

Biological control of mesquite (*Prosopis* species) (Fabaceae) in South Africa

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The biological control programme against *Prosopis* species (Fabaceae) (mesquite) in South Africa has reached a stage where the already-established agents, *Algarobius prosopis* (LeConte) and *Neltumius arizonensis* (Schaeffer) (both Coleoptera: Chrysomelidae: Bruchinae), are considered to be inadequate. Other potential agents have been identified, including nine beetle species, four moths and a gall midge. Of these, a straight-snouted weevil, *Coelocephalopion gandolfoi* Kissinger (Coleoptera: Brentidae: Apioninae), whose larvae attack seeds within green pods, is considered especially promising and has been subjected to host-range tests. The biology, ecology and host range of a flowerbud galler, *Asphondylia prosopidis* Cockerell (Diptera: Cecidomyiidae), have also been investigated. Some pathogens have been considered, as either classical biological control agents or as mycoherbicides. Ongoing debates about the relative value and costs of the trees continue to hamper progress with the planned escalation of biological control. Recent assessments show that the costs of mesquite will soon outweigh the benefits in most situations, opening opportunities to clear additional agent species for release. The results of studies since 1999 on the established and the prospective agents on mesquite are reviewed, while considering the issues that need to be addressed to enable the biological control programme to proceed.

Key words: Bruchinae, Apioninae, Cecidomyiidae, pathogens, invasive alien trees.

INTRODUCTION

Several species of thorny, leguminous trees in the genus *Prosopis* L. (Fabaceae), commonly called mesquite or prosopis, have become invasive in the arid northwestern parts of South Africa over the past half-century. Originally introduced from North and South America in the late 1800s, they were promoted as useful trees and widely distributed and planted until 1960. Their main uses include provision of shade for livestock, timber for furniture and construction, pods for fodder, wood for fuel and charcoal, and a nectar source for honey production (Zimmermann 1991; Zimmermann *et al.* 2006). Widespread, deliberate planting provided multiple sources of seed which were spread far and wide, both endozoochorously and through flooding events. These invasive trees now occur over several million hectares in the Northern Cape, Western Cape, Free State and North West provinces, forming extensive, impenetrable thickets over large areas. Besides overrunning grazing land, consuming excessive quantities of ground-water and negatively affecting biodiversity, the plants within dense infestations no longer provide

the services that make them useful (*i.e.* they have no flowers or pods, they are too small and diffuse to provide shade and their trunks are too thin to be useable for timber, fuel-wood or charcoal).

Taxonomy and phylogeny

Zimmermann (1991) reviewed the taxonomy and the means of introduction and spread of *Prosopis* species in South Africa. He noted that six taxa are recognized to be naturalized, with *Prosopis velutina* Wootton (Fig. 1) and *Prosopis glandulosa* var. *torreyana* (Benson) Johnst. (Fig. 2) being the most troublesome. While *Prosopis juliflora* (Sw.) DC. and *Prosopis glandulosa* var. *glandulosa* J.Torrey are also invasive, they are less so than the first two species, and *Prosopis chilensis* (Molina) Stuntz and *Prosopis pubescens* Benth. rarely show signs of invasiveness (Harding 1987; Harding & Bate 1991). Of the six taxa, *P. chilensis* is native to Peru, Bolivia, central Chile and northwestern Argentina, *P. juliflora* is native to northern South America and Central America and the other four species are native to southwestern North America.

Although these taxonomic placements have

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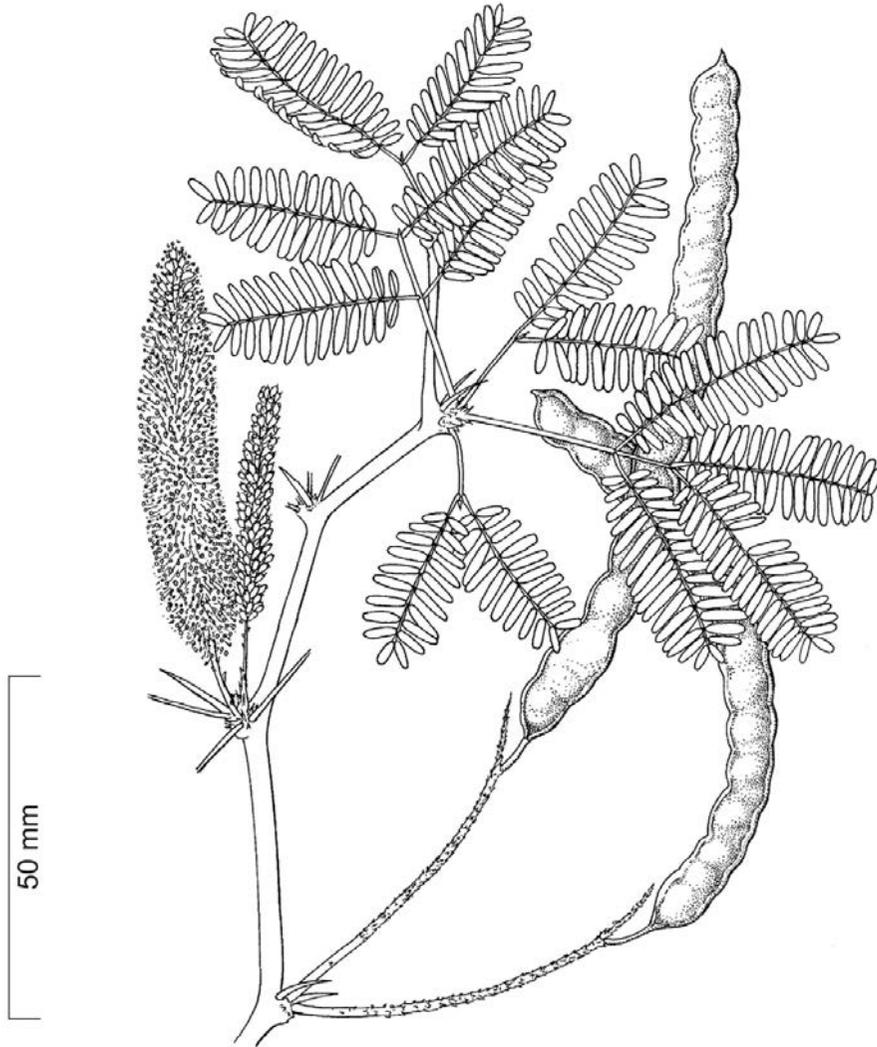


Fig. 1. *Prosopis velutina*. (Drawn by G. Condy; first published in Henderson & Harding (1992), ARC-Plant Protection Research Institute, Pretoria.)

been recognized, the identity and provenance of much of the material brought into South Africa in the late 19th and early 20th centuries is uncertain. From the start, mixtures of seeds from at least three species were imported from North America, allowing hybridization and giving rise to taxonomic uncertainty (Harding 1987). The only South American species, *P. chilensis*, came to South Africa from Namibia whence it had been introduced during an agroforestry project. Difficulty in identifying individual species (Pasiiecznik *et al.* 2006) has heightened and prolonged the taxonomic confusion. Proper identification of the target pest

may have implications for the success of biological control, in terms of ensuring compatibility of agents with their host-plant species (Zwölfer & Harris 1971; Volchansky *et al.* 1999; Lym & Carlson 2002; Manrique *et al.* 2008; Mathenge *et al.* 2010). Molecular studies which have elucidated much of the phylogeny and relationships within the genus *Prosopis* (Catalano *et al.* 2008) may provide the clarity that is needed.

The genus *Prosopis*, which contains about 45 species, has a centre of diversity in the Americas. The genus is divided into five sections, with the two main ones, *Algarobia* and *Strombocarpa*,

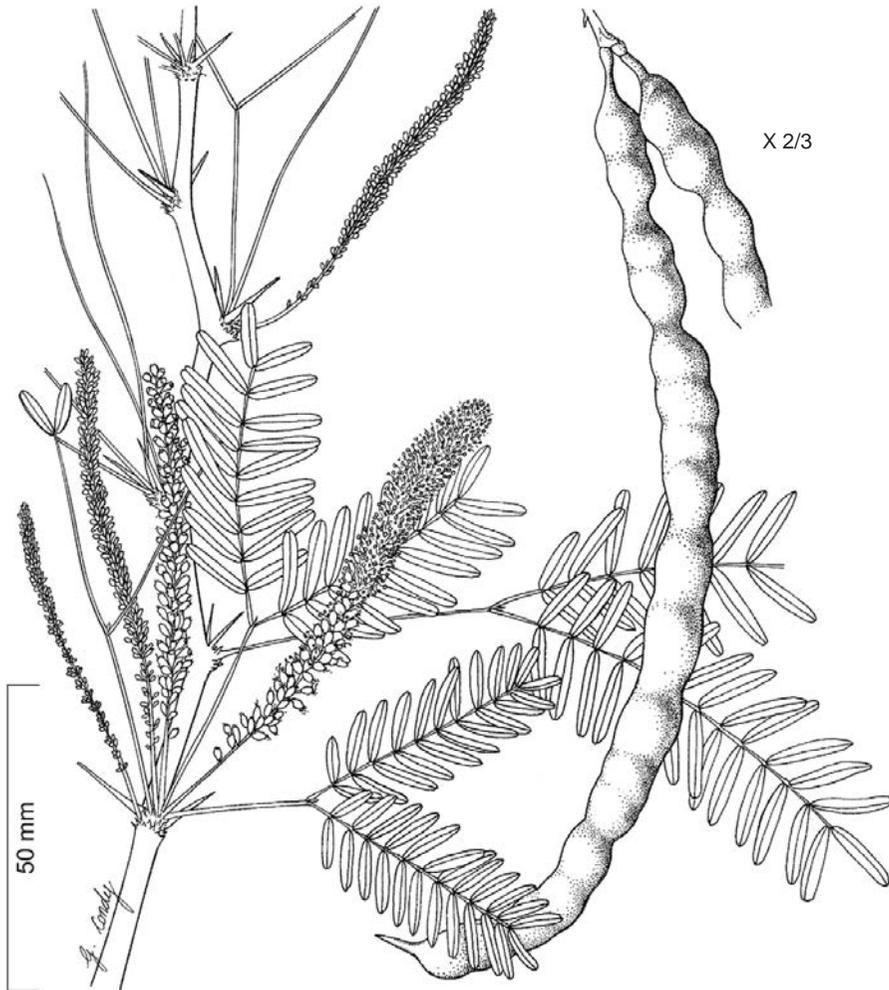


Fig. 2. *Prosopis glandulosa* var. *torreyana*. (Drawn by G. Condy; first published in Zimmermann (1991), ARC-Plant Protection Research Institute, Pretoria.)

native to the Americas and containing about 90 % of the species within the genus (Catalano *et al.* 2008). Section *Monilicarpa* comprises only one species endemic to central Argentina, while sections *Anonychium* and *Prosopis* are restricted to the Old World, ranging from the Sahel region of Africa through to India and containing one and three species, respectively (Catalano *et al.* 2008). Phylogenetic analyses indicated that the genus *Prosopis* is polyphyletic and that the Old World species of *Prosopis* are not closely related to American species of *Prosopis*, having diverged >30 Mya (Catalano *et al.* 2008).

All of the invasive *Prosopis* species in South Africa, except for *P. pubescens* (section *Strombocarpa*,

series *Strombocarpae*), are members of section *Algarobia*, series *Chilensis*. This would explain the hybridization that has complicated matters in South Africa. It also presents a positive aspect for biological control because any oligophagous agents that feed across several species within the series should be ideal for controlling the mix of invasive species in South Africa, without presenting any risk to the Old World species which are distantly related to American *Prosopis* species (Catalano *et al.* 2008). New World *Prosopis* species are in fact more closely related to a shrub *Xerocladia viridiramis* (Burch.) Taub. (Fabaceae) which is endemic to Namibia and Namaqualand, than they are to Old World *Prosopis* species.

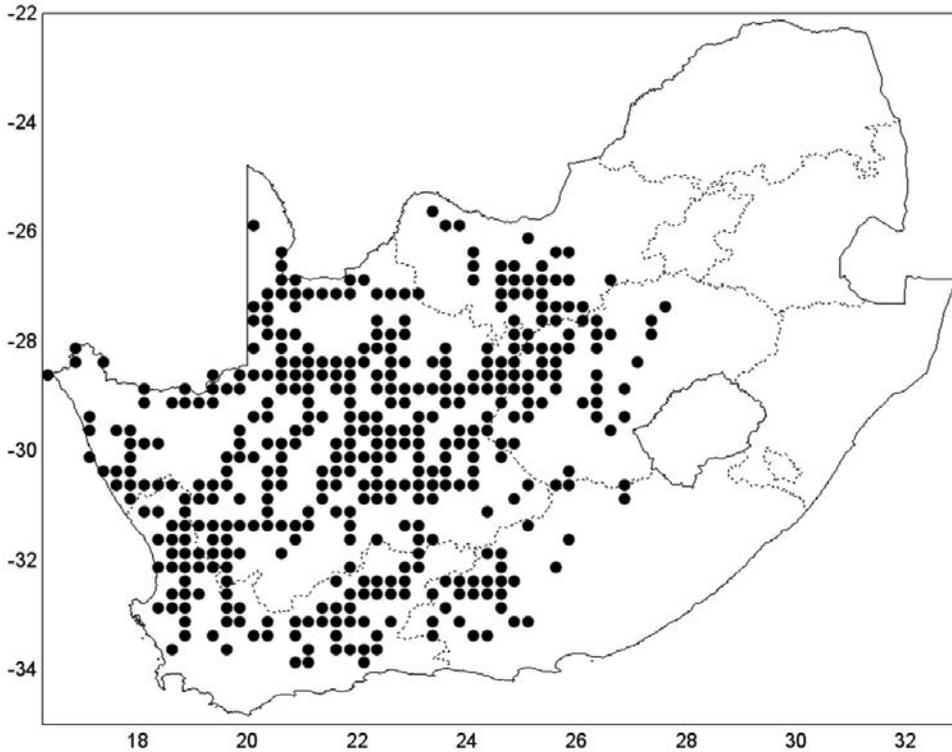


Fig. 3. Distribution of *Prosopis glandulosa* var. *torreyana*, *P. velutina* and their hybrids in South Africa. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

Spread, densification, and area infested

Estimates of the historical rate of spread of *Prosopis* species in South Africa range from 3.5–18 % per annum although, at times, the rate of spread may be as high as 30–40 % (Wise *et al.* 2011). Once mesquite has established in an area, the density of the infestations increase at annual rates of 2.5–10 % (Wise *et al.* 2011). Mesquite is now present through much of the western half of South Africa (Fig. 3), and several estimates of the area of the entire country or of individual provinces infested with this weed have been made over the past decade. Versfeld *et al.* (1998) estimated the total area of occurrence, nationally, to be 1 800 000 ha, of which approximately 55 % is in the Northern Cape Province, translating into a 'condensed area' of 173 149 ha. Although Kotzé *et al.*'s (2010) figure for the total area infested by mesquite in South Africa agrees closely with that of Versfeld *et al.* (1998), their estimate of condensed area, at 422 687 ha, is much higher. However, because their methodologies differ, the areas estimated by Versfeld *et al.* (1998) and Kotzé *et al.* (2010) are not

directly comparable. Van den Berg (2010) estimated the area infested in the Northern Cape Province to be almost 1 500 000 ha, which Wise *et al.* (2011) divided into those in uplands comprising 1 022 000 ha with an average density of 21 % cover, and in the floodplains comprising 453 000 ha, at an average density of 33 % cover.

Estimates of the future realized-range of mesquite in South Africa diverge widely. Wise *et al.* (2011) estimated that the potential area in South Africa suitable for *P. glandulosa* var. *torreyana* and the *P. glandulosa* var. *torreyana* × *velutina* hybrid is in the region of 56 million ha, including 85 % (32 million ha) of the Northern Cape Province, whereas van den Berg (2010) gives a much lower figure of 5 million ha likely to be invaded in this province.

Henderson (2007) ranked invasive alien plants in South Africa using a biome-based approach. *Prosopis* species were the tenth most prominent species in South Africa, the most prominent in the Nama-Karoo Biome (the second largest biome in South Africa), and the third most prominent in the Succulent Karoo Biome. *Prosopis* species were

within the top ten invasive species in riparian and wetland habitats. Other recent assessments also rank *Prosopis* species among the most problematic of the invasive plant species in South Africa (Robertson *et al.* 2003; Nel *et al.* 2004).

The spread of mesquite and the formation of expansive infestations have been enhanced by livestock and game which consume the ripe seed-pods and disperse scarified seeds. Mesquite seed is long-lived and may accumulate over time in sizeable seed banks which persist for at least 20 years (Martin 1970). In South Africa, the size of seed banks varies across the distributional range of mesquite and is affected by the presence or absence of livestock, with accumulations of as many as 2500 seeds/m² in some areas (Roberts 2006).

Costs and benefits of mesquite

Changes in priorities over time led to changes in perceptions of the problems caused by invasive alien plants. Impacts of *Prosopis* species on water resources and biodiversity in southern Africa have received relatively recent, heightened recognition. Mesquite invasions alter the hydrology of water-impooverished ecosystems, and have been estimated to use approximately 192 million m³ of water annually (Le Maitre *et al.* 2000), the equivalent of approximately 1100 mm of rainfall, which is four times the average amount that falls in the affected areas (Versfeld *et al.* 1998; Zimmermann *et al.* 2006). The plants cope with the resulting deficit by utilizing ground water which in turn lowers the water table and further alters the ecology of affected regions, especially by causing extensive mortality of *Acacia erioloba* E.Mey. (Fabaceae), a keystone indigenous species which is particularly abundant along drainage lines (Robertson & Woodborne 2002; Schachtschneider 2010). Both botanical and avian diversity were lower in dense mesquite stands compared to native *Acacia* woodland along drainage lines in the Kalahari region of South Africa (Dean *et al.* 2002).

Wise *et al.* (2011) indicated that the main uses for mesquite in the Northern Cape Province currently are: (i) pods for livestock consumption, (ii) pods for medicinal purposes, and (iii) firewood. They distinguished between upland and floodplain areas in the Northern Cape because mesquite infestations reach a greater density in the floodplains and the plant's incremental water usage (*i.e.* how much more water mesquite uses compared to native vegetation) is also higher in the floodplains.

They calculated that, currently, the net economic return from mesquite on both floodplains and uplands is positive because the average densities of mesquite are quite low, and thus the benefits delivered by pods and firewood exceed the deleterious effects on water and pasture. However, current clearing efforts are having no impact on the infestations. If the *prosopis* infestations continue to increase in density and extent at current rates, the net returns will become negative in floodplains within about 8–16 years. Further, under a 'pessimistic' scenario of per-annum spread and densification rates in the floodplains of 30 % and 10 %, respectively, and in the uplands 15 % and 5 %, over the next 25 years the positive returns from upland areas will not compensate for negative returns from the floodplain areas, leading to an overall negative economic impact. Wise *et al.* (2011) suggested that in order to maintain a net economic gain, it would be better to focus clearing efforts in floodplain areas, but also to develop cheaper control methods.

Another recent study (Dube 2009) assessed the value that sheep farmers in the Northern Cape Province placed on mesquite pods and the economic impacts that a 50 % and 100 % reduction in pods would have on them. The use of pods for human medicinal purposes was included in the study. Although the farmers in question did place some value on pods, they generally considered that the negative impact of mesquite due to water loss was of much greater importance. The use of pods for medicinal purposes would probably be negatively affected by pod reductions greater than 50 %.

Control and management options

Several control methods have been investigated for management of mesquite, including mechanical removal, felling and herbicide treatment of cut stumps, foliar spraying of saplings, and burning (Harding 1987; van Klinken *et al.* 2009). None of these are affordable or practical on a large scale and costs of control generally far exceed the value of invaded land. Wise *et al.* (2011) estimated that in South Africa US\$109.1 million and US\$76.6 million (US\$1 = c. R7 in March 2011) would be needed to clear the invaded uplands and floodplains respectively. Clearing costs per hectare vary from US\$13–534 depending on the densities of the infestations. Zimmermann *et al.* (2006) discussed utilization of mesquite pods and wood as a

management tool but concluded that the remote areas in which *prosopis* mostly grows and the lack of harvestable material generally, makes this option uneconomical.

Biological control

A biological control programme was initiated against mesquite in South Africa in the mid-1980s. To date the programme has focused on seed-feeding insects which could theoretically regulate expansion of the weed while allowing it to persist and be exploited for its useful assets and services. By reducing seed production, and therefore the recruitment rates of young plants, it was envisaged that sparse populations of large, widely-spaced, useful trees could be retained without dense thickets forming. This strategy resulted in the introduction and release of three beetle species, *Algarobius prosopis* (LeConte) and *Algarobius bottimeri* Kingsolver, in 1987 and 1990, respectively (Zimmermann 1991), and *Neltumius arizonensis* (Schaeffer) in 1992 (Impson *et al.* 1999) (all Coleoptera: Chrysomelidae: Bruchinae). *Algarobius bottimeri* persisted for a short period after release but eventually failed to establish (Hoffmann *et al.* 1993; Impson & Hoffmann 1998). Biological control of *Prosopis* species in South Africa during the 1980s and 1990s was reviewed by Zimmermann (1991), Moran *et al.* (1993) and Impson *et al.* (1999). In aggregate, biological control efforts in South Africa have not been successful in alleviating the *prosopis* problem. Van Klinken *et al.* (2009) provide a more recent global perspective on invasive species of mesquite and their control. The present review deals exclusively with developments within South Africa during the period from 1999 to the present.

Initiatives over the past ten years

In 2001, a workshop held in Kimberley, South Africa, to discuss the 'Status and long-term management of *prosopis*' was attended by over 50 stakeholders representing many disparate spheres of society and government (Anon. 2001; Zimmermann & Pasiecznik 2005; Zimmermann *et al.* 2006). One of the resolutions emanating from this workshop was to broaden the possibilities for biological control by accepting that agents which might prevent flower and seed-pod production altogether, could be considered. This opened the way for phytophages that use the buds, flowers and immature pods to be investigated to reduce

seeding, densification and dispersal of mesquite. The Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI) was consequently commissioned to conduct research on insect and pathogen species attacking the reproductive parts of *Prosopis* species in both North and South America. Two recent cost:benefit studies (Dube 2009; Wise *et al.* 2011) also recommended that further biological control agents be investigated. However, the status of mesquite in South Africa, and introduction of agents that will damage plant parts other than seeds, remains controversial.

In any event, nine beetle species, four moths and one gall midge collected from *Prosopis* species in Argentina, within the section *Algarobia*, series *Chilensis* (six species), *Sericanthae* (one species), *Pallidae* (one species) and *Ruscifoliae* (two species), were assessed (Mc Kay & Gandolfo 2007). One of these, the straight-snouted weevil *Coelocephalapion gandolfoi* Kissinger (Kissinger 2005) (Coleoptera: Brentidae: Apioninae), whose larvae attack seeds within green pods on the trees, was considered especially promising and host-range tests were conducted. At the same time a study was conducted in the U.S.A. on aspects of the biology, ecology and host range of the flowerbud galler, *Asphondylia prosopidis* Cockerell (Diptera: Cecidomyiidae), which was another species considered as a promising agent. Pathogens were investigated as both classical biological control agents and as mycoherbicides. Further assessment of the agents already established in the field was also conducted (Roberts 2006; van Klinken *et al.* 2009). These developments are reviewed below.

PROSPECTIVE BIOLOGICAL CONTROL AGENTS

Coelocephalapion gandolfoi

The apionid, *C. gandolfoi*, was collected from nine species of *Prosopis* (all section *Algarobia*) over a latitudinal gradient of 1500 km in Argentina, under a contract between the ARC-PPRI and the South American Biological Control Laboratory of the United States Department of Agriculture (USDA-SABCL) in Buenos Aires. Adult weevils are small and brown to black in colour. Reproductively mature adults first appear at the beginning of spring (late September). They feed on the young green pods and leaves, and oviposit near the seeds inside the tender pod tissues (Mc Kay & Gandolfo 2007; F. Mc Kay, D. Gandolfo & A. Witt, unpubl.).

Newly-hatched larvae enter the seeds where they complete their life cycle, with adult progeny emerging from the ripening pods about 40 days after oviposition. By then the pods are unsuitable for further oviposition. Laboratory tests using young pods suggest that the newly-enclosed adults are reproductively immature. The species is probably univoltine, with adults feeding on mesquite foliage through the summer and going into quiescence with the onset of winter (F. Mc Kay, D. Gandolfo & A. Witt, unpubl.). Levels of seed damage, determined using *Prosopis flexuosa* DC. in the field, were high, with 99 % of trees, 90–96 % of pods, and 51–100 % of seeds within the pods being damaged. The females preferred ovipositing on undamaged pods.

Adult host specificity was determined in the laboratory, both in Argentina and South Africa (F. Mc Kay, D. Gandolfo & A. Witt, unpubl.). Because it was not possible to breed the insect in the laboratory, field-collected adults were used for all tests. Oviposition on severed green pods and feeding on pods and on bouquets of foliage was observed. Reproductively immature adults were used only to evaluate feeding preferences. Initially, no-choice tests were performed on 45 test plant species and six *Prosopis* species controls. The test plants were selected to achieve representation within the three Leguminosae subfamilies, but African *Acacia* species were prioritized. Large numbers of eggs were laid on pods of the four control species exposed to reproductively mature adults, and moderate to intense feeding damage was recorded on the four control species exposed to immature adults. No eggs were laid on any of the test plant species, but a negligible amount of feeding by the adults was noted on several species of test plants. Follow-up, paired-choice tests were conducted on 15 species of test plants on which feeding had been recorded in the no-choice tests. Although there was still some feeding on the pods of five of these species, this remained negligible in comparison to that recorded on the control plants.

The field host range of *C. gandolfoi* was also evaluated in Argentina using *Prosopis kuntzei* Harms ex Hassler (section *Algarobia*, series *Sericanthae*), *Prosopis torquata* (Cav. ex Lag.) DC. and *Prosopis strombulifera* (Lam.) Benth. (both section *Strombocarpa*, series *Strombocarpaceae*) and using *Leucaena leucocephala* (Lam.) de Wit (Fabaceae). No damage was found on these four species, despite the presence of damage on nearby

host species (F. Mc Kay, D. Gandolfo & A. Witt, unpubl.).

It appears that *C. gandolfoi* is adequately host specific for release in South Africa. Climate matching between its native range and the region of infestation by *Prosopis* species in South Africa is apparently close (F. Mc Kay, D. Gandolfo & A. Witt, unpubl.). Several other Apionidae species have been used, some successfully, as biological control agents against invasive alien plants in the Fabaceae and other families (Julien & Griffiths 1998; Hoffmann & Moran 1991; Urban *et al.* 2011). Given that all invasive *Prosopis* species in South Africa are within the section *Algarobia*, series *Chilensis*, and the weevil attacks a number of species within the same taxon in their native range, they can be expected to successfully utilize the invasive species within South Africa. However, given that the majority of *Prosopis* species in South Africa are of northern hemisphere provenance, *C. gandolfoi* would still be considered as a largely 'new association' agent (*sensu* Hokkanen & Pimentel 1989). That this need not be viewed as a drawback is evidenced by the success of *Evippe* sp. no. 1 (Lepidoptera: Gelechiidae), established and effective on *Prosopis* species in Australia (van Klinken *et al.* 2009), which is also a new-association biological control agent.

Mc Kay & Gandolfo (2007) stated that: 'although larvae destroy the seeds, pods still develop, apparently without losing much of their value as fodder'. Given the ongoing uncertainty regarding the introduction of new biological control agents which will reduce pods as a resource, *C. gandolfoi* appears well placed to reduce seed set without reducing pod production, although it may be necessary to determine in more detail whether pods in Argentina do lose any nutritive value once they have been attacked by the weevil. By utilizing the pods while they are still attached to the trees, *C. gandolfoi* will avoid the problem faced by the *Algarobius* bruchine beetles of having to compete with vertebrate granivores for pods that have fallen to the ground.

Cecidomyiidae

The gall midge, *A. prosopidis*, was recommended as a potential biological control agent for South Africa by DeLoach (1992). It has a natural range in southwestern North America, and has been recorded attacking several *Prosopis* species, predominantly within the section *Algarobia*, series

Chilensis. Adult females lay eggs in flower buds and galls form thereafter from ovarian tissue, each containing a single larva and preventing flowering and hence seed set. Thus in the presence of midges, racemes of galls can replace racemes of flowers. Pupation occurs within the gall. Following the resolution at the 2001 Kimberley workshop in South Africa, New Mexico State University (NMSU) was contracted by the ARC-PPRI to conduct further studies on the midge, in particular its biology and methods for mass-rearing, mortality factors and impact in the field, and some host-range studies (both surveys and manipulative).

During this study it became apparent that the *A. prosopidis* system was considerably more complex than anticipated. Previous researchers had noted three gall forms, and in the current study a fourth was identified (Thompson 2009; Park 2010). These consisted of one 'perseverant' form, which sometimes persisted on the tree for over two years (named PV), and three 'abortive' forms, which became detached from the trees after as little as a month after initiation. These were a large teardrop (LT) form, from which the original *A. prosopidis* was described; a small teardrop (ST) form, and the previously unrecorded barrel form (AB). More than one gall type can sometimes be found on a single raceme.

In order to characterize the midges from each of these gall forms, a molecular study on insects from the four gall forms collected off *P. glandulosa* was conducted using a mitochondrial (COI) locus. This provided strong evidence that each of the four gall forms was associated with a different *Asphondylia* species, with *A. prosopidis* causing only LT galls (Thompson 2009; Park 2010). Examination of the pupae indicated that morphological differences between the four species were visible (Park 2010).

PV-gall midges are univoltine and have little potential as biological control agents because field populations are generally low (Thompson 2009) and adults only emerge early in the flowering season and thus have no effect on most of the flowers that are set. The lifecycle of the three abortive forms was similar during summer, with a minimum developmental duration of 23 days under midsummer conditions and up to six generations over the entire summer. However, overwintering strategies differ, with AB midges overwintering successfully as first instar larvae, whereas no successful overwintering for LT or

ST midges was recorded, leading to the suspicion that they may use an alternate host. Cold weather in autumn and winter kills many immature midges within galls on the trees, with about 50 % overwintering mortality of AB and PV midges (Thompson 2009).

The proportion of total galls that each gall-form comprised varied from year to year over the three years that surveys were conducted (2005–2007). Abortive galls represented the majority (90.7–92.1 %), within which LT increased from 7.6–59.1 % and AB decreased from 52.7–18.0 % over the three years (Thompson 2009). On average, 38.7–52.6 % of abortive gall forms were parasitized, compared to 10.5–16.1 % of PV galls. The LT and ST galls were more heavily parasitized (maximum 77.0 %) than AB galls (maximum 33.6 %). Some galls within all the forms were found to be empty, indicating other mortality factors were also affecting the midges.

Like many cecidomyiid species, it appears that the *Asphondylia* species forming AB galls is monogenic, *i.e.* a single female produces progeny of only one gender. Of 53 racemes collected from the field, 90 % produced only one gender of midge (Park 2010). The highest number of male and female galls on a single raceme was 81 and 51, respectively.

Many *Asphondylia* species are associated with communities of fungi in their galls (Adair *et al.* 2009). It is probable that some of these fungi are symbionts which aid in larval development. Molecular characterization of the fungus growing within LT galls (*i.e.* *A. prosopidis sensu stricto*) indicated that it was *Botryosphaeria dothidea* (Morig. ex Fr.) Ces & de Not. (Botryosphaerales: Botryosphaeriaceae), previously isolated from *Asphondylia* galls on a range of other plant species in South Africa, Europe, South America and Australia (Adair *et al.* 2009; Park 2010).

Studies of the impact of the *A. prosopidis* midge complex on mesquite in the southwestern U.S.A. were not encouraging. Surveys of trees in the field indicated generally low rates of galling. Of several hundred *P. glandulosa* trees inspected during the growing season over three years, 7.2–11.3 % bore galls, of which 6.9–8.0 % were abortive and 2.2–6.0 % perseverant (Thompson 2009). The total racemes galled on these trees was far lower, varying from 0.008–0.05 % of all racemes counted on all the trees. However, typically when a raceme was attacked, no seed pods were produced. Trees in

less water-stressed environments (including those in 'landscape' settings which had been planted and, or, irrigated) were noted to be more frequently galled (e.g. 45 %) and often to have much higher gall loads (up to 4000). Also, mesquite trees flower most prolifically in spring when galling intensity is lowest. A winter survey over three states (Texas, Arizona, New Mexico) in 2007 indicated higher percentages (average 27 %) of trees with PV galls (Thompson 2009).

In terms of host range, most galls were found on *P. glandulosa* (varieties *glandulosa* and *torreyana*), *P. velutina* and their hybrids (both species are in section *Algarobia*, series *Chilensis*). Infrequently galls were found on *P. pubescens* (section *Strombocarpa*, series *Strombocarpaceae*) trees. *Acacia constricta* Benth. (25 plants), *Acacia smallii* Isley (both Fabaceae) (5 plants), and *Fallugia paradoxa* (D. Don) Endl. ex Torr. (Rosaceae) (25 plants), were inspected in the field (Thompson 2009). None had *A. prosopidis*-like galls. Attempts at inducing galling through the release of adults into field cages with flowering mesquite trees provided inconsistent results, preventing manipulative host-range testing from being conducted.

Prosopidicola mexicana Crous & C.L. Lennox (Diaporthales: Valsaceae) and other pathogens

Zimmermann *et al.* (2006) reviewed recent research on pathogens as biological control agents and mycoherbicides of mesquite. A promising disease causing flattening of the pods and seed decay was collected in Mexico and the U.S.A. (Texas) off *P. glandulosa* (Lennox *et al.* 2004) and described as *Prosopidicola mexicana* Crous & C.L. Lennox. Although it was isolated from diseased pods, it was able to attack foliage under quarantine conditions and could therefore not be investigated further while a moratorium is in place on agents attacking non-reproductive parts of the plant (A. Wood, pers. comm.). The mycoherbicide BioChon™, containing *Chondrostereum purpureum* (Pers.) Pouzar (Polyporales: Meruliaceae), was tested on mesquite in quarantine at the ARC-PPRI, as the product is European, but it was not effective. The stump inoculant, StumpOut™, containing *Cylindrobasidium laeve* (Pers.: Fr.) Chamuris (Agaricales: Physalacriaceae), was tested in the field, but also was not effective. This is not surprising as StumpOut is ineffective against species that coppice strongly from the crown region (A. Wood, pers. comm.).

Foliage-feeding agents deployed in Australia

There are no conflicts of interest with regards to the biological control of *Prosopis* species in Australia. This has allowed the release of two foliage-feeding agents, *Evippe* sp. no. 1 and *Prosopidopsylla flava* Burckhardt (Hemiptera: Psyllidae) (van Klinken *et al.* 2009). Both species have established, but *Evippe* sp. no. 1 is by far the most successful agent. Should restrictions on the release of agents attacking stems, foliage and roots be lifted in South Africa in the future, agents that have proved damaging in Australia should be considered for release in South Africa with little additional pre-release research work necessary.

RECENT RESEARCH ON THE ESTABLISHED BIOLOGICAL CONTROL AGENTS IN SOUTH AFRICA

Both *A. prosopis* and *N. arizonensis* persist on mesquite throughout South Africa but *A. bottimeri* has not persisted (Impson & Hoffmann 1998). The failure of *A. bottimeri* may have been a consequence of release in areas (Free State Province) that are unfavourable for the beetles, as is suggested by low *A. prosopis* populations in these areas (Roberts 2006). The relative scarcity of *N. arizonensis* (it seldom accounts for more than 10 % of the total seed destruction by the bruchines in a year) (Roberts 2006) is attributed to competition with *A. prosopis* (Impson & Hoffmann 1998) and indigenous egg and larval parasitoids, particularly the egg parasitoid *Uscana* sp. (Hymenoptera: Trichogrammatidae), which may account for as much as 80 % egg loss at certain times (Coetzer & Hoffmann 1997; Roberts 2006).

The oviposition behaviour of *A. prosopis* may explain its predominance in the system. Eggs are deposited and concealed in cracks and fractures in the pods, making them less vulnerable to egg parasitoids than the eggs of *N. arizonensis* which are attached, fully exposed, on the pod surfaces (Strathie 1995). Furthermore, unlike *N. arizonensis* which requires newly-formed, pristine pods on which to deposit its eggs (Strathie 1995), for *A. prosopis*, pods remain suitable for oviposition for a much longer period and continue to be used as they weather and disintegrate. It is assumed that both *A. prosopis* and *N. arizonensis* are equally susceptible to larval parasitism, with 24 species of hymenopteran parasitoids having been reared from pods containing bruchine larvae (Hoffmann

et al. 1993; Coetzer 1996; Roberts 2006). The incidence of these parasitoids is generally low and they do not account for more than 4 % cumulative loss of bruchine larvae over the course of the year.

In recent years, there has been an investigation into the presumption that the greatest curb on population expansion, and therefore efficacy, of *A. prosopis* and *N. arizonensis* is removal of the food source, the mature seed pods, by game and livestock, predominantly sheep. Although as much as 85 % of mesquite seed is destroyed on ingestion by sheep (Harding 1991), many scarified seeds are disseminated in dung in and around mesquite stands, readily germinating with the onset of rain. These seeds were assumed to be no longer available to the bruchines, but Roberts (2006) discovered that as much as 70 % of seed contained within dung is located, oviposited on, and supports larval development of *A. prosopis*. Roberts (2006) also showed that the use of dung-borne seed, dispersed away from tree canopies and warmed by sunlight, enables *A. prosopis* populations to complete at least two generations during winter when temperatures in fallen pods and dung pellets in the shade of trees are too low for larval development. In summer, the temperatures in dung exposed to sunlight become too extreme for *A. prosopis* larvae and only dung in shade is used during this period of the year (Roberts 2006).

Although the beetles utilize seed contained within dung, seasonal temperature constraints and eventual disintegration of the dung pellets with time, leaves many seeds that are not usable and these enter the seed bank. The situation is confounded by as-yet-unidentified extraneous factors which affect seed survival. For example, in the southern and central areas of the range of mesquite, the soil seed banks are much higher in the presence of livestock (approximately 2000 seeds/m²) than in their absence (approximately 110 seeds/m²), while the reverse is true for the northeastern areas, around Kimberley, where seed banks are higher in the absence of livestock (1000 seeds/m²) than in their presence (140 seeds/m²) (Roberts 2006).

Roberts (2006) studied the dynamics of seeds and seedlings in both xeric and mesic areas where mesquite occurs in South Africa. In the arid to semi-arid areas, mesquite seeds germinate with the onset of rains, giving rise to cohorts of seedlings, most of which die unless there is a sustained period of rainfall, which never happened during

the three-year below-average rainfall period (2002–2005) under investigation. The germination events result in a dramatic decline in the size of seed banks until they are recharged with the next annual crop of seeds. Despite high levels of seed destruction due to stock ingestion and bruchine damage, there are still sufficiently large numbers of seed available for mesquite populations to expand and increase in density during favourable rainfall periods in arid areas. In more mesic areas where levels of seed destruction are generally lower, recruitment of seedlings occurs consistently on an annual cycle, a combination which enhances the invasive potential of mesquite and accounts for its greater rates of proliferation under these conditions compared to arid and semi-arid areas.

The role of biological control in overall management of mesquite

The stochasticity of the interactions between livestock, climate and biological control make it difficult to assess how much, if any, effect *A. prosopis* is having on the population dynamics of *Prosopis* species in South Africa. Recent evidence has shown that seeds may not be as long-lived as previously thought, in that two years after trees had been cleared from a site there were no seeds left in the soil (Roberts 2006). This reinforces perceptions that if livestock and wild animals are excluded from infestations, giving *A. prosopis* an opportunity to destroy almost all of the seeds produced each year, much could be achieved in curbing the rates of spread and densification of *prosopis* stands. In reality, this is unlikely to be possible and biological control still needs the official sanction to be expanded to include additional guilds of agents.

MESQUITE AND ITS BIOLOGICAL CONTROL ELSEWHERE IN AFRICA

Prosopis species from the Americas have been promoted as agroforestry species in the tropical arid and semi-arid regions of Africa since the early 20th century, but more intensively since the 1970s (Babiker 2006; Choge & Ngujiri 2006). They have become highly invasive but can nevertheless still be useful if exploited optimally (Geesing *et al.* 2004).

There has been considerable confusion as to the identity and distribution of American *Prosopis* species in tropical Africa. It appears that *Prosopis pallida* (H.B. ex Willd.) Kunth (section *Algarobia*,

series Pallidae) is more widely distributed than previously thought, having often been misidentified as *P. juliflora* (section Algarobia, series Chilensis) (Pasiiecznik *et al.* 2006). *Prosopis pallida* is less invasive and more useful than *P. juliflora*.

The use of classical biological control on *Prosopis* species in regions of Africa remains controversial for two reasons. Firstly, despite the large phylogenetic distance between the American and Old World taxa (Catalano *et al.* 2008), there is concern that such agents will attack species of *Prosopis* indigenous to Africa and Asia (Pasiiecznik & Felker 2006). For example, *Prosopis africana* (Guill. & Perr.) Taub. is an important but over-exploited agroforestry species through the Sahel region (Tchoundjeu *et al.* 1998). *Algarobius prosopis* is already present in northeastern Africa and the Arabian Peninsula, and although it attacks the seeds of introduced *Prosopis* species, it has not been recorded from *P. africana* or *Prosopis cineraria* (L.) Druce. (Babiker 2006; Ali & Labrada 2006). Secondly, there is concern that the introduction of biological control agents will lead to a reduction in introduced species of *Prosopis*, particularly those that are less invasive, such as *P. pallida*, thereby compromising their usefulness. However, as is the case for most classical biological control projects using seed-attacking agents, the agents are unlikely to reduce the value of the trees. Rather, they may increase usefulness by reducing propagule production, thereby thinning the trees so that flower and pod production and wood quality increases. It is likely that *C. gandolfoi* will attack *P. pallida*, given that it was collected off *P. affinis* Spreng. (also series Pallidae) in Argentina.

Although several indigenous insect species attack *P. juliflora* in Ethiopia, classical biological control is needed (Bedada & Tessema 2009). High levels of seed destruction by unidentified bruchines were recorded by Geesing *et al.* (2004) around the Niger part of Lake Chad.

DISCUSSION AND CONCLUSIONS

Infestations of mesquite, *Prosopis* species, continue to spread and become denser in the arid and semi-arid northwestern regions of South Africa, and although the trees continue to provide services, they also have substantial negative impacts.

Despite a resolution having been taken at a workshop in Kimberley in 2001, that new biological control agents attacking the reproductive parts of

the plant should be investigated for possible release in South Africa, there still appears to be controversy as to whether it would be acceptable to release agents which would cause a reduction in flower and pod production. Nevertheless, two agents have been considered. Laboratory trials and field surveys on *C. gandolfoi* indicate that the host range of the weevil is restricted to species of *Prosopis* in three series of the section Algarobia. Given that all invasive *Prosopis* species in South Africa lie within its host range, it is likely to attack them all if released. Although seeds are destroyed, it does not appear to damage the pods significantly, although this has not been quantified. In field surveys in Argentina, the weevil was widespread, present on a high proportion of trees, and in a high proportion of the pods and seeds on those trees, indicating that it may be an effective biological control agent. Because recent molecular studies show that the Old World *Prosopis* species are phylogenetically far removed from New World species, it is highly unlikely that they will be suitable as hosts to the weevil, thus allaying fears that these important agroforestry species will be compromised. However, introduced species of useful mesquite, such as *P. pallida*, will likely be attacked. It is probable that an application for release of *C. gandolfoi* will be submitted to the relevant South African permitting agencies within the coming year.

Work on the flowerbud-galling midge, *A. prosopidis*, originating in southwestern North America, has revealed it to be a complex of probably four species. The biology and consequently their suitability for biological control is variable from species to species. It appears as though *Asphondylia* sp. producing barrel-form galls is the most promising as a biological control agent. Little host-range testing has been achieved to date, but it remains likely that the insect is largely restricted in its range to *Prosopis* species within section Algarobia, series Chilensis. However, galling rates in the field in America, particularly on water-stressed trees, were low. Whether this has negative implications for its efficacy as a biological control agent in drier parts of the invasive range of *prosopis* is unknown. Furthermore, it may be a more controversial species to release, given that it would reduce flower and pod availability. For these reasons, this project has been discontinued.

The seed-feeding bruchines *A. prosopis* and *N. arizonensis* are now widespread in the field in

South Africa, with *A. prosopis* being by far the more abundant and accounting for the majority of seed destruction. In the more arid parts of the invasive range of mesquite in South Africa, *A. prosopis* appears to have the potential to have a significant impact on the size of soil seed banks.

Elsewhere in Africa, alien *Prosopis* species are becoming an increasingly serious problem, although they consistently provide useful services. *Algarobius prosopis* is established in parts of this range on introduced species. Although there have been intentions of collaboration with South Africa in biological control research from other countries in Africa, this is yet to happen, due largely to controversy surrounding the introduction of biological

control agents onto mesquite species which are regarded as useful plants.

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