impact is therefore seen as being negligible. Until the public can distinguish between native and introduced grasses and is made aware of the impact they have on native ecosystems, grasses will continue to be ignored unless a problem in agricultural situations.

Selection of biological control agents for grasses

According to Moran (1980), the arthropod complex on simple plants should be dominated by endophagous species, e.g. *Opuntia* spp. where 79% of the phytophagous species are borers (Lepidoptera and Coleoptera) (Moran 1980). Grasses, being simple plants, should therefore also be dominated by endophages. However, according to Tscharntke & Greiler (1995) grasses are dominated by ectophages, which is what we found on *Sporobolus* spp. in our surveys. However, in *P. australis*, there are virtually equal numbers of ectophages and endophages (Tewksbury *et al*. 2002), probably because the large culms provide niches for a large number of arthropods. Endophagous species are also abundant in other large semi-aquatic grasses like *S. alternifolia* and *C. epigejos*.

Unlike the situation in many dicotyledons, where the arthropod fauna is often dominated by species in the Coleoptera (Curculionidae and Chrysomelidae) (Syrett *et al*. 1996), grasses have a relatively poor beetle fauna (Tewksbury *et al*. 2002). Only eight beetle species have been collected on *P. australis* worldwide (Tewksbury *et al*. 2002). However, in smaller grasses, like *Sporobolus* spp. and *Nasella trichotoma*, beetles are relatively abundant, but the majority of these are generalist pollen feeders. Diptera (Agromyzidae, Chloropidae) are generally more common in grasses than in dicotyledons, with 32 species in the Chloropidae, most of them endophagous, collected on *P. australis* (Tewksbury *et al*. 2002). Herbivores with apparent specialization on *S. alternifolia* are mainly hemipterans with only 2 of the 24 arthropod species being coleopterans (Mordellidae, Curculionidae) (F.S. Grevstad, University of Washington, pers. comm.).

Host specificity of agents on grasses

Chewing insects on grasses are generally oligophagous (Bernays & Berbehenn 1987), but many other taxa are monophagous. There is a close association between many species in the Cecidomyidae and particular grass hosts (Barnes 1946) and many grass-feeding homopterans also have a small host range (Southwood & Leston 1959, Gibson 1976). Many stem-boring and stem-galling dipterans found in grasses have a limited host range (Nye 1959, Mowat 1974), with more than 20 monophagous chloropid species attacking *P. australis* (Tewksbury *et al.* 2002). Other families with a large number of monophagous species on *P. australis* are the Agromyzidae and Delphacidae, while species in the Pseudococcidae, Coccidae and Noctuidae are generally polyphagous (Tewksbury *et al.* 2002). Of the nine endophagous insects collected on *C. epigejos*, two are considered to be monophagous (Eurytomidae, Chloropidae) (Dubbert et al. 1998).

Many species in the Eurytomidae are known to be host specific. Martinez *et al*. (1999) found 18 different species of eurytomids in 10 sympatric species of grasses, with no species occurring in more than one species of grass. The position in which the larvae develop on the culm is also specific for many species (Boucek 1988) as demonstrated by the endophages on *C. epigejos* (Dubbert *et al*. 1998).

Many pathogens on grasses also only have a single host with head smuts and many rusts being extremely host specific (Valverde *et al*. 1999). The host specificity of biotrophic pathogens in general can be extremely narrow, sometimes being restricted to a particular biotype as demonstrated with the rust *Puccinia chondrillina* Bubak & Syd. released for the control of skeleton weed in Australia (Burdon *et al*. 1981). A pathogen that exhibits biotype selectivity within a single species should not infect plants from closely related species.

Level of damage caused by agents on grasses

Arthropods on grasses can be extremely damaging and result in the death of the attacked plant. A sap-sucker, *Prokelesia marginata* (Van Duzee) (Homoptera: Delphacidae), recently released for the control of *S. alternifolia* on the west coast of the United States, was placed in cages with *S. alterniflora* plants from Willapa Bay (Daehler & Strong 1997) and *S. anglica* plants from Puget Sound (Wu *et al*. 1999). Attacked plants from both species were severely stunted or died.

Although eurytomids are not known to kill plants they can reduce crop yields substantially. *Eragrostis teff* (Zucc.) Trotter was introduced to the United States where it was attacked by the stem-boring eurytomid *Eurytomocharis eragrostidis* (Howard),,, causing a reduction in forage yields of over 70% in one year (McDaniel & Boe 1990). Spears & Barr (1985) also found that *Tetramesa* spp. reduced seed weight in *Aristida longiseta* Steud., *Sitanion hystrix* (Nutt.) J.G. Smith, *Sporobolus cryptandrus* (Torr.) A. Gray and *Stipa comata* Trin. & Rupr. by 47, 33, 46 and 60%, respectively. This resulted in a reduction in seed germination for all four species with as many as 99% of seeds of *A. longiseta* not germinating (Spears & Barr 1985).

A stem-borer, *Tetramesa* sp. (Hymenoptera: Eurytomidae), collected on *S. pyramidalis*, *S. africanus* and *S. natalensis* in southern Africa, was also found to be damaging. Of 144 *S. pyramidalis* culms randomly collected at a particular site, 33% were infested with *Tetramesa* sp. larvae. The inflorescences of 60% of these infested culms were malformed. The culms of infested plants were also significantly shorter: 470 mm ($n = 48$) versus 656 mm ($n = 96$) df = 79, $t = –6.385$, $P < 0.001$).

Numerous pathogens damage cereal crops throughout the world, with smuts and rusts being particularly abundant. A smut, *Sporisorium ophiuri*, which is being considered for the control of *Rottboellia cochinchinensis* in Costa Rica, is very damaging and as a sole agent could reduce the density of itchgrass by 90%, with an annual infection rate of about 88% (Smith *et al*. 1997). This level of infection is unlikely to be achieved consistently, but indicates how damaging a smut can be. Infected plants have significantly fewer tillers and leaves and flower earlier than healthy individuals.

Of the five primary pathogens collected on the three *Sporobolus* spp., the smut *Ustilago sporoboli-indici* L. Ling appears to be the most promising agent. The other pathogens, a leaf rust (*Uromyces tenuicutis* McAlp.), tar spot (*Phyllachora sylvatica* Sacc. & Speg.), choke disease (*Parepichloë cinerea* Berk. & Br.) and ear blight (*Bipolaris crustacea* (Henn.) Alcorn) are already present in Australia (R. Shivas, Curator: Plant Pathology Herbarium, Queensland, Australia, pers. comm.) while the smut has only ever been recorded in parts of Africa, Asia and the Philippines (K. Vánky, pers. comm.). Research into the use of *B. crustacea* as a mycoherbicide found that it was not suitable anyway because of its low rates of infection and the timing of infection in relation to seed production (Hetherington & Irwin 1999).

Ustilago sporoboli-indici produces sori on the leaves and stems and usually prevents the production of an inflorescence. The disease appears to be systemic and usually all shoots of an infected plant are affected and sterile. In preliminary surveys, 10 randomly collected *S. pyramidalis* plants at each of five localities were separated into individual tillers, and only 6% (15/250) of infested tillers had inflorescences compared to 50% (547/1085) of uninfested tillers. The culms of infested tillers were also significantly shorter than uninfested tillers: 74.6 cm ($n = 15$) versus 101.8 cm ($n = 547$); df = 14, $t = 3.46$, $P < 0.002$. In transect surveys at five localities, an average of 54% (range = 15–70%) of grass clumps had at least one infested tiller.

Conclusions

There does not appear to be any valid reason why grasses should not be considered as targets for classical biological control programs. Recent surveys on a number of grass species clearly demonstrate that there are large number of arthropods, especially on large species, and that many of them are monophagous. We are optimistic that some of the agents we have selected as potential biocontrol agents for *Sporobolus* spp. will be both damaging and host specific.

Acknowledgements

Thanks to Drs R. Shivas and K. Vánky for assistance in field surveys, and to Drs W.A. Palmer, R. McFadyen, M.P. Hill, J.H. Hoffmann, C. Moran and colleagues in ARC–PPRI for valuable comments on the manuscript.

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