

RESEARCH ARTICLE

Implications of the changing phylogenetic relationships of *Acacia* s.l. on the biological control of *Vachellia nilotica* ssp. *indica* in Australia

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Plant relationships have implications for many fields including weed biological control. The use of DNA sequencing and new tree building algorithms since the late 1980s and early 1990s have revolutionised plant classification and has resulted in many changes to previously accepted taxonomic relationships. It is critical that biological control researchers stay abreast of changes to plant phylogenies. One of the largest plant genera, *Acacia*, has undergone great change over the past 20 years and these changes have ramifications for weed biological control projects in a number of countries. *Vachellia nilotica* (prickly acacia) is a major weed in Australia, originating from the Indian subcontinent and Asia, and it has been a target for biological control since 1980. Once a member of *Acacia*, a large (>1,000 spp.) and iconic group in Australia, prickly acacia is now part of the genus *Vachellia*. Current knowledge suggests that *Vachellia* is more closely related to mimosoid genera than it is to *Acacia* s.s. There has also been a recent reclassification of legume subfamilies with subfamily Mimosoideae now part of subfamily Caesalpinioideae, and four new subfamilies. In this paper we review the changes that have occurred to this group since the prickly acacia biological control project began and discuss the implications for the project. A new host test list for quarantine testing is proposed. Developed following the modernisation of the centrifugal-phylogenetic method, it is shorter than past lists, containing 46 species, although still lengthy because of the expectations of regulatory bodies, which are slower to accept advances in scientific knowledge. The list includes five *Vachellia* species, six "Mimoseae" species and 26 *Acacia* species. The number species from legume subfamilies other than the new Caesalpinioideae is greatly reduced.

KEYWORDS

Fabaceae, host test list, Mimoseae, weed biological control

1 | INTRODUCTION

Considered the father of taxonomy, Linnaeus published the first hierarchical classification of plants using binomial nomenclature (*Species Plantarum*) in 1753. The Linnaean binomial naming system and classification is still used today. Since the time of Linnaeus, plant taxonomies have been based on morphological similarities but more recently biochemical similarities have become more important. Taxonomic classifications provide a convenient method of arranging organisms into groups, and have historically been the only means available of organising plants. Linnaean groupings are based on similarity, but this does

not necessarily reflect evolutionary relationship (Briese, 2003; Kelch & McClay, 2004; Withgott, 2000). In the second half of the 20th century the use of cladistics and phylogenetic trees to determine plant relationships became increasingly common (Rouhan & Gaudeul, 2014; Withgott, 2000). Cladistical groupings are based on derived characters, rather than similarity which may not be because of shared evolutionary history. The use of DNA sequencing and new tree building algorithms since the late 1980s and early 1990s have revolutionised plant classification and has resulted in many changes to previously accepted taxonomic relationships (Rouhan & Gaudeul, 2014). Examples include splitting Euphorbiaceae into several families

(Euphorbiaceae Jussieu *sensu stricto* (s.s.), Pandaceae Engl. & Gilg., Phyllanthaceae Martynov, Picrodendraceae Small, Putranjivaceae Meirner and Peraceae Klotzsch; Angiosperm Phylogeny Group, 2009; Wurdack, Hoffmann, & Chase, 2005), expanding Malvaceae to include the former families Bombacaceae, Tiliaceae and Sterculiaceae (Judd & Manchester, 1997), the inclusion of the former family Asclepiadaceae in Apocynaceae (Endress & Bruyns, 2000), the expansion of *Euphorbia* to include a number of former genera including *Chamaesyce*, *Cubanthus*, *Elaeophorbia*, *Endadenium* and *Synadenium* (Horn et al., 2012) and the inclusion of the former genus *Dryandra* in *Banksia* (Mast & Thiele, 2007). The number of published scientific papers on plant phylogenies continues to increase (Briese, 2005; Web of Science). Changes to plant groupings will continue to be made as our knowledge grows.

Plant relationships have implications for many fields including weed biological control. Phytophagous insects generally feed on closely related host plants as they often share similar features (e.g., chemistry, morphology; Bernays & Chapman, 1994; Nishida, 2014). Host specificity testing of potential weed biological control agents provides valuable information regarding potential risks to non-target plants, and it has been a crucial part of weed biological control since the 1920s (Dodd, 1940). Since it is impractical to test every plant species, a test list is developed. Initially, these lists were not compiled systematically but rather consisted of crop and ornamental species that were economically important at the time (Dodd, 1940). As knowledge of host selection developed, test lists became more "biologically relevant" and focused on determining host range (Briese, 2003; Harris & Zwölfer, 1968). For the past 40 years, researchers have developed test lists following the centrifugal phylogenetic method (CPM; Wapshere, 1974). The CPM emphasises the testing of species most closely related to the target and then successively more distant taxa. Despite the name, test plant selection relies on hierarchical taxonomic groupings (and testing members from as many groups as possible) as well as the inclusion of unrelated "safeguard" species (Briese, 2005; Kelch & McClay, 2004; Kleinjan & Hoffmann, 2013). The CPM has been modernised, shifting the focus from taxonomic groupings to phylogenetic relationships, taking into consideration ecological and biogeographic filters, and removing unrelated "safeguard" species (Briese, 2003, 2005; Meheliš et al., 2015). The modernisation takes advantage of the huge advances made in plant phylogenetic relationships and host selection behaviour since the CPM was developed and shifts the focus to defining the host range rather than determining whether or not individual plant species were "safe" (Briese, 2005).

One of the largest plant genera, *Acacia*, has undergone great change over the past 20 years and these changes have ramifications for weed biological control projects in a number of countries. Molecular studies have demonstrated that *Acacia sensu lato* (s.l.) is paraphyletic and should be split into a number of genera (Murphy, 2008). Most Australian *Acacia* s.l. species are now believed to be more closely related to members of the Mimosoid tribe Ingeae than to African *Acacia* s.l. species (Bouchenak-Khelladi, Maurin, Hurter, & van der Bank, 2010). South Africa, Portugal and Australia have weed biological control programmes targeting species within *Acacia* s.l. (Impson, Kleinjan, Hoffmann, Post, & Wood, 2011; Marchante, Freitas, & Hoffmann,

2011; Palmer, Lockett, & Dhileepan, 2012). The implications of recent phylogenetic changes on the biological control of Australian *Acacia* species in South Africa has been discussed (Kleinjan & Hoffmann, 2013).

In Australia, prickly acacia (*Vachellia nilotica* ssp. *indica* (Benth.) Kyal. & Boatwr.; formerly *Acacia nilotica* ssp. *indica* (Benth.) Brenan) has been a target for weed biological control since 1980 (Marohasy, 1993). Historically, prickly acacia has been a difficult target for biological control because of the large number of native *Acacia* species in Australia (>1,000) and their high cultural, economic and environmental value (Maslin, 2018). Unlike targets such as members of the Cactaceae, for which there are no native species in Australia, a high level of specificity is required for suitable prickly acacia agents. In light of the changes to *Acacia* s.l. and the testing of potential new biological control agents, we reassess the composition of host test lists used historically for testing potential prickly acacia biological control agents. We also propose a new test list for testing future potential agents.

1.1 | *Vachellia nilotica*

Vachellia nilotica is a widespread species found in the drier areas of Africa and the Indian subcontinent. It is a highly variable species with nine subspecies recognised (Brenan, 1983). Subspecies are differentiated mainly by the shape, size and degree of pubescence of the pods. The degree of pubescence of young branchlets, the habit of the tree, and the shape of the crown are also important characteristics. Six of the subspecies are found in Africa and three in the Indian subcontinent and Asia (Dhileepan, 2009). Biochemical and molecular studies suggest that *V. nilotica* populations in Queensland are the subspecies *indica* (Brenan, 1983; Hannan-Jones, 1999; Wardill et al., 2005). *Vachellia nilotica* ssp. *indica* is native to India, Pakistan, Bangladesh, Yemen, Oman and Myanmar and has been introduced into Australia, Angola, Ethiopia, Indonesia, Iran, Iraq, Nepal, New Caledonia, Somalia, Tanzania, and Vietnam, although Brenan (1983) noted that its habitats in Ethiopia and Somalia appeared to be natural (Dhileepan, 2009; Mackey, 1997). It has been cultivated in Iran and Vietnam (Brenan, 1983). *Vachellia nilotica* ssp. *indica* was introduced into Australia sometime in mid-1800s, with the first herbarium record for the species collected in 1874 (Australasian Virtual Herbarium, 2017). It was promoted as a shade and fodder tree in western Queensland from the 1920s and was first declared noxious in 1957 (Mackey, 1997). It is now a serious weed of northern Australia and has been declared a Weed of National Significance (<http://weeds.ala.org.au/WoNS/pricklyacacia/>). *Vachellia nilotica* infests over 7 million hectares of the Mitchell grass downs in western Queensland, as well as scattered coastal infestations in Queensland, the Northern Territory and Western Australia (Bolton, 1989; Mackey, 1997). It costs primary producers AUD\$9m per year because of decreasing pasture production and hindering the mustering of livestock and also threatens to transform one of Australia's last remaining large expansive grasslands (Burrows, Carter, Scanlan, & Anderson, 1990; Spies & March, 2004).

Prickly acacia has been a target of weed biological control in Australia since 1980. Following field surveys in Pakistan, Kenya and South Africa, six agents were released. Only two of these, a seed-feeding bruchid beetle, *Bruchidius sahlbergi* Schilsky, from Pakistan

and a leaf-feeding geometrid moth, *Chiasmia assimilis* (Warren), from Kenya and South Africa, have become established (the other four agents failed to establish; Dhileepan, 2009). Neither agent provides effective control in the widespread inland infestations of prickly acacia, prompting field exploration for new potential agents. In the early 2000s, field surveys were conducted in India and resulted in four insects being imported into quarantine (Dhileepan et al., 2014). These insects were either not sufficiently host specific or could not be established (Dhileepan et al., 2014; Taylor & Dhileepan, 2018). The search for new agents, focussing on gall-inducers, was redirected to Ethiopia and Senegal, based on plant genotype and climate matching (Dhileepan et al., 2018). Several potential agents have been identified. Two of these have been imported into our quarantine facility: a gall thrips from Ethiopia and a stem-galling fly from Senegal.

1.2 | Historical plant relationships

Acacia was first described (although broadly) by Miller in 1754 (Maslin, 2018). Bentham (1842; cited in Maslin, 2018) more clearly defined the limits of the genus and his circumscription of *Acacia* remained relatively unchanged until 1972. The genus was typified on *A. scorpioides* (L.) W. Wight (= *A. nilotica* (L.) Delile) in 1913 (Orchard & Maslin, 2003; Thiele et al., 2011). *A. nilotica* remained the type for *Acacia* until 2005. Vassal (1972; cited in Maslin, 2018) recognised three subgenera: subgenus *Acacia* (of which prickly acacia was a member), subg. *Phyllodineae* (syn. *Heterophyllum*; the majority of Australian species) and subg. *Aculeiferum*. Pedley's, 1978 classification drew on Bentham's and Vassal's work. He too recognised three subgenera. The large subg. *Phyllodineae* was further split into seven sections.

When the initial biological control work was conducted, prickly acacia was known as *A. nilotica*. *Acacia* s.l. consisted of around 1,350 species, the vast majority of which (>1,000 species) occur in Australia. Pedley (1986) proposed that *Acacia* s.l. be split into three genera: *Acacia* (= subg. *Acacia*), *Senegalia* (= subg. *Aculeiferum*) and *Racosperma* (= subg. *Phyllodineae*). The classification was not widely adopted, but it did stimulate further research on the generic status of *Acacia*.

Acacia s.l. was a member of the monogeneric tribe Acacieae; one of five tribes within the subfamily Mimosoideae (Acacieae, Ingeae, Mimoseae, Parkieae and Mimozygantheae; Murphy, Brown, Miller, & Ladiges, 2010). Two of the other tribes occur in Australia. The Mimoseae tribe contains four genera (nine species) native to Australia and

four naturalised genera (Orchard & McCarthy, 1998). The Ingeae tribe is represented in Australia by eight genera including 20 native species and three naturalised species. The Mimosoideae was one of three subfamilies in the legume family (Fabaceae/Leguminosae). The peas, Faboideae, are represented in Australia by ~1,500 species in 136 genera and include a number of agriculturally important species (Crisp, 2009). The Caesalpinoideae is represented by 127 species in 22 genera (including six naturalised genera; Orchard & McCarthy, 1998).

1.3 | Current phylogenetic relationships

Studies have now demonstrated that *Acacia* s.l. is indeed polyphyletic and the genus has been split into seven genera (*Acacia* Martius, *Vachellia* Wight & Arn., *Senegalia* Raf., *Parasenegalia* Seigler & Ebinger, *Pseudosenegalia* Seigler & Ebinger, *Acaciella* Britton & Rose and *Mariosousa* Seigler & Ebinger; Miller, Terra, Riggins, Ebinger, & Seigler, 2017). In 2005, *Acacia* was retypified so that the majority of *Acacia* s. l. (i.e., *Acacia* subg. *Phyllodineae*) retained the name *Acacia* (see Maslin, 2015; Maslin, Miller, & Seigler, 2003; Miller & Seigler, 2012; Table 1). Species within *Acacia* subg. *Acacia* (including prickly acacia) have been transferred to the genus *Vachellia* Wight & Arn. species within subgenus *Aculeiferum* have been transferred to *Senegalia*, *Acaciella*, *Parasenegalia*, *Pseudosenegalia* and *Mariosousa* (Miller et al., 2017).

The *Vachellia* genus is of Afro-Asian origin and contains 164 species (Kodala & Wilson, 2006). There are 11 species found in Australia of which nine are native (*V. bidwillii* (Benth.) Kodala, *V. clarksoniana* (Pedley) Kodala, *V. ditricha* (Pedley) Kodala, *V. douglasica* (Pedley) Kodala, *V. pachyphloia*, *V. pallidifolia* (Tindale) Kodala, *V. suberosa* (A. Cunn. ex Benth.) Kodala, *V. sutherlandii* (F. Muell.) Kodala, and *V. valida* (Tindale & Kodala) Kodala) (Pedley, 2002). Two other species (*V. nilotica* ssp. *indica* and *V. farnesiana* (L.) Wight & Arn.¹) are naturalised (Kodala & Wilson, 2006; Maslin, 2018). All native *Vachellia* species are restricted to northern Australia; *V. bidwillii* is the only species found south of the tropics (Maslin & Pedley, 1988). They occur in both semi-arid and moist-tropical climatic zones.

The native *Vachellia* species present in Australia are believed to be descended from individuals that migrated into Australia prior to European colonisation (Tomlinson, 2014). There is limited phylogenetic information available on Australian *Vachellia*. However, a study involving *V. bidwillii* suggested that it is closely related to several African *Vachellia* species including *V. nilotica* (Miller & Bayer, 2001). Several Australian *Vachellia* species (*V. clarksoniana*, *V. ditricha*, *V. valida*) have previously been confused with *V. bidwillii*.

The traditionally accepted tribes within the Mimosoideae are now considered to be polyphyletic or paraphyletic (Legume Phylogeny Working Group, 2013; Luckow, Miller, Murphy, & Livshultz, 2003; Miller & Seigler, 2012), but as new subgroups are yet to be formalised, they are partially retained here. Molecular work suggests that *Vachellia* is nested within the old Mimoseae and is sister to *Neptunia* Lour. and other basal Mimoseae including *Prosopis*, *Desmanthus* and *Leucaena* (Figure 1; Bouchenak-Khelladi et al., 2010; Legume Phylogeny Working Group, 2013; Miller & Burd, 2014; Murphy, 2008). As such, *V. nilotica* is now believed to be more closely related to species within

TABLE 1 Generic and subgeneric names of *Acacia* s.l. pre-retypification, at the time of the initial biocontrol programme against prickly acacia (Pedley, 1978), and now, post-ratification; including the number of known Australian native species (Maslin, 2018; Miller et al., 2017)

Pedley (1978)	Species	Post-ratification	Species
<i>Acacia</i> subg. <i>Acacia</i>	7	<i>Vachellia</i>	9
<i>Acacia</i> subg. <i>Phyllodineae</i>	950	<i>Acacia</i> (s.s.)	1,057
<i>Acacia</i> subg. <i>Aculeiferum</i>			
Section <i>Filicinae</i>	0	<i>Acaciella</i>	
Section <i>Spiciflorae</i>	1	<i>Senegalia</i> (s.s.)	2
"skleroxyla" group	0	<i>Parasenegalia</i>	0
pro parte	0	<i>Pseudosenegalia</i>	0
"coulteri" group	0	<i>Mariosousa</i>	0

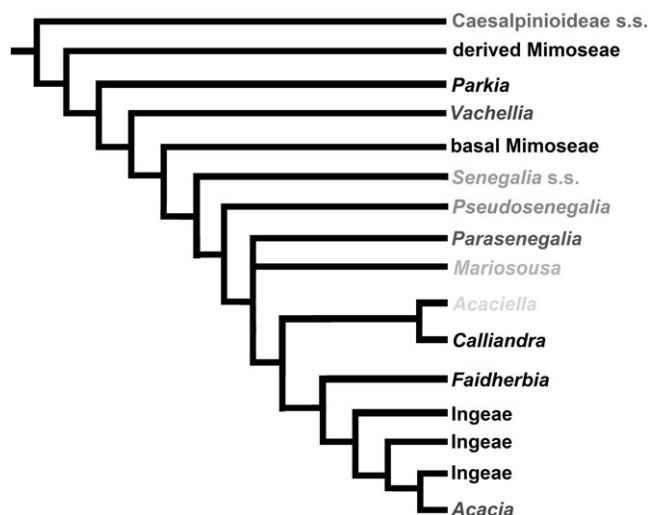


FIGURE 1 Schematic representation of relationships within the former Mimosoideae with *Acacia* s.l. highlighted in grey text and Caesalpinioideae (Kleinjan & Hoffman, 2013; LPWG, 2013; Miller & Burd, 2014; Miller et al., 2017)

the Mimosaeae than it is to Australian *Acacia* (s.s.) species and other members of *Acacia* s.l.

The Mimosaeae contains four genera (10 species) native to Australia (*Neptunia*, *Dichrostachys*, *Entada* and *Adenanthera*) and four naturalised genera (*Prosopis*, *Mimosa*, *Leucaena* and *Desmanthus*; Atlas of Living Australia, 2017; Orchard & McCarthy, 1998). *Neptunia* is a small genus (11 species) of small shrubs or subshrubs. Five *Neptunia* species are endemic to Australia, mostly restricted to the northern half of the continent, and another two (*N. oleracea* Lour. and *N. plena* (L.) Benth.) have become naturalised (Department of Employment, Economic Development and Innovation, 2016). *Entada* spp. are lianas restricted to the rainforests of northern Queensland. *Dichrostachys spicata* (F. Muell.) Domin is a shrub found across northern Western Australia and the Northern Territory with scattered populations in Queensland. *Adenanthera abrosperma* F. Muell. is endemic to Northern Queensland.

Acacia (s.s.) is well removed from *Vachellia*. It is nested within the former Ingeae tribe and is in a grade (paraphyletic group) with *Acaciella*, *Mariosousa* and *Senegalia* (Figure 1; Brown, 2008; Kyalangalilwa, Boatwright, Daru, Maurin, & van der Bank, 2013; Maslin, 2018). There are currently 1,053 described *Acacia* species (s.s.) in Australia (1,176 including infraspecific taxa; Maslin, 2018). The sections within *Acacia*

(s.s.), as defined by Pedley (1978) are not considered natural groupings (Murphy, 2008), but are retained here as there is currently no phylogenetically based classification for this large group. Some relationships have been resolved and are summarised by Murphy (2008). Nearly half of the Australian *Acacia* species have plurinerved phyllodes (515 species; sections *Juliflorae* and *Plurinerves*; Maslin, 2018; Maslin & Pedley, 1988). Both sections are widespread across Australia although more *Juliflorae* species occur north of the Tropic of Capricorn and more *Plurinerves* species occur south of the Tropic. Section *Phyllodineae* (uninerved phyllodes) is the largest group with 421 species. It too is a widespread group, although is predominantly in temperate regions. Section *Lycopodiifoliae*, a small group morphologically distinct from other species, largely distributed in northern Australia (Maslin & Pedley, 1988; Murphy et al., 2010). Section *Alatae* is a small group from south-western Australia and is usually incorporated into *Phyllodineae*. Species with bipinnate leaves (71 in total) belong to the sections *Botrycephalae* and *Pulchellae*. They are mostly temperate species found in the southern half of the continent (*Botrycephalae* in south-eastern Australia and *Pulchellae* in south-western Australia). Despite morphological similarities, the two bipinnate groups are not sister groups (Murphy, 2008). Both are nested within clades of phyllodinous species, which suggests that there have been two separate reversals to bipinnate leaves.

Relationships within the large grade comprising *Acacia* s.s., the old Ingeae tribe, *Mariosousa*, *Acaciella*, *Senegalia*, *Parasenegalia* and *Pseudosenegalia* are largely unresolved (Brown, 2008). An exception is the sister relationship between *Acacia* s.s. and *Paraserianthes lophantha* (Willd.) I. C. Nielsen, a fast growing small tree from south-western Western Australia (Figure 1; Brown, Murphy, & Ladiges, 2011). The Ingeae is represented in Australia by 21 native species (seven genera), as well as several naturalised species (e.g., *Inga edulis* Mart., *Pithecellobium dulce* (Roxb.) Benth.). The largest genus is *Archidendron*, a group of 10 species restricted to the east coast of the continent.

The remaining groups of the former *Acacia* s.l. are poorly represented in Australia. *Acaciella* is represented by two naturalised species with isolated populations. *Senegalia* is represented in Australia by two rare endemic species and two naturalised species (Maslin, 2012). No *Mariosousa*, *Parasenegalia* or *Pseudosenegalia* species occur in Australia.

The Legume Phylogeny Working Group (LPWG) has recently published a new subfamily classification of Fabaceae that follows a traditional Linnaean approach, but is compatible with clade-based classifications (Legume Phylogeny Working Group, 2017). Traditional subfamilies Mimosoideae DC and Faboideae Rudd ($\equiv$ Papilionoideae DC) are monophyletic, but are nested within the paraphyletic subfamily Caesalpinioideae. The Legume Phylogeny Working Group (2017) has reclassified Fabaceae into six subfamilies; four new subfamilies have been separated from Caesalpinioideae and the former subfamily Mimosoideae is now a clade within Caesalpinioideae (Figure 2). The former Caesalpinioideae (s.l.) was the smallest of the old legume subfamilies in Australia so, with the exception of the mimosoid component, the new subfamilies are relatively small. Caesalpinioideae s.s. is represented in Australia by six native genera and several naturalised genera, including the widespread genus *Senna* Mill. The Dialioideae is represented in Australia by three genera (e.g., *Labichea* Gaudich. ex

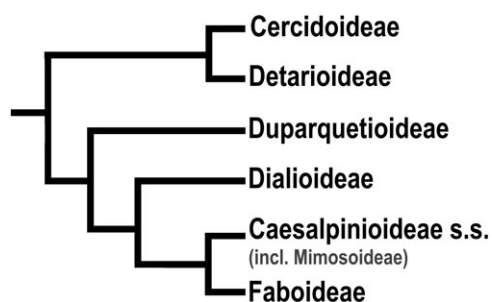


FIGURE 2 Newly classified subfamilies in Fabaceae as defined by the Legume Phylogeny Working Group (LPWG, 2017). The former three subfamilies are in different grey text

DC), the Detarioideae by five small genera, and the Cercidoideae by two genera (e.g., *Bauhinia* L.). The new subfamily Duparquetioideae contains a single species, *Duparquetia orchidacea* Baill., which is not found in Australia. The Faboideae remains a large group with ~1,500 species in Australia, including numerous agriculturally important species.

2 | HOST TEST LISTS

2.1 | Historical host test lists

We reviewed the test lists for five of the six agents released in Australia against prickly acacia (Table 2). At the time of the initial testing, prickly acacia was believed to be closely related to Australian *Acacia* species (Marohasy, 1993). Australian herbaria at the time and later the "Flora of Australia" followed the familial classification of Cronquist (1981). As such, the subfamilies within Fabaceae were considered distinct families (Orchard & McCarthy, 1998; Orchard & Wilson, 2001a,b).

Early in the biological control programme, three native *Acacia* subg. *Acacia* species and one naturalised species were known to occur in Queensland (Willson, 1982). A total of 54 non-target species were tested in the early 1980s against the seed feeding beetle *B. sahlbergi* (Willson, 1982). Unlike more recent test lists, only 15% of test species were from *Acacia* subg. *Phyllodineae* (Table 2). The test list was dominated by economically important species, as was common at the time; almost half are from the subfamily Faboideae ($\equiv$ Fabaceae used in later test lists), and nine unrelated economic species. One Mimoseae species was tested, the invasive fodder species *Leucaena leucocephala* (Lam.) de Wit.

By modern standards the test list for *B. sahlbergi* is lacking. Despite this limitation, the fact that seed of neither *V. bidwillii* nor *V. farnesiana* were attacked by larvae during testing or were any of the *Acacia* species tested (Willson, 1982) means that the testing was

adequate. It was also noted by researchers that because of the size of the beetle, species with small seeds would not be able to support development. This precludes many *Acacia* subg. *Phyllodineae* and *Nepentunia* species. A check of *Vachellia* spp. pods co-occurring with infested prickly acacia plants would be informative and would likely confirm host testing results.

A small gracilariid moth with tip-boring larvae (*Cuphrodes profluens* Meyrick) was tested and released around the same time as *B. sahlbergi* but failed to establish in the field (Dhileepan, 2009). We did not see the test list for this agent but is likely to be similar to the list for *B. sahlbergi*.

Tested 10 years after *B. sahlbergi*, the test list for *Homichloda barkeri* (Jacoby) (a chrysomelid beetle approved for release in 1994, which failed to establish in the field; Lockett & Palmer, 2003), contained 47 test species including the three *Acacia* subg. *Acacia* species, 19 *Acacia* subg. *Phyllodineae* species and five species from Mimoseae (Marohasy, 1994; Table 2).

Test lists used for testing potential prickly acacia biological control agents in the late 1990s and early 2000s relied on information presented in the "Flora of Australia," which included nine *Acacia* subg. *Acacia* species (seven native species and two introduced; Orchard & Wilson, 2001a,b). The approved test lists for *Chiasmia* spp. and *Cometaster pyrrula* (Hopffer) contained 66 species, although additional species were tested. The test lists included six *Acacia* subg. *Acacia* species, at least 30 *Acacia* subg. *Phyllodineae* species (mostly from section *Botrycephalae*), and six Mimoseae species (Table 2; Palmer et al., 2007; Palmer & Senaratne, 2007). Representatives from the Caesalpinioideae and the Faboideae were also included, but fewer than in the *B. sahlbergi* test list (Table 2). Two species from outside the legume groups were included in the testing of *Chiasmia* spp. as they were known hosts of congeners (Palmer, 1998). These species were retained for the testing of *C. pyrrula* as outgroups (Table 2; Palmer & Senaratne, 2007).

TABLE 2 The composition of host test lists used for testing some of the prickly acacia biocontrol agents historically and the proposed new test list

Taxonomic group	<i>Bruchidius sahlbergi</i>	<i>Homichloda barkeri</i>	<i>Chiasmia</i> spp.	<i>Cometaster pyrrula</i>	Phylogenetic group	Proposed new list
Mimosaceae					Subfamily Caesalpinioideae	
Acacieae					Mimosoid clade	
<i>Acacia</i> subg. <i>Acacia</i>	2	3	6	6	<i>Vachellia</i>	5
<i>Acacia</i> subg. <i>Phyllodineae</i>	8	19	34	35	Basal "Mimoseae"	4
<i>Acacia</i> subg. <i>Aculeiferum</i>	2	0	1	1	Derived "Mimoseae"	2
Mimoseae	1	5	6 ^a	9	<i>Senegalia</i> s.s.	1
Ingeae	1	4	4 ^a	2	"Ingeae"	2
Caesalpinioideae	8	8	8	8	<i>Acacia</i>	26
Fabaceae	24	8	15	14	<i>Peltophorum</i> clade	1
Unrelated	8	0	2	2	Cassieae clade	1
					Subfamily Faboideae	2
					Subfamily Dialioideae	1
					Subfamily Cercidoideae	1
Total	54	47	74	77	Total	46

^a Palmer, Lockett, Senaratne, and Mc Lennan (2007) list eight Mimoseae and two Ingeae as they erroneously assigned *Albizia* and *Carthorium* to Mimoseae.

The need for a high level of specificity was recognised early in the prickly acacia biological control project and this has resulted in the rejection of numerous potential agents (Dhileepan et al., 2015; Marohasy, 1993; Palmer et al., 2012; Palmer & Witt, 2006). With the exception of the *B. sahlbergi* test list, the past host test lists used for testing potential prickly acacia agents have included a good representation of both *Vachellia* and Mimoseae, the groups now known to be most closely related to prickly acacia. Specifically, the test list for *C. assimilis*, one of the two agents that have established in Australia, contained five native subg. *Acacia* (now *Vachellia*) species and four native Mimoseae (Table 2; Palmer et al., 2007). None of these species were found to support development of this agent.

2.2 | Proposed new host test list

Until relatively recently in Australia, host test lists needed approval prior to the commencement of host testing. Approval of the test lists is no longer required which in theory allows more flexibility for researchers to develop a list that is consistent with accepted plant phylogenetic relationships and allows alterations to the list where species cannot be sourced or easily propagated. However, the new process is a double-edged sword. In Australia, once host specificity testing has been completed (if the agent is considered sufficiently host-specific) an application to release the biological control agent, including a report detailing the host testing and discussing any risk posed, is submitted to regulatory bodies within the Australian federal government. A draft risk analysis produced by regulatory bodies and the proponent's report on host testing is distributed to state and territory governments, the CSIRO and registered stakeholders for comment and is posted online for public comment. Any of these stakeholders can question the integrity and completeness of the test list and request that additional species be tested. Although the CPM for selecting test plants has been superseded to better reflect our current knowledge, regulatory bodies still adhere to the 40-year-old guidelines (Briese, 2005; Sheppard, Heard, & van Klinken, 2005). We are still expected to test plants from as many related taxonomic groups as possible (rather than focusing on the degree of relationship between target and non-target species) and include safeguard species. A lengthy test list is not necessarily more informative, and including safeguard species has been demonstrated to be redundant, but unfortunately regulatory bodies and the wider community are slower to accept scientific advances. It is for this reason that the proposed new test list remains lengthy and includes species that may not necessarily assist in defining the host range of potential biological control agents.

The test list used for testing *Chiasmia* spp. and *C. pyrrula* contained a sound selection of species from relevant taxonomic groups. Consequently, the new proposed host test list does not greatly differ from this, although it is somewhat shorter. The proposed host test list contains 46 species and better reflects currently accepted phylogenetic relationships while considering the size of the various groups in Australia (Tables 2 and 3). The degree of phylogenetic separation (see Briese, 2003, 2005) is included although because of the uncertainty with relationships within and between many legume groups these are approximate. Four native *Vachellia* species are included in the list plus *V. farnesiana*. The remote distribution of native *Vachellia* species

makes sourcing these species difficult as none are in cultivation. *V. sutherlandii* and *V. bidwillii* (and *V. farnesiana*) occur in the Mitchell grass downs in western Queensland and are therefore sympatric with the major prickly acacia infestation. *V. sutherlandii* in particular is common in north-western Queensland where it forms groves in grassland or open woodland plains (Maslin, 2018). Some of the other *Vachellia* species may co-occur with prickly acacia over part of their range (e.g., *V. ditricha* and *V. pachyphloia*). Wardill et al. (2005) raised the possibility of hybridisation between prickly acacia and native *Vachellia*, although the authors are not aware of any investigation into this.

Similar to the past test lists we have included species from each of the four native Mimoseae genera. Two species of *Neptunia* are included because of their close relationship to *Vachellia* and because they were found to be suitable hosts for some of the recently tested agents (the scale *Anomalococcus indicus* Ramakrishna Ayyar and leaf-webbing moth *Phycita* sp. B; Taylor & Dhileepan, 2018; K. Dhileepan, unpublished data). Additionally, *N. dimorphantha* Domin and *N. monosperma* F. Muell. ex Benth. are found on the Mitchell grass downs. Two other basal Mimoseae are included in the list (*Leucaena leucophala*, which has become widely naturalised in Queensland and *D. spicata*) as well as two derived Mimoseae (*A. abrosperma* and *Entada phaseoloides* (L.) Merr.).

Acacia species necessarily remain as a significant part of the proposed test list, even though they are not as closely related to *Vachellia* (and therefore prickly acacia) as once thought; *Acacia* is approximately five degrees of separation from *Vachellia*, although still in the same subfamily. *Acacia* is by far the most speciose Caesalpinioideae clade in Australia. It also has high cultural, economic and environmental value and it is for this reason that regulatory bodies (and indeed the general public) demand assurance that they are not at risk. The host test list contains 26 *Acacia* species with all sections represented. Bipinnate species feature heavily (despite representing only 7% of Australian *Acacia* species and being largely allopatric to prickly acacia infestations), because of their morphological similarity to prickly acacia. The most northerly occurring native *Acacia* species with bipinnate leaves are *A. storyi*, *A. deanei* subsp. *deanei*, *A. glaucocarpa*, *A. pedleyi* and *A. chinchillensis*. The ability to obtain non-target plants (or seeds or cuttings for propagation) for host testing is an additional criterion for including a species on a host test list. We have been able to source seeds of *A. deanei* subsp. *deanei*, *A. chinchillensis* and *A. glaucocarpa* for recent testing of potential agents so they are included in the revised test list. The remaining *Acacia* s.s. species are phyllodinous. They are either common ornamental species or species that occur in the north of the country, with 11 species occurring on the Mitchell grass downs (Atlas of Living Australia, 2017). All can be procured as plants or seeds.

As mentioned previously, the remaining groups of the former *Acacia* s.l. (*Acaciella*, *Senegalia*, *Parasenegalia*, *Pseudosenegalia*, *Mariosousa*), are poorly represented in Australia. The two naturalised *Acaciella* species have isolated populations and are both prohibited species in Queensland (Queensland Biosecurity Act 2014), so they have not been included in the test list. We have included one *Senegalia* species, but this is unlikely to be native; *Senegalia albizioides* (Pedley) Pedley is endemic to the remote Cape York Peninsula in Far North Queensland, where it occurs in or on the margins of rainforest and *S. pennata* subsp. *kerrii* (I. C. Nielsen) Maslin is restricted to the tip of Cape York Peninsula.

TABLE 3 Proposed host plant test list for host specificity testing of prickly acacia biological control agents in Australia

Species	Status	Degree of phylogenetic separation
Order Fabales		
Family Fabaceae Lindl.		
Subfamily Caesalpinioideae DC		
Mimosoid clade (= Mimosoideae de Candolle)		
Genus <i>Vachellia</i>		
<i>V. nilotica</i> ssp. <i>indica</i> (Benth.) Kyal. & Boatwr.	TW	0
<i>V. bidwillii</i> (Benth.) Kodela	N	0
<i>V. ditricha</i> (Pedley) Kodela	N	0
<i>V. farnesiana</i> (L.) Wight & Arn.	I	0
<i>V. sutherlandii</i> (F. Muell.) Kodela	N	0
<i>V. valida</i> (Tindale & Kodela) Kodela	N	0
Basal "Mimoseae"		
<i>Dichrostachys spicata</i> (F. Muell.) Domin	N	1
<i>Leucaena leucocephala</i> (Lam.) de Wit	I	1
<i>Neptunia dimorphantha</i> Domin	N	1
<i>N. monosperma</i> F. Muell. ex Benth.	N	1
Derived "Mimoseae"		
<i>Adenantha abrosperma</i> F. Muell.	N	2
<i>Entada phaseoloides</i> (L.) Merr.	N	2
Genus <i>Senegalia</i>		
<i>Senegalia</i> sp.	E	3
"Ingeae"		
<i>Albizia lebbek</i> (L.) Benth.	N	4
<i>Parachidendron pruinsum</i> (Benth.) I. C. Nielsen	N	4
Genus <i>Acacia</i>		
Section <i>Botrycephalae</i>		
<i>A. baileyana</i> F. Muell.	N	5
<i>A. cardiophylla</i> A. Cunn. ex Benth.	N	5
<i>A. chinchillensis</i> Tindale	N	5
<i>A. deanei</i> subsp. <i>deanei</i> (R. T. Baker) M. B. Welch, Coombs & McGlynn	N	5
<i>A. glaucocarpa</i> Maiden & Blakely	N	5
<i>A. irrorata</i> Sieber ex Spreng.	N	5
<i>A. oshanesii</i> F. Muell. & Maiden	N	5
<i>A. spectabilis</i> A. Cunn. ex Benth.	N	5
Section <i>Juliflorae</i>		
<i>A. aneura</i> F. Muell. ex Benth.	N	5
<i>A. cambagei</i> R. T. Baker	N	5
<i>A. chisholmii</i> F. M. Bailey	N	5
<i>A. holosericea</i> A. Cunn. ex G. Don	N	5
<i>A. shirleyi</i> Maiden	N	5
Section <i>Lycopodiifoliae</i>		
<i>A. spondylophylla</i> F. Muell.	N	5
Section <i>Phyllodineae</i>		
<i>A. conferta</i> A. Cunn. ex Benth.	N	5
<i>A. falcata</i> Willd.	N	5
<i>A. podalyriifolia</i> A. Cunn. ex G. Don	N	5
<i>A. salicina</i> Lindl.	N	5
<i>A. victoriae</i> Benth.	N	5
Section <i>Plurinerves</i>		
<i>A. complanata</i> A. Cunn. ex Benth.	N	5
<i>A. coriacea</i> DC	N	5

TABLE 3 (Continued)

Species	Status	Degree of phylogenetic separation
<i>A. excelsa</i> Benth.	N	5
<i>A. simsii</i> A. Cunn. ex Benth.	N	5
<i>A. stenophylla</i> A. Cunn. ex Benth.	N	5
Section Pulchellae		
<i>A. drummondii</i> Lindl.	N	5
<i>A. pulchella</i> R.Br.	N	5
Peltophorum clade		
<i>Delonix regia</i> (Boj. ex Hook.) Raf.	OI	6
Cassieae clade		
<i>Senna artemisioides</i> subsp. <i>helmsii</i> (Symon) Randell/subsp. <i>oligophylla</i> (F. Muell.) Randell	N	7
Subfamily Faboideae Rudd		
<i>Hardenbergia violacea</i> (Schneev.) Stearn	N	8
A crop species (e.g., <i>Phaseolus</i> sp., <i>Cajanus cajan</i> (L.) Millsp.)	C	8
Subfamily Dialioideae LPWG		
<i>Petalostylis labicheoides</i> R.Br.	N	9
Subfamily Cercidoideae LPWG		
<i>Bauhinia hookeri</i> F. Muell.	N	10

Note. C: crop; E: exotic, non-invasive; I: invasive; N: native; O: ornamental; TW: target weed.

Outside of the former Mimosoideae, the test list is greatly reduced compared to past test lists. As Mimosoideae has merged with Caesalpinoideae (s.s.) to form the new Caesalpinoideae (s.l.), a native and an ornamental species from the Caesalpinoideae (s.s.) have been included in the proposed test list: the widespread species *Senna artemisioides* (Gaudich. ex DC) Randell and the common exotic street tree *Delonix regia* (Boj. ex Hook.) Raf. In anticipation of requests for a broader test list, we have included several species from other legume subfamilies including the large subfamily Faboideae (syn. Papilionoideae). No non-leguminous species are included in the new test list.

This is a timely review of the host test list and the result is a relatively concise list that reflects current knowledge of phylogenetic relationships amongst *Acacia* s.l., while still meeting likely concerns of regulatory bodies. The list will no doubt evolve as relationships within the legumes are further resolved. This is a flexible list that acts a framework which can be modified as needed. In reality, the list of species actually tested for a potential agent will be greater than the 46 specified here; at least eight species were added to the prescribed lists for *Chiasmia* spp. and *C. pyralis*. Reasons for this may include feeding and/or prolonged survival on a test species (congeners may be added) or requests by stakeholders.

3 | CONCLUDING REMARKS

Our understanding of plant relationships and evolutionary history is growing every day and accepted relationships within and between many groups are changing (Stevens, 2018). Whereas in the past, test lists were often prescribed lists (certainly in Australia) that may have been used for multiple agents, these days a greater level of flexibility is required. Sites such as the Angiosperm Phylogeny Website (APW; Stevens, 2018) should be checked regularly as significant changes to

plant groupings can and do occur, and these can affect test list composition. The APW follows the widely accepted Angiosperm Phylogeny Group (APG) classification (see Angiosperm Phylogeny Group, 2016 for their most recent classification), and is regularly updated.

While it is critical for researchers to stay abreast of scientific advances, biological control scientists are constrained by a risk-averse political and regulatory environment (Hinz, Schwarzländer, Gassmann, & Bouchier, 2014; Moran & Hoffmann, 2015), as it is these bodies who are responsible for approving the release of weed biological control agents. Although the CPM for selecting test plants has been superseded to better reflect our current knowledge of host-choice behaviour and plant relationships; regulatory bodies, and indeed some weed biological control researchers, still adhere to the 40-year-old guidelines (Briese, 2005; Sheppard et al., 2005). Unfortunately, there is still an expectation to test plants from as many related taxonomic groups as possible (rather than focusing on the degree of relationship between target and non-target species) and include safeguard species. The reality is that a lengthy test list is no more informative; it purely serves to provide a degree of comfort to regulatory bodies and the general public, who are slower to accept scientific advances.

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ENDNOTE

¹*V. farnesiana* is believed to have been introduced to Australia prior to European settlement and as such it has been considered to be native.

However, it is now recommended that species be considered alien (Bean, 2007).

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