

Phylogenetics and the conservation and utilisation of *Acacia* in Western Australia

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SUMMARY

The genus *Acacia* is a dominant component of the Australian flora and many species have been identified as requiring conservation management, and as having potential for utilisation for a wide range of purposes. Phylogenetics is particularly valuable in the south-west of Western Australia where the complex evolutionary history has resulted in a diverse flora with both relictual and recently evolved components. Phylogenetic analysis contributes to conservation of plants through identification of unique evolutionary lineages, determination of phylogenetic value for conservation priority setting, and identifying phylogenetically independent comparisons between rare and widespread species. Phylogenetic analysis also contributes to utilisation of plants through the identification of genetic and taxonomic units, particularly for species complexes where variation is unresolved. The contribution of phylogenetic analysis to these aspects of effective conservation management and efficient utilisation strategies are discussed with examples from various *Acacia* species in Western Australia.

INTRODUCTION

The genus *Acacia* is a dominant component of the Australian flora and hence *Acacia* species predominate in conservation of the diverse Australian flora, particularly in south-west western Australia which is a centre of diversity for *Acacia* (Hopper and Maslin 1978). Acacias also have a dominant role in utilisation as they are adapted to a wide range of environments, and as such they have been extensively planted overseas (McDonald *et al.* 2001; Midgley and Turnbull 2002). Some species have also been utilised in Australia (McDonald *et al.* 2001) and several are important for commercial revegetation purposes in Western Australia (Byrne and Broadhurst 2002). Whilst genetic analysis in general makes an important contribution to conservation and management strategies, phylogenetic analysis in particular is valuable in south-west Western Australia in the conservation and management of a diverse flora that has been subject to evolutionary forces over long time frames resulting in both relictual and recently derived species (Hopper and Maslin 1978).

Phylogeny is the relationship between groups of organisms as reflected by their evolutionary history, and phylogenetics uses genetic data to determine evolutionary relationships at lower taxonomic levels such as between species and between populations within species. Phylogenetic analysis can contribute to the conservation and utilisation of flora in several ways. Below species level it can identify different genetic lineages with unique evolutionary histories as conservation management units or evolutionary significant units (ESU's) (Coates 2000; Ryder 1986). A knowledge of phylogenetic relationships

between species allows determination of the phylogenetic value (the degree of genetic distinctiveness) of species to assess priority for conservation activity (Byrne *et al.* 2001), and also enables appropriate comparisons to be made between rare and widespread taxa in assessment of their genetic diversity (Gitzendanner and Soltis 2000). A knowledge of phylogeny and the differentiation of genetic and/or taxonomic units is critical in the domestication of all species, but in particular for species complexes where genetic and morphological variation have not been resolved. Genetic studies of species for domestication have frequently found genetic differentiation within the species, which can be significant enough to identify separate entities requiring taxonomic revision, e.g. the tropical *A. aulacocarpa* (McGranahan *et al.* 1997; McDonald and Maslin 2000).

This review examines aspects of phylogenetics relevant to the conservation and utilisation of flora in Western Australia, especially in the south-west, with particular reference to understanding the evolutionary biology of *Acacia*.

PHYLOGENETICS AND EVOLUTIONARY HISTORY IN WESTERN AUSTRALIA

Unlike many areas of the world, the south-west of Western Australia has had a stable geological history with no major glaciation events (Hopper *et al.* 1996). The subdued landscape has no significant mountains and is dominated by a semi-arid zone between the high rainfall mesic region in the extreme south-west corner and the desert to the north and east (Hopper 2000). However, the area has

experienced climatic instability during the Pleistocene due to cyclic contraction and expansion of the arid and mesic zones, leading to a mosaic of habitats and edaphic complexity, particularly in the transitional semi-arid zone (Hopper *et al.* 1996). The area has a large, highly diverse flora characterised by both relictual taxa that have persisted through landscape stability and lack of glaciation, and more recently evolved components resulting from speciation in association with climatic oscillations (Hopper 1979, 2000). The complex mosaic of soil types and habitats has led to a high degree of natural isolation and fragmentation within the flora, causing significant local endemism and a high turnover of taxa across the landscape, affecting both relictual and recently evolved components.

The evolutionary history of the region would be expected to have had significant effects on the structuring of genetic diversity within the flora. In a naturally fragmented landscape many species persist in geographically restricted and disjunct distributions. Genetic studies using nuclear isozyme markers on Western Australian species that are rare and restricted, particularly those with disjunct distributions, have commonly revealed different genetic lineages (Coates 2000). Phylogenetic studies using chloroplast DNA (cpDNA) have confirmed the evolutionary distinctiveness of these lineages (Byrne *et al.* 1999, 2001), and indicate that genetic processes associated with historical eco-geographic barriers to gene flow may have led to the formation of distinct evolutionary lineages in many species. These evolutionary lineages often warrant separate conservation management (Soltis and Gitzendanner 1999) and should be treated as conservation management units or ESUs (Coates 2000). Identification of these lineages enables conservation action to be focused at this level where necessary, thus ensuring that the protection of distinct lineages is addressed. Evolutionary lineages may be present even in the absence of morphological differentiation (Byrne *et al.* 1999, Coates 2000). For example, populations of *Acacia anomala* that occur in two areas 30 km apart are genetically divergent and represent separate evolutionary lineages (Coates 1988). These populations also show differences in reproductive strategy, the northern populations reproducing sexually and the southern ones clonally.

In contrast, extensive gene flow between populations of species that are widely distributed would generally be expected to limit the geographic structuring in such species. Given the evolutionary history of south-west Western Australia, however, widespread species in the region may be expected to show some structuring in genetic diversity. Most studies of the nuclear genome of such species have revealed little genetic differentiation between populations (e.g. Byrne 1999; Byrne *et al.* 2002b; Hines and Byrne 2001) but phylogenetic studies using cpDNA have shown substantial differentiation in the chloroplast genome in these species (Byrne *et al.* 2002a; Byrne *et al.* 2002c; Byrne and Hines unpublished data). This is because analysis of the chloroplast genome can provide insights into the historical processes influencing population structure (Avise 2000; Schaal *et al.* 1998) since maternally inherited organelle markers retain information

about past population history in present day population structures (Ennos *et al.* 1999). The differentiation observed in the chloroplast genome in the widespread species in Western Australia indicates that they have also been affected by historical isolation and fragmentation as would be expected from the history of the region.

For example, *Acacia acuminata* is a widespread species complex that has three described taxa and several informal variants. Two of the described taxa have been treated as either separate species (*A. acuminata* and *A. burkittii*) or subspecies (Kodala and Tindale 1998; Maslin 2001). Here I follow the *Flora of Australia* treatment which ranks them as subspecies (Tindale and Kodala 2001). *Acacia acuminata* subsp. *acuminata* has broad phyllodes and compressed seeds and occurs in the south west of the distribution; subsp. *burkittii* has terete phyllodes and large globose seeds and occurs from the southern arid zone of Western Australia to western New South Wales (Maslin *et al.* 1999). The third taxon, *A. oldfieldii*, has striated pods and is restricted to the Moresby Range north of Geraldton. A variant with narrow phyllodes occurs between typical subsp. *acuminata* and subsp. *burkittii*, and a small-seeded variant occurs in the north of the species' distribution. A phylogenetic study of the *A. acuminata* complex revealed a very high level of diversity in the chloroplast genome and an unexpectedly high level of intra-population variation (Byrne *et al.* 2002c). The phylogeny of *A. acuminata* showed that the variation was not specific to taxa within the complex (Fig. 1), and the pattern of distribution of the variation suggests that the lack of congruence between taxa and cpDNA variation is caused by lineage sorting of ancestral polymorphisms rather than hybridisation, although ancient hybridisation may be a factor in the origin of a variant with narrow phyllodes. The phylogeny identified two separate lineages that were geographically based, the main lineage being distributed throughout the range of the species and the second restricted to the centre of the range. Nested clade analysis (Templeton *et al.* 1995) identified past fragmentation as the primary cause of the differentiation between the two lineages, which is consistent with climatic instability during the Pleistocene. Another species where significant differentiation in cpDNA has been observed is *A. verrucula* (Byrne *et al.* 2001), the southern population at Ravensthorpe being genetically divergent from the other populations sampled. The Ravensthorpe population occurs in an upland region of exceptional species richness and high endemism (Hopkins *et al.* 1983; Hopper *et al.* 1996), and it has been suggested that the divergence of the flora in this region has been influenced by geographic isolation following landscape dissection, combined with climatic fluctuation (Hopkins *et al.* 1983). The genetic divergence of the Ravensthorpe population identified by cpDNA analysis is consistent with this hypothesis (Byrne *et al.* 2001).

The association of phylogenetic lineages with geographic distribution is the basis of phylogeography. Such studies have also identified distinct, geographically separated lineages in the widespread York Gum, *Eucalyptus loxophleba*, (Byrne and Hines unpublished data) and

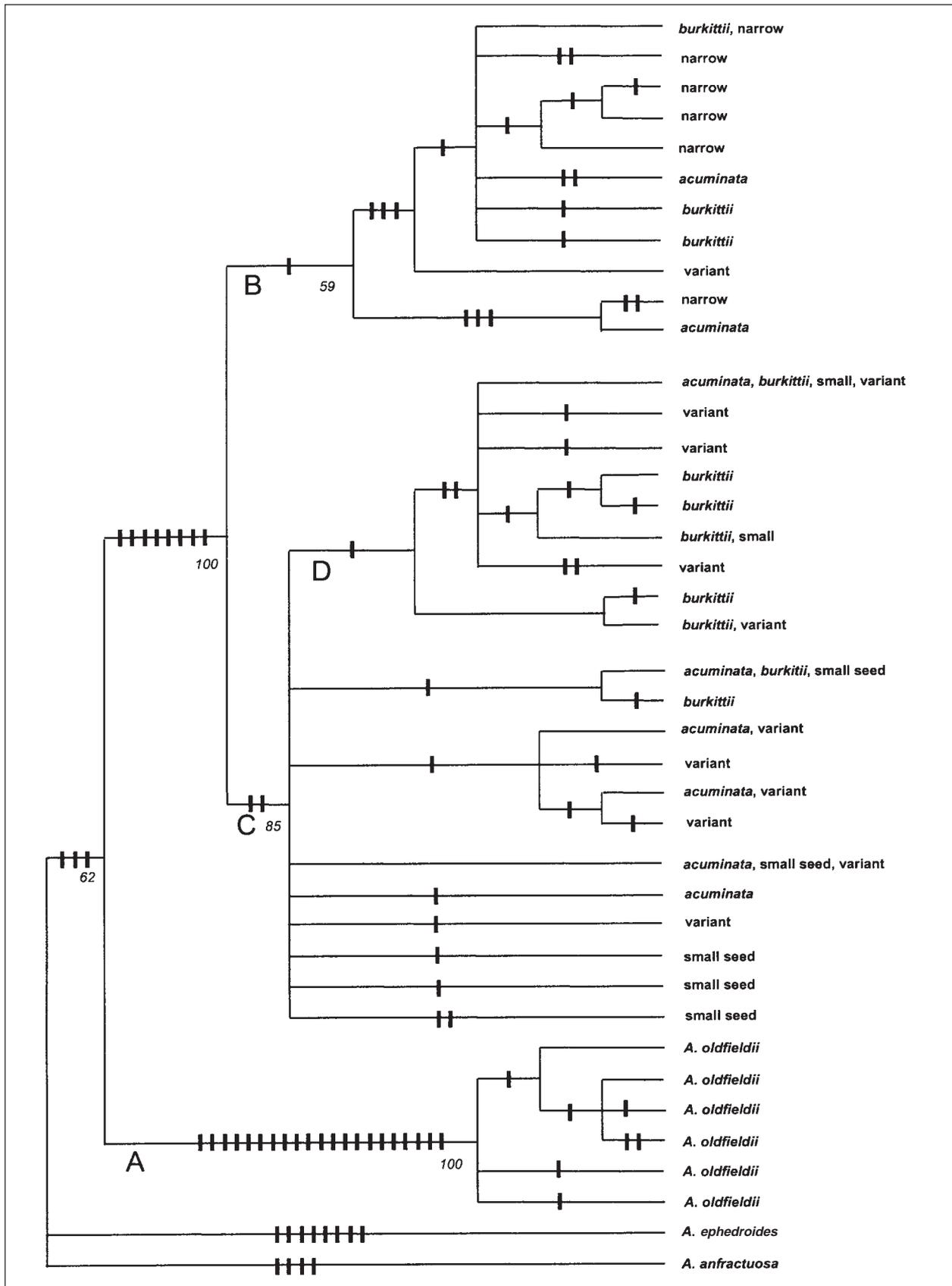


Figure 1. Phylogenetic parsimony tree of haplotype relationships in the *Acacia acuminata* complex including *A. oldfieldii*. Bars on lines represent mutations. Numbers below lines represent bootstrap confidence values (%). Letters at nodes represent major clades. Taxa to right of branches contain the haplotype on that branch. *Acacia ephedroides* and *A. anfractuosa* were used as the outgroups.

Sandalwood, *Santalum spicatum*, (Byrne *et al.* 2002a). Comparative phylogeographic studies such as these can identify major historical events that have had significant effects on the flora throughout the region. The identification of two lineages within all the widespread species so far studied suggests that there may have been contraction to broad refugial areas in the north and south of the south-west region. These refugial areas may not be as discretely defined as those resulting from periods of glaciation, as the climatic changes resulting from oscillations between the mesic and arid zones would not be expected to be as intense as during glaciation. However, the presence of distinct geographically located lineages suggests that the climatic changes have been significant enough to lead to isolation through range contraction in both the arid and mesic directions. The effects of historical isolation are still evident in the chloroplast genome, even though subsequent favorable climatic conditions have allowed range expansion of the lineages and established the widespread distributions present today.

PHYLOGENETIC RESOLUTION FOR CONSERVATION AND UTILISATION

Both efficient utilisation and effective conservation strategies rely on being able to identify, define and name specific units (Maslin this proceedings). A lack of understanding of taxonomic units and their genetic relationships hinders the utilisation and domestication of native species (Byrne and Broadhurst 2002), and conservation management activity is focused on taxonomic species since they are generally the primary units for conservation (Coates and Atkins 2001). The flora in south-west Western Australia contains many species complexes with a high degree of unresolved morphological variation. Resolution of taxonomic and genetic units within these complexes is important so that their commercial potential can be fully utilised and/or the conservation status of units appropriately recognised.

Currently three *Acacia* species complexes have commercial potential and are of interest for utilisation in agroforestry programs to address land degradation problems associated with salinity in Western Australia (Byrne and Broadhurst 2002). Resolution of the taxonomic and genetic units in these complexes is required for efficient domestication of the species so that selection for appropriate traits may be made from taxa displaying the desired characteristics (Byrne and Broadhurst 2002). One of these species complexes is *Acacia acuminata* which has three described taxa and several informal variants as described above. A combined genetic/taxonomic study was carried out to resolve the morphological variation present within the complex (Broadhurst and Coates 2001; Byrne *et al.* 2002c; Maslin *et al.* 1999). A study of the nuclear genome (Broadhurst and Coates 2001) showed that *A. oldfieldii* is highly significantly different from the *A. acuminata* complex. Within the rest of the complex the small-seeded form is also genetically distinct from the

two subspecies, subsp. *acuminata* and subsp. *burkittii*, which form separate clusters, with the narrow phyllode variant intermediate between the two but closer to subsp. *acuminata*. Identification of the taxa within the complex enables appropriate assessment of desired traits and performance of taxa, and provides a basis for the selection and breeding for these characteristics.

Another species complex of interest for agroforestry is *A. microbotrya*. A preliminary study of genetic variation in the *A. microbotrya* complex showed some genetic differentiation between the recognised variants, var. *microbotrya* which occurs mainly in the south of the distribution and var. *borealis* which occurs to the north of var. *microbotrya* (Elliot *et al.* 2002). A full study encompassing the range of geographic distribution and morphological variation, and including other variants and taxa, is currently being undertaken.

Resolution of species complexes is also important to establish their conservation status. The rare *A. sp.* 'Dandaragan' is currently gazetted as a phrase name and listed as critically endangered, but there is some uncertainty about its taxonomic status in relation to the common *A. microbotrya*. *Acacia sp.* Dandaragan is restricted to a ridge outside Dandaragan on the western edge of the range of the widespread *A. microbotrya* complex, and may be a morphological variant of, or the end of a morphological cline from, *A. microbotrya*. Research showed *A. sp.* Dandaragan to be morphologically and genetically distinct from the *A. microbotrya* variants at a level expected of subspecies or species (Elliot *et al.* 2001) and confirmed the independent status of the taxon. The identity and conservation status of rare species may be masked by the unresolved morphological variation present in species complexes such as *A. microbotrya* and phylogenetic studies provide assistance in resolving these taxonomic ambiguities.

PHYLOGENETICS AND SETTING PRIORITIES IN CONSERVATION

Conservation management operates in a framework of setting priorities due to competition for land use and limited funding for conservation activities (Coates and Atkins 2001). Most often the driving force is the degree of threat to specific taxa (Hopper 2000) but many authors have suggested that all taxa are not equal and that some means of assessing their biodiversity value should be used (Crozier 1992; Faith 1992; Humphries *et al.* 1995; Vane-Wright *et al.* 1991). Phylogenetic diversity is one such means of assessing biodiversity value, whether priorities are placed on phylogenetic distinctiveness (Vane-Wright *et al.* 1991), character richness (Faith 1992) or taxa from rapidly evolving clades (Erwin 1991).

The phylogenetic value of relictual species and recently evolved species are quite different, even though both categories of species may be rare and restricted. Two rare species of *Acacia* (*A. sciophanes*, *A. lobulata*) occurring at the north-western edge of the range of their more common

widespread relatives were thought to represent recent speciation due to their morphological similarity, restricted distributions and occurrence in an area of high speciation. A study of the phylogenetic relationships using chloroplast DNA between the pairs of taxa showed that they had quite different evolutionary patterns (Byrne *et al.* 2001). *Acacia sciophanes* shares a common ancestor with its more common relative *A. anfractuosa* (Fig. 2) but the two species have diverged relatively recently (Byrne *et al.* 2001). The level of cp DNA diversity within the species was comparable even though *A. sciophanes* has a much more restricted distribution than *A. anfractuosa*. In contrast, phylogenetic relationships between the second pair of species with a similar distribution pattern in the same area showed that the rare *A. lobulata* was genetically very distinct from the more widespread *A. verrucula*, and they have been separated from a common ancestor for a long period, in the order of 3 million years (Byrne *et al.* 2001). *Acacia lobulata* was also distinct from several other taxa from the *A. flavipila* alliance including an eastern Australian species, *A. ixiophylla*, which coalesced to a common ancestor with *A. verrucula* and another species in the alliance (Fig. 3). *Acacia lobulata* does not have close affinities with any other species and may represent a relictual species with no extant close relatives. The study also showed that *A. lobulata* had some cpDNA variation despite being highly restricted, suggesting that it has been separated for long enough for mutations to arise in the slowly evolving chloroplast genome. *Acacia lobulata* and *A. verrucula* were believed to be close relatives due to the presence of reticulate venation on the phyllodes, although

A. verrucula has flat and *A. lobulata* terete phyllodes. This is likely to be an example of morphological convergence masking the evolutionary relationships between these taxa.

Another rare species that occurs at the edge of the distribution of its widespread presumed relative is *A. oldfieldii* which is restricted to two populations in the Moresby Range north of Geraldton. It is morphologically similar to the widespread complex *A. acuminata* (discussed above), but a nuclear study showed it to be significantly divergent from taxa in that complex (Broadhurst and Coates 2001). A phylogenetic study using cpDNA confirmed the distinctiveness of *A. oldfieldii* (Byrne *et al.* 2002c) as there were a high number of mutations (26) differentiating it from the other taxa in the *A. acuminata* complex (Fig. 1). This degree of divergence was unexpected given the low level of morphological differences between them and is another example of a relictual species with a restricted distribution.

These studies show that similarities based on morphology and geographic distributions are not necessarily reliable in identifying relictual species or recent speciation, whereas phylogenetic analysis can readily do so by determining the degree of evolutionary divergence between species. Recently derived species will show little divergence from their close relatives, while relictual species will show greater levels of divergence. The nucleotide divergence between species of Western Australian acacias that have been studied using cpDNA variation are given in Table 1, and demonstrate examples of both ancient relictual species, and those more closely related to other species through recent evolution from a common ancestor.

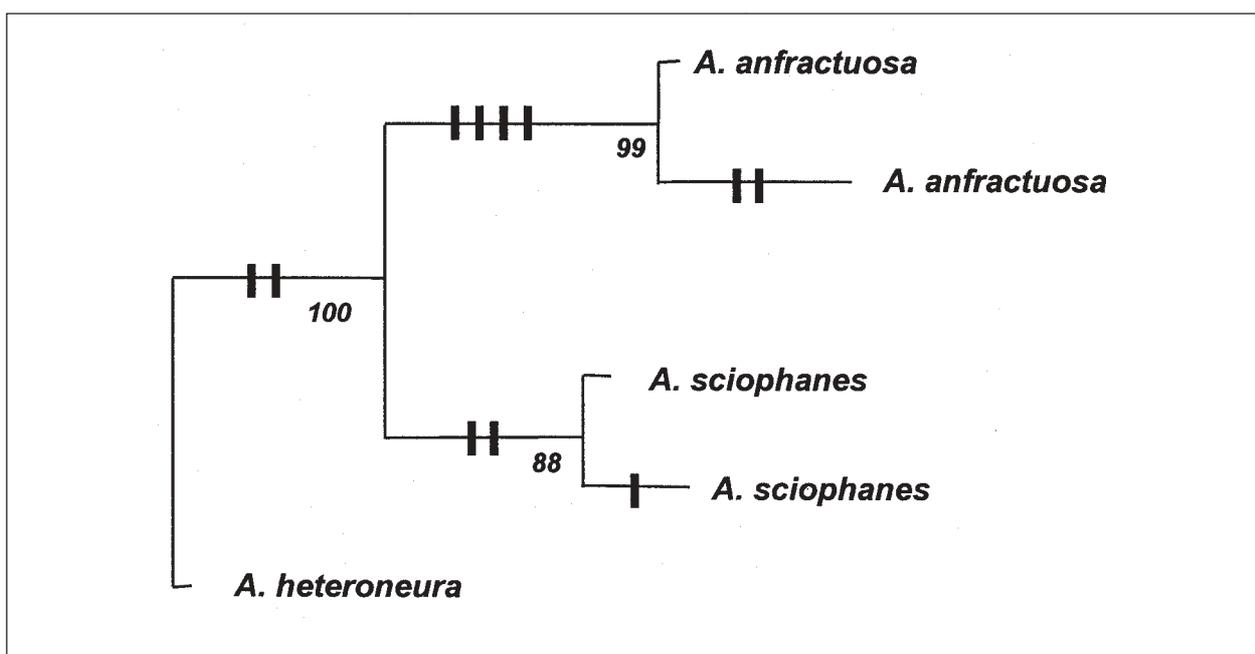


Figure 2. Phylogenetic parsimony tree of haplotype relationships in *Acacia sciophanes* and *A. anfractuosa*. Bars on lines represent mutations. Numbers below lines represent bootstrap confidence values (%). *Acacia heteroneura* was used as the outgroup and is from the same alliance as *A. sciophanes* and *A. anfractuosa*.

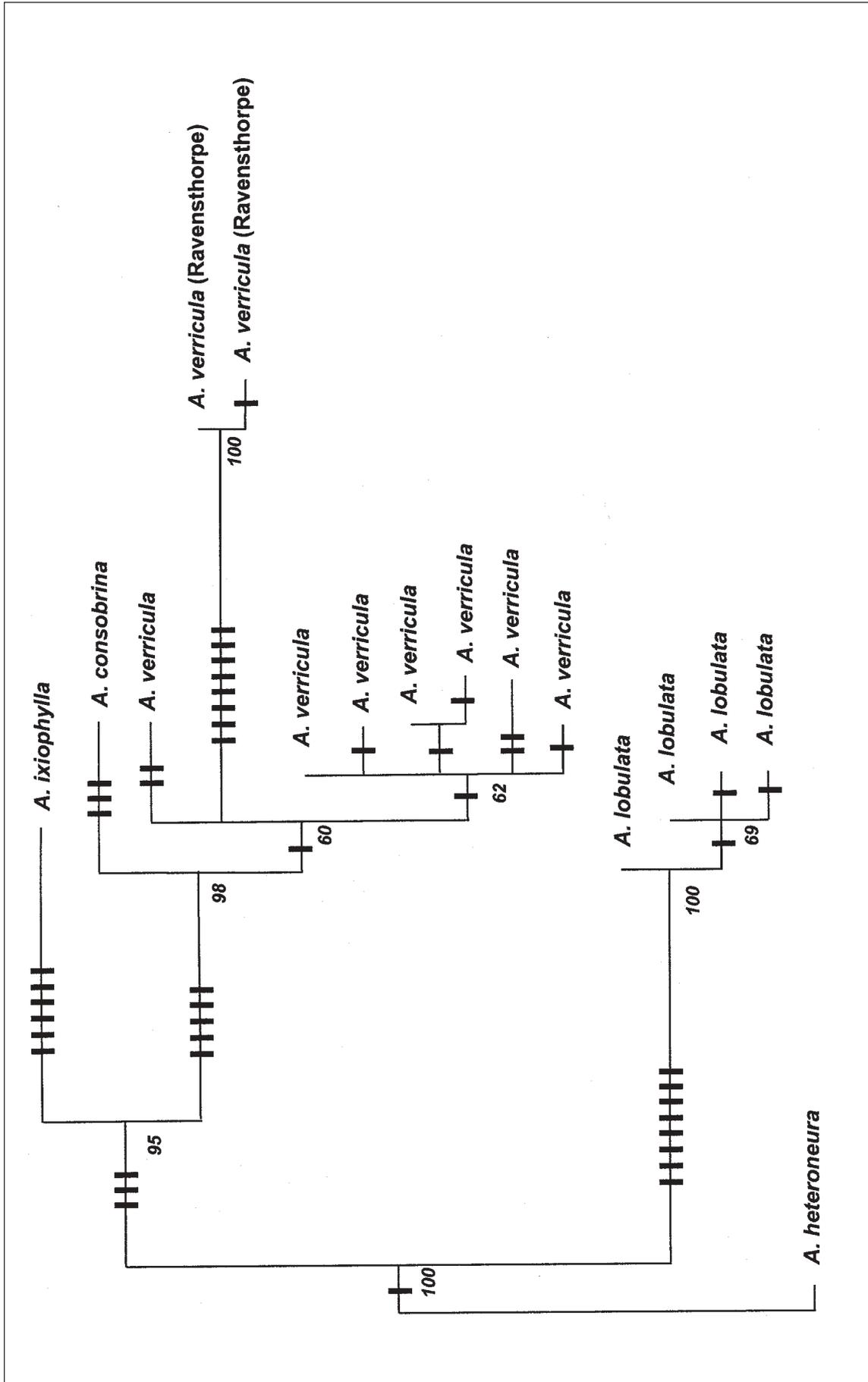


Figure 3. Phylogenetic parsimony tree of haplotype relationships in *Acacia lobulata* and *A. verrucula*. Bars on lines represent mutations. Numbers below lines represent bootstrap confidence values (%). *Acacia heteroneura* was used as the outgroup and is from a different alliance. *Acacia ixiophylla* is an eastern Australian species from the *A. flavipila* alliance. *Acacia consobrina* is another Western Australian species from the *A. flavipila* alliance.

PHYLOGENETICS AND SPECIES COMPARISONS IN CONSERVATION

A goal of conservation programs is to conserve genetic diversity so that the evolutionary potential of the species is maintained (Hamrick *et al.* 1991). Hence a focus of genetic studies of rare species has been the level of genetic diversity within populations and species. Comparison of the levels of genetic diversity has often shown rare species to have lower levels of genetic diversity compared to widespread plants with similar life history traits (Hamrick and Godt 1989), but the range in levels of diversity varies greatly. Rather than comparisons to a mean for rare or widespread species, Karron (1987) pointed out that it was more logical to make comparisons between congeneric species. Comparison between rare species and a widespread common relative helps to elucidate the particular aspects that limit the success of rare species (Gitzendanner and Soltis 2000) and this applies to comparisons of ecological parameters as well as genetic diversity. Felsenstein (1985) has also suggested that comparisons of congeners should use fully resolved phylogenies to ensure that the studies utilise the full power of phylogenetically independent comparisons.

Genetic studies have shown that several rare acacias in Western Australia are not depauperate in terms of genetic diversity compared with the levels of diversity generally observed in *Acacia* species, including many from eastern Australia (Buist *et al.* this proceedings). The rare species do, however, show lower levels of diversity when compared to their widespread relatives in phylogenetically independent comparisons (see Buist *et al.* this proceedings). For example, *A. sciophanes* and *A. anfractuosa* have similar morphological characteristics with the same sparse wispy, ghost-like form. *Acacia anfractuosa* is distributed over a 300 km range in the semi-arid zone of south-west Western Australia, and *A. sciophanes* is restricted to two populations on the western edge of that range. A study of genetic diversity in the two species showed that *A. anfractuosa* maintained average genetic variation within and between populations, whereas *A. sciophanes* showed lower levels of variation within populations and greater level of variation between populations in relation to their geographic distance (Tischler 1998). The rare *A. oldfieldii* also showed lower levels of genetic diversity than any taxon of the *A. acuminata* complex presumed to be its closest widespread relative (Broadhurst and Coates 2001). Properly resolved phylogenies make it easier to identify species pairs between which appropriate phylogenetically independent comparisons can be made for both genetic and ecological data. Comparisons between rare species and their close common relatives indicate how they differ, and therefore contribute to determining those aspects of a species' biology that may be factors in its rarity.

TABLE 1

Nucleotide divergence between *Acacia* species, and between lineages in *A. acuminata*.

SPECIES/LINEAGE	NUCLEOTIDE DIVERGENCE (%)
<i>A. sciophanes</i> – <i>A. anfractuosa</i>	0.072
<i>A. lobulata</i> – <i>A. verrucula</i>	0.334
<i>A. lobulata</i> – <i>A. ixiophylla</i>	0.382
<i>A. verrucula</i> – <i>A. ixiophylla</i>	0.152
<i>A. oldfieldii</i> – <i>A. acuminata</i>	0.287
<i>A. acuminata</i> lineage B – <i>A. acuminata</i> lineage C	0.083

CONCLUSIONS

Phylogenetic analysis is particularly valuable in an ancient, stable landscape such as the south-west of Western Australia, both for conservation of the flora and for efficient utilisation of native species for commercial production and revegetation. Phylogenies provide appropriate comparisons of genetic and ecological data between rare species and their widespread congeners, identify the phylogenetic value of species for setting conservation priorities and differentiate between relictual and recently evolved species. Phylogeny is also valuable in identifying and clarifying taxonomic ambiguities within both rare and widespread species, and comparative phylogeography is beginning to identify significant patterns in the evolutionary history of the south-west region.

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