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***Chrysanthemoides monilifera* (L.) T. Norl. – Bitou bush and boneseed**

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ABSTRACT

Chrysanthemoides monilifera invades native vegetation of southern Australia and is a major threat to the integrity of natural ecosystems. Two subspecies have mostly allopatric distributions; boneseed (subsp. *monilifera*) occurs throughout south-eastern Australia and bitou bush (subsp. *rotundata*) is mainly restricted to coastal habitats in New South Wales. Twelve potential agents have been studied, and some released, as part of a biological control program for *C. monilifera*. Four agents are established on bitou bush (the bitou tip moth *Comostolopsis germana*, the leaf roller moth *Tortrix* sp., the bitou seed fly *Mesoclanis polana* and the bitou tortoise beetle *Cassida* sp. 3) and affect certain plant growth parameters, but have not yet caused substantial decline of infestations. One other agent (the boneseed leaf buckle mite *Aceria* sp.) is possibly established on boneseed. Four agents have failed to establish (three leaf beetles *Chrysolina scotti*, *C. sp. B* and *C. picturata* and the lacy-winged seed fly *Mesoclanis magnipalpis*). The bitou leaf beetle *Ageniosa electoralis* was rejected. Testing of the systemic rust fungus *Endophyllum osteospermi* is in progress and testing of the boneseed seed fly *Mesoclanis dubia* is incomplete.

Key words: *Chrysolina*, *Mesoclanis*, *Comostolopsis*, *Tortrix*, *Aceria*, *Endophyllum*, *Cassida*, *Ageniosa*

INTRODUCTION

Chrysanthemoides monilifera (L.) T. Norl. (Asteraceae: Calenduleae) is a perennial, woody shrub indigenous to southern Africa. Two subspecies, *C. m.* subsp. *monilifera* (L.) T. Norl. (boneseed) and *C. m.* subsp. *rotundata* (DC.) T. Norl. (bitou bush), are

naturalised in southern Australia (Figure 1) where they invade natural ecosystems. Boneseed is widespread and occurs in a broad range of bioregions and vegetation types, but is most abundant on sandy or gravelly soils of coastal hills and plains. Infestations are extensive in the Mount Lofty Ranges, South Australia (SA); the Mornington Peninsula and You Yang Range, Victoria and around Hobart and Launceston in Tasmania. Bitou bush occupies over 80% of the New South Wales (NSW) coastline and is the dominant plant over 400 km, particularly in the northern coastal regions (Thomas and Leys 2002). The most significant bitou bush infestations occur from Jervis Bay in the south to Tweed Heads in the north and these landmarks coincide with southern and northern containment lines of a national management strategy (Downey 2004; Cherry *et al.* 2008). Small isolated infestations are known beyond the containment lines on the southern NSW coast, Menindee (western NSW) and at Frankston and Mallacoota (Victoria), and these are targets for eradication. Both subspecies are Weeds of National Significance (WoNS) in Australia. Infestations of boneseed occur in New Zealand, where it is listed under the New Zealand Biosecurity Act 1993, and in California, Sicily, St Helena and southern France (Weiss *et al.* 1998). The impact of *C. monilifera* on natural ecosystems in Australia is severe and has received considerable attention in recent times, particularly for bitou bush. Grazing is detrimental to *C. monilifera* (Scurr *et al.* 2008) and this partially explains why it has negligible impacts on grazing industries.

Impact (bitou bush)

Bitou bush invasion threatens at least 158 species, 26 ecological communities and 3 endangered plant populations in NSW (Downey *et al.* 2009). Bitou bush can dominate native vegetation and alter the characteristics and functioning of ecosystems in a variety of ways. These include: cooler, moister, darker micro-habitats, increased leaf litter decomposition rates and altered nutrient cycling (Lindsay and French 2004a, 2005); suppression of indigenous plant germination, seedling growth and recruitment (Ens *et al.* 2009; French *et al.* 2008); reduced plant species richness in foredune shrublands and forested hind dunes (Mason and French 2008); increases in some moisture-loving invertebrate guilds, decreased beetle diversity and changes in abundance of ants, earwigs, centipedes and native cockroaches (French and Eardley 1997; Wilkie *et al.* 2007); negative effects on plant-foraging bird species, less

abundant scavengers and less diverse raptors in bitou bush invaded habitats (French and Zubovic 1997; Gosper 2004; Owers 1999).

Impact (Boneseed)

In Australia, invasion of native vegetation by boneseed reduces floristic and soil-seed bank diversity and emergence levels of native and exotic plant species (Thomas *et al.* 2005). Similarly, in New Zealand boneseed seedling abundance increases dramatically following canopy disturbance, while native seedling abundance is reduced (McAlpine *et al.* 2009). Grassy woodland, valley grassy forest and lowland forest vegetation communities in Victoria are vulnerable to invasion by boneseed, where dense infestations eliminate most indigenous ground flora and prevent virtually all overstorey regeneration (Muyt 2001). Infestations in the You Yang Range directly threaten the endangered orchid *Pterostylis truncata* Fitzg. (brittle greenhood, Orchidaceae) (Bramwells 2003).

BIOLOGICAL CONTROL HISTORY

Groves (2008) provided details on the historical events associated with the biological control of *C. monilifera* in Australia and this review augments his account. In 1974, the Australian Weeds Committee declined a proposal for initiating research on biological control of *C. monilifera*. A decade later, a national conference on *Chrysanthemoides* (Love and Dyason 1985) was hosted by two NSW Government agencies and an outcome was that a biological control program should be developed. In 1986, the then Council of Nature Conservation Ministers (CONCOM) secured funding from state and federal government agencies to develop and implement the biological control program. A collaboration was formed between the CSIRO, responsible for overseas exploration, and the Keith Turnbull Research Institute (now Department of Primary Industries, Victoria), which carried out host-testing and evaluation of potential agents in its quarantine facility in Melbourne. Other State agencies in NSW, Tasmania and SA were engaged to release approved agents and monitor their establishment and impact. In 1987, surveys and ecological studies commenced in South Africa to assess the phytophagous biota associated with *Chrysanthemoides* species. This phase ran for over a decade and was based mostly at Cape Town, South Africa. One hundred and thirteen species of arthropods and four

species of pathogenic fungi were found to attack *C. monilifera* and the closely-related *Chrysanthemoides incana* (Brum. f.) T. Norl. (Scott and Adair 1992). Forty-two of the arthropods found and the four pathogens were identified as potential agents based on expected host specificity, severity of damage to host, climate matching and level of predation, and 12 of these have been fully or partially evaluated for release in Australia. Nine agents were approved for release from 1989 to 2008; two moths, four beetles, two flies and one mite species (details below). One beetle was rejected, one rust fungus is being tested and tests on one fly are incomplete.

PLANT TAXONOMY

The genus *Chrysanthemoides* contains two species, *C. monilifera* and *C. incana*, and both are indigenous to southern Africa. The published taxonomy of *C. monilifera* recognises six subspecies and most have distinct habitat requirements and geographic distributions. Subspecies are distinguished by a combination of floral, vegetative and growth form characteristics (Norlindh 1943). Additional infraspecific entities are purported to occur in South Africa (Griffioen 1995), but critical examination of morphological and genetic characters is required to confirm this. Barker *et al.* (2009) offer some support for the recognition of infraspecific taxa based on DNA sequence data, but *Chrysanthemoides* remains unresolved as monophyletic. Hybridisation between taxa in South Africa is also suggested from molecular evidence (Barker *et al.* 2009), which partially explains why it is difficult to assign some plants to described taxonomic entities.

In Australia, analysis of morphological data indicates that bitou bush and boneseed are relatively homogeneous with no obvious patterns of phenotypic variation, although boneseed is recognised as having greater phenotypic variation than bitou bush (Simmons and Flint 1986). Nonetheless, putative hybridisation between bitou bush and boneseed is reported from several locations, but most recently documented at Daveys Bay (Victoria), where a hybrid swarm occurs over approximately 20 ha (Adair and Butler 2010). Such hybridisation could potentially complicate or jeopardise biological control if hybrids have a lower susceptibility to agents with particularly high levels of host specificity.

RELEASED AGENTS

***Comostolopsis germana* Prout (Lepidoptera: Geometridae) (bitou tip moth)**

Larvae of *Comostolopsis germana* feed in the apices of *C. monilifera* stems and branches. Individual larvae construct loose canopies with white silk and leaves and feed on young foliage, soft stems, and buds. Pupation usually occurs within folded leaves on or near the host. The insect is multivoltine and several generations develop over a favourable season. Adults are green with white wavy lines on both fore and hind wings and rest appressed on foliage during the day (Figure 2), taking flight for short distances when disturbed.

The bitou tip moth is specific to *C. monilifera* and *C. incana* (Adair and Scott 1989). In South Africa, it is most prevalent in warmer regions of the Eastern Cape and KwaZulu Natal and more abundant on bitou bush and *C. m.* subsp. *pisifera* (L.) T. Norl. than on other subspecies or *C. incana*. Between 1989 and 1992, the moth was released at 77 sites in NSW, and establishment was confirmed at 44 sites (Downey *et al.* 2007). It has now colonised most of the range of bitou bush in NSW. Releases were also made on boneseed at 37 sites in Victoria, SA and Tasmania, but the insect failed to establish. Predation pressure, poor climatic matching between the insect's origins in South Africa and release locations in south-east Australia, and host preferences have been implicated in lack of establishment (Adair and Edwards 1996; Weiss *et al.* 1998; Downey *et al.* 2007).

Using an insecticide exclusion technique (Adair and Holtkamp 1999), Holtkamp (2002) showed that densities of 100 bitou tip moth larvae m^{-2} can reduce seed production of bitou bush by more than 50% and sometimes by more than 80%. Larval densities up to 400 m^{-2} have been recorded and found to significantly reduce bitou bush flowering and fruiting (Holtkamp 1997).

***Chrysolina* spp. (Coleoptera: Chrysomelidae) (leaf beetles)**

Of the eight Chrysomelinae known from *Chrysanthemoides* in South Africa (Adair and Scott 1991), three species of *Chrysolina* were selected for host-specificity testing (Figure 3). The general biology of the three species is similar, although their distributions and host preferences in South Africa are distinctive. Elongate eggs are laid in clusters on the leaves of the host plant or in the soil around the plant base. The larvae and adults primarily feed on young foliage and stems in the upper canopy, but mature leaves are also eaten. Adults and larvae shelter on the underside of leaves, in

leaf folds or litter beneath the canopy. They drop from the host plant when disturbed, possibly as a predator avoidance strategy. All three species are specific to *C. monilifera* and are multivoltine with generation times ranging from 64 to 226 days at 22°C. Adults are mostly nocturnal. Larvae pupate in the soil within a cocoon constructed from soil particles and debris. There are four larval instars. In addition to the criteria mentioned above their selection also included consideration of the 'new association' hypothesis discussed by Hokkanen and Pimentel (1984).

Chrysolina scotti Daccordi (formerly referred to as *Chrysolina* sp. A) (black boneseed leaf beetle). The black boneseed leaf beetle is distinguished by shiny black elytra with a narrow white band along the lateroventral margin. The species is known from the Eastern Cape Province of South Africa between Plettenberg Bay and Grahamstown, where it feeds on *C. monilifera* subsp. *pisifera*. Outbreak populations can cause severe defoliation and death of the host and the only parasitoid recorded in South Africa was a species of Tachinidae, which was rare (Adair and Scott 1991). The climate match index between the insect's natural distribution and areas of *C. monilifera* in south-eastern NSW is high. In host-specificity tests the black boneseed leaf beetle developed on both bitou bush and boneseed, but higher emergence rates occurred on boneseed.

The black boneseed leaf beetle was first released at Studley Park, Melbourne in 1989 and was subsequently released at eighteen sites in Victoria, one site in SA, five in NSW, and ten sites in Tasmania, but the species failed to establish at any site (R Adair unpublished data). In southern Victoria, arboreal-foraging ants and spiders are principal predators of eggs (Meggs 1995) and this undoubtedly adversely affected establishment of the beetle. In contrast, when chrysomelids under consideration for use as biological control agents were assessed for relative susceptibility to ant predation in South Africa using the canopy-foraging ant *Crematogaster peringueyi* Emery (Formicidae), tests indicated a range of behaviours or attributes would enable them to defend against predatory ants (J Scott *pers. comm.* 1990).

***Chrysolina* sp. B (painted boneseed leaf beetle).** The elytra of this undescribed species are white with irregular and deeply dissected black blotches in four traverse bands. The thorax is mostly white with an 'M-shaped' black dorsal band. The beetle is restricted to near-coastal areas on the west coast of the Western Cape Province of

South Africa in habitats with calcareous soils. The natural hosts of the painted boneseed leaf beetle are *C. m.* subsp. *pisifera* and *C. incana*. The species was approved for release in 1994 (Adair and Scott 1997) and distributed to four sites in Victoria, two in Tasmania, eight in NSW (Downey *et al.* 2007). None were released in SA. The insect has not been subsequently recovered from any of these sites.

***Chrysolina picturata* (Clark) (blotched boneseed leaf beetle).** In contrast to the painted boneseed leaf beetle, the blotched boneseed leaf beetle can be distinguished by four elytral bands of irregular white shapes on a black background. The thorax is wholly black (Adair and Scott 1997). It is known from the Western Cape Province near Cape Agulhas in habitats with alkaline soils derived from calcareous sands, marine clays or limestone. The natural hosts in South Africa are boneseed and *C. m.* subsp. *pisifera*. The beetle was approved for release in 1992 and subsequently distributed to seven sites in Victoria and two sites in SA. No establishment has been recorded (Downey *et al.* 2007).

***Cassida* sp. 3 (Coleoptera: Chrysomelidae) (bitou tortoise beetle)**

One described and three undescribed species of *Cassida* are recorded from *Chrysanthemoides* in South Africa, and all are foliage feeders. The bitou tortoise beetle (Figure 3) was selected by matching the host subspecies and target climate in Australia (Kleinjan and Scott 1996). In South Africa, adults and larvae feed on bitou bush and are known from the Eastern Cape. Larvae form shallow, feeding pits in the leaf surface and remain firmly attached. Both larvae and adults are green and are well camouflaged on the foliage of bitou bush. The bitou tortoise beetle was approved for release in 1995 and released at 12 sites in NSW (Downey *et al.* 2007). The tortoise beetle has established and is present at most of the initial releases sites, but numbers remain low and impact on bitou bush appears to be negligible.

***Mesoclanis* spp. (Diptera: Tephritidae) (seed flies)**

The genus *Mesoclanis* is restricted to southern Africa and is only associated with *Chrysanthemoides* (Munro 1950). Species of *Mesoclanis* are distinguished principally by wing pigmentation patterns and are illustrated by Munro (1950) (Figure 4). Three species were considered as biological control agents for *C. monilifera* in Australia (Scott and Adair 1992; Adair and Edwards 1996; Edwards and Brown 1997). The

larvae of *Mesoclanis polana* Munro (bitou seed fly), *Mesoclanis magnipalpis* Bezzi (lacy-winged seed fly) and *Mesoclanis dubia* Walker (boneseed seed fly) feed in capitula of *C. monilifera*. White, cigar-shaped eggs are inserted between buds and larvae bore through flowers, developing ovules, and to a lesser extent, receptacle tissue. Pupation mostly occurs within ovules (Adair and Bruzzese 2000), but may also occur amongst disc florets (*M. dubia*) or within the receptacle (*M. polana*) (Edwards and Brown 1997). *Mesoclanis polana* is found on bitou bush in the Eastern Cape and KwaZulu Natal and does not utilise boneseed in South Africa. Across the southern and the eastern seaboard, the *M. magnipalpis* is known from bitou bush, boneseed, *C. m. subsp. pisifera* and *C. incana*, but is most prevalent in southern localities, while the *M. dubia* is known from bitou bush and boneseed (Edwards and Brown 1997; Munro 1950; T Morley unpublished data).

***Mesoclanis polana* (bitou seed fly).** *Mesoclanis polana* was released in 1996 and, following ten releases of between 50 and 800 flies each, by 1998 the fly had dispersed over 1200 km, occupying virtually the entire range of bitou bush in Australia (Edwards *et al.* 1999). Although this fly can be reared on boneseed, emergence rates are low and it has not been recovered from boneseed in the field in Australia, even from regions where bitou bush and boneseed infestations are sympatric and *M. polana* is abundant (T Morley unpublished data).

The impact of *M. polana* on seed production was monitored at eight latitudinally distinct sites in NSW between 1996 and 2004 (Edwards *et al.* 2009). High and persistent levels of seed reduction (58–86%) occurred in northern NSW, while considerably lower seed reduction (6–11%) occurred at southern sites. At most sites in this study, seed destruction levels were continuing to rise, suggesting higher levels of destruction may be achieved. In a separate study, Stuart *et al.* (2002) found reductions of 23–31% in seed production between 2001 and 2002.

***Mesoclanis magnipalpis* (lacy-winged seed fly).** *Mesoclanis magnipalpis* was approved for release in Australia in 1997. Using flies derived from *C. m. subsp. pisifera* in South Africa, several releases totalling several hundred flies were made between 1998 and 2000 on boneseed and boneseed × bitou bush hybrids in Victoria, and on boneseed in SA. No establishment was detected from these releases although the fly was twice recovered in the same season as release (A Bruzzese *pers. comm.*

2004). In 2005, substantially larger numbers of the fly (also derived from *C. m. subsp. pisifera*) were released on boneseed in Victoria and in southern range of bitou bush in NSW (Morley 2005), where populations of *M. polana* are least abundant. Although some adults were recovered from boneseed sites during the same season as the releases, no flies were subsequently found. The reasons for this establishment failure are unknown, but some possibilities are discussed in Morley and Morin (2008). A further attempt to introduce the *M magnipalpis* was made in 2009 and comprised flies collected from boneseed in the Western Cape. Sixty-two flies were released in spring of that year at Frankston, Victoria into a field cage containing 100 small flowering boneseed plants. At the time of writing (September 2010), no signs of *M. magnipalpis* had been observed for the 2010 flowering season and this introduction attempt seems to have failed (Morley 2010).

Further research is required to resolve survival strategies of *M. magnipalpis*. Larger releases of the fly collected from the boneseed in the Western Cape may be warranted. It would also be worthwhile to release on bitou bush in southern NSW flies that are sourced from bitou bush in its southern distribution in South Africa

***Tortrix* Linnaeus sp. (Lepidoptera: Tortricidae) (leaf roller moth)**

Tortrix sp. is widespread in South Africa and is recorded from all six subspecies of *C. monilifera* (Scott and Brown 1992) with no clear preference for climate or *Chrysanthemoides* taxa. Larvae feed in shoot apices where they construct feeding shelters by joining together with silk two or more neighbouring leaves. Leaves and stems within and around the shelter are consumed, often resulting in the death of terminal leaves and shoot tips. One to several larvae may occur in each shelter, particularly in the early stages of development. There are six larval instars and pupation occurs within leaf folds, and adpressed leaves or stems. Egg clusters are laid on leaf blades with a transparent waxy covering. The moth is multivoltine and usually has three generations per year, with oviposition peaks in July, November and late January.

In South Africa *Tortrix* sp. is the most damaging insect of *C. monilifera*, with outbreaks occurring over many hectares, often significantly reducing seed production and killing whole bushes (Scott and Adair 1990). Host plant records and field observations in South Africa indicated that it was restricted to *Chrysanthemoides* (Scott and Brown 1992; Edwards 1997). However, in laboratory and cage tests,

development was completed on 36 plant species from 11 families. To predict the likely field host range, open-field studies were undertaken in South Africa using five different approaches, some of which were novel (Edwards 1997; R Adair unpublished data). The results of these tests indicated that although the moth has a strong preference for oviposition and development on *C. monilifera*, there is a possibility that some oviposition could occur on plants located in very close proximity to *C. monilifera* and that limited larval development could also be expected on *Calendula* and *Gazania* spp., if they occurred in close proximity to *Chrysanthemoides*. Approval for release of *Tortrix* sp. was granted on the basis of this risk assessment.

The first release was made at the You Yang Range, Victoria in April 2000 and further releases were made at 112 sites across south-eastern Australia until 2004. In NSW, the leaf roller moth is established on bitou bush at up to nine sites, with up to 70 larvae/m² recorded (Downey *et al.* 2007; H Cherry *pers. comm.* 2010). No establishment has occurred elsewhere. Low establishment success has been attributed to competition between neonates and predation, most likely by ants (Swirepik *et al.* 2004). In predator-exclusion experiments, up to 18 times more *Tortrix* sp. larvae and pupae were recorded when protected from predators (Ireson *et al.* 2002) and there were significantly more predatory arthropods and higher mortality of the moth at dune than headland sites (Strakosch 2004). Although eggs of the moth are often heavily parasitised by *Trichogramma* sp. (Hymenoptera) in South Africa (P Edwards and P Müller unpublished data) there has been no record of attack on eggs in Australia.

Tortrix sp. is the subject of a Weed Warriors program in NSW, which began in 2006. Weed Warriors engages students, weed officers, land managers and community groups to rear, release and monitor biological control agents (Schembri *et al.* 2008).

***Aceria* sp. (Acari: Eriophyidae) (boneseed leaf buckle boneseed mite)**

Aceria sp. induces formation of erinea (a type of gall) on the leaf blades of *C. monilifera*. Erinea are dense patches of hair-like structures whose formation disrupts normal leaf expansion resulting in disfigurement by twisting or buckling. Erineum formation commences on shoot meristems before leaves become visible (Morley and Morin 2008). In South Africa, the mite has been recovered from boneseed, bitou bush, *C. m.* subsp. *pisifera* and *C. incana* and these mite populations probably represent host-specific biotypes.

Following extensive host-specificity testing of the mite in South Africa and quarantine in Australia, taxonomic problems with the eriophyids associated with *C. monilifera* erinea contributed to the delayed approval of its release in Australia. Smith Meyer (1981) attributed erineum formation on *C. monilifera* to *Aceria neseri* Meyer, but no mite that corresponded with that description was found from more than 1000 specimens sampled from a culture reared in quarantine in Australia and associated with boneseed leaf buckle mite erinea (T Morley and J Davies unpublished data). Unfortunately, Smith Meyer's *A. neseri* holotype specimen is badly damaged and cannot be viewed for comparison with its description or other mites. *Aceria* sp. was released from quarantine in 2008, with more than 90 releases made up to autumn 2010 in Victoria, SA and Tasmania. Small colonies have persisted 12 months after release at four sites in Victoria and one site in Tasmania, and these are promising signs of establishment.

AGENTS TESTED BUT NOT RELEASED

***Ageniosa electoralis* (Vogel) (Coleoptera: Chrysomelidae) (bitou leaf beetle)**

The only agent rejected after completion of host-testing evaluation was the bitou leaf beetle *Ageniosa electoralis* (Figure 3). This beetle is restricted to coastal areas of KwaZulu Natal, South Africa, where it can cause extensive defoliation on bitou bush. Adults and larvae feed on young foliage and stems of the host and are mostly nocturnal. The adults are shiny dark green-black. Round dark eggs are laid in the leaf litter and soil around the base of the host plant. Pupation occurs in the soil in cocoons of cemented soil particles. In host-specificity tests, larvae were able to complete development and produce adults on seven species of plant including globe artichoke *Cynara scolymus* L. (Asteraceae) and carrot *Daucus carota* L. (Apiaceae). The bitou leaf beetle was rejected as a potential biological control agent pending additional information on the likelihood of attack on non-target hosts under field conditions (Adair and Scott 1993). Given failure of *Chrysolina* spp. released for biological control of *Chrysanthemoides*, further evaluation of the bitou leaf beetle is a low priority.

***Mesoclanis dubia* (boneseed seed fly).**

Of the *Chrysanthemoides* seed flies, least is known about the ecology and biology of *Mesoclanis dubia* (Figure 4). Twenty-one percent ($n=262$) of seed flies from bitou bush fruit samples from St Francis Bay (Eastern Cape Province, South Africa) in 1993 and 1994 were *M. dubia* (Edwards and Brown 1997), whereas this species comprised 55% ($n=303$) of flies from boneseed fruit samples collected from Stellenbosch and Paarl (Western Cape Province) in 2009 (T Morley unpublished data). All remaining flies in these samples were *M. magnipalpis*. Preliminary host testing indicated that *M. dubia* oviposits readily on boneseed soon after emergence (R Adair unpublished data). More comprehensive testing is necessary to fully assess the potential of this fly for biological control of boneseed in Australia.

AGENTS UNDERGOING EVALUATION

***Endophyllum osteospermi* (Doige) A.R. Wood (Uredinales: Pucciniaceae) (boneseed rust fungus)**

The boneseed rust fungus is a systemic pathogen that is restricted to a small group of related plants in the Calendulae: *C. m.* subsp. *monilifera*, *rotundata*, *pisifera*, *canescens* (L.) T. Norl. and *subcanescens* (L.) T. Norl., *C. incana*, an undescribed taxon and three *Osteospermum* L. species (Wood 1998).

The fungus has a latent period ranging from 6 months to 3 years after infection of a host before symptoms manifesting as witches' brooms develop (Wood *et al.* 2004; Morin and Wood 2009). Witches' brooms are deformed branches with multiple swollen stems, short internodes and small chlorotic leaves that produce fewer flowers and drupes (Wood 2002; Wood 2006). In a field study in South Africa, vegetative growth, number of buds, flower heads, fruiting heads and drupes of symptomless branches of infected bushes were 15–99% less than those of similar branches of uninfected bushes (Wood 2002), indicating that infected branches act as resource sinks. Plants severely infected over a few years died prematurely.

A three-tier system was developed to evaluate the host specificity of the fungus. This was a novel approach and was adopted because of the long latent period before symptoms appear (Wood 2006; Morin and Wood 2009). The first tier of tests involved inoculation of detached, young leaves of test species and microscopic examination four days later. Germination of spores and penetration of epidermal cells by the fungus occurred on boneseed and bitou bush and three other closely-related

species, but also on four species outside the Calenduleae: *Gazania rigens* (L.) Gaertn., *Gerbera jamesonii* L., *Bedfordia arborescens* Hochr. (all Asteraceae) and *Eucalyptus cladocalyx* F.Muell. (Myrtaceae) (Wood 2006).

Second-tier tests utilising leaves still attached to whole potted plants were performed on six non-target species that were penetrated in first-tier tests. These second-tier tests involved microscopic examinations of leaves two weeks after inoculation to determine if the rust had successfully colonised and were repeated several times in South Africa and under quarantine in Australia in 2007 and 2008. None of the tests, however, were successful because the various leaf clearing and staining techniques tried could not detect early signs of rust colonisation (Morin and Wood 2009). In light of these difficulties, a third tier of tests was initiated, whereby inoculated plants are kept for several years to allow symptoms to develop.

In South Africa during 2008 and 2009 and under quarantine in Australia in spring 2009 (one test species) whole potted plants were inoculated repeatedly with the fungus over a few weeks and, at the time of writing (September 2010), had been maintained for up to two years. Witches' brooms developed on some boneseed plants within one year of inoculation, but on none of the other species, (A Wood and L Morin unpublished data). An application for release in Australia will be prepared if, when these third-tier tests are satisfactorily completed, the risk to non-target species seems acceptable. Climate modelling predicts that the greatest impact of the rust fungus is likely to be on boneseed populations in Tasmania and southern Victoria, areas where the plant is highly invasive (Wood *et al.* 2004).

OTHER PROMISING AGENTS

The beetle *Obereopsis pseudocapensis* Breuning 1955 (Coleoptera: Cerambycidae) attacks stems of *C. m.* subspp. *rotundata* and *pisifera* in the southern Cape coast and Eastern Cape (Neser and Morris 1985; Adair and Edwards 1996). Larvae bore internally within upper shoot tips where they eat vascular tissue and cause stem death. Adults oviposit in leaf midveins and young larvae tunnel into nearby stem tissue. Preliminary testing and field observations indicate this insect is specific to *C. monilifera* and can cause considerable damage.

Two moth species are known to cause similar damage to that of *O. pseudocapensis*. An undetermined tip wilt moth (Gelechiidae) feeds internally within

the stem apices on *C. m.* subsp. *monilifera* and *pisifera*. (Adair and Edwards 1996) and larvae of an undetermined stem-girdling moth (Pyralidae) feed on the same hosts, but external feeding as well as internal feeding causes stems to wilt (Scott and Adair 1992; Scott and Adair 1990). Their host-specificities are not known.

Several other damaging insect species also feed internally on *C. monilifera* in South Africa and investigation is warranted for the root and crown-boring beetle *Sphenoptera* Dejean sp., (Coleoptera: Buprestidae) (Neser and Morris 1985), the shoot apex galling cecidomyid *Cecidomyia deformans* Schiner (Diptera: Cecidomyiidae) and the peduncle galling cecidomyid, *Lasioptera* Meigen sp. (Diptera: Cecidomyiidae).

ENDEMIC NATURAL ENEMIES

While no endemic phytophagous arthropods cause significant herbivory damage to *C. monilifera* in Australia, there are at least 55 fungal species associated with bitou bush (Cother *et al.* 1996). The cosmopolitan generalist fungus, *Sclerotinia sclerotiorum* (Lib.) de Bary is associated with bitou bush dieback in Australia and its potential for inundative biological control was investigated and rejected in the early 1990s (Cother *et al.* 1996; Cother 2000). The anamorphic fungus *Hendersonia osteospermi* Wakef. causes necrotic spots on the foliage of *C. monilifera* in South Africa (Crous *et al.* 2000) and its teleomorph was recently isolated from bitou bush in Australia and described as the new species *Austropleospora osteospermi* R.G. Shivas & L. Morin (Morin *et al.* 2010). *Austropleospora. osteospermi* is implicated, together with other fungi, in bitou bush dieback in Australia and further investigation is required (Morin *et al.* 2010).

DISCUSSION

Comostolopsis germana and *M. polana* have reduced the reproductive capacity of bitou bush in NSW (Holtkamp 2002; Edwards *et al.* 2009). However, further agents with potential to reduce canopy density and cause structural damage to bitou bush infestations are required. French *et al.* (2008) found that bitou bush seedling establishment success compared to that of native plants is a major contributor to bitou bush invasiveness, suggesting agents that target seedlings might effectively suppress

bitou bush infestations. None of the agents so far released on boneseed have established, although there are early signs of establishment of the recently released mite, *Aceria* sp. The mite and *E. osteospermi*, which is currently under investigation, offer reasonable prospects that biological control agents will be established on boneseed in the near future.

A range of factors are likely to have contributed to the failure of agents on *C. monilifera*. Predation by indigenous invertebrates appears to have hampered establishment or dispersal of the *Chrysolina* spp. and *Tortrix* sp. These insects feed or shelter in the canopy and appear susceptible to Australian predators. Predatory mites are implicated in the decline of release stocks of *Tortrix* sp. (Ireson *et al.* 2002), and might also hinder establishment of *Aceria* sp. The selection of future biological control agents for *C. monilifera* should avoid poorly concealed external feeders and focus closely on endophagous guilds. Incorrect climate and host matching also appears to have contributed to establishment failure of some agents. In retrospect, the ‘new association’ hypothesis (Hokkanen and Pimentel 1984) that led to concentrated effort on the evaluation of leaf beetles failed to deliver effective agents, and greater emphasis on exploring a more diverse range of insect feeding guilds may have yielded better results.

Indirect effects on non-target invertebrate species of agents released for bitou bush have been extensively studied (Carvalho *et al.* 2007). Their introduction have led to changes in invertebrate community structure by increasing abundance of native parasitoids (Carvalho *et al.* 2007), although the magnitude of such perturbations will probably diminish if bitou bush infestations ever decline significantly.

The integration of biological control and other forms of management is likely to be required for adequate suppression of *C. monilifera* and this is recognised by many (e.g. Adair and Edwards 1996; Groves 2008). Control of bitou bush in NSW with low doses of aerially applied herbicides (Toth *et al.* 1993) enabled larger areas to be treated than previously and accelerated the containment of this invasive plant. Interactions between herbicide applications and biological control agents of bitou bush seem likely. Ainsworth and Holtkamp (1999) observed high numbers of the *C. germana* on bitou bush seedlings following aerial spraying and noted that larvae on sprayed plants would perish due to lack of fresh foliage. They also found that *M. polana* avoided bitou bush sprayed with glyphosate.

Fire can be used to kill boneseed (Lane and Shaw 1978; Melland *et al.* 1999), and depending on intensity, partially kill stands of bitou bush (Vranjic and Groves 1999). Canopy-dwelling agents of *C. monilifera* will be killed by fire and re-colonisation will occur when regenerating hosts become phenologically acceptable, depending on proximity of viable agent populations in unburnt areas and agent dispersal capabilities. Otherwise, programs using wild or laboratory-reared agents may be required to hasten re-colonisation.

Population modelling (Kriticos *et al.* 2003; Noble and Weiss 1989; Stuart 2002) suggests that pre-dispersal seed destruction by biological control agents might need to be greater than 95% in order to significantly impact bitou bush infestations, even when integrated with other control methods. However a recent assessment of predicted bitou bush seed longevity (Schoeman *et al.* 2010), where the value of this parameter was suggested to be much lower than that assumed in models above, perhaps adds to uncertainty of such models' predictions.

Estimated costs to 2005 of the biological control program for *C. monilifera* were \$7.1 million in 2005 dollar terms, with the potential to result in a net present value (NPV) of \$47.9 million and a benefit cost ratio (BCR) of 10.3 (Page and Lacey 2006). However, accrued benefits are one-twentieth of those predicted, resulting in NPV of \$2.5 million and a BCR of 0.5 at a 5% discount rate (Page and Lacey 2006). Nominal investment in this program between 2005 and 2010 was in the order of \$1.5 million and was focused on the boneseed leaf buckle mite, the boneseed rust fungus and the lacy-winged seed fly.

The program for biological control of *C. monilifera* received strong nationally co-ordinated financial support from 1987 to 2000, which has progressively declined since then. Although the search for and testing of new agents and mass-rearing and distribution of released agents has diminished, a more broad national *C. monilifera* management program is facilitated through the WoNS program and biological control activities link with this. We believe that introduction of the boneseed rust fungus, lacy-winged seed fly (possibly different biotypes for boneseed and bitou bush) and the boneseed seed fly should continue to be pursued and that other natural enemies of *C. monilifera*, particularly the endophages mention above, have potential as biological control agents in Australia. Further quantification of the impacts of *C. monilifera* invasions, particularly for boneseed, is warranted and we agree with Groves (2008)

that documenting change in biodiversity metrics as a result of successful biological control will be a significant challenge.

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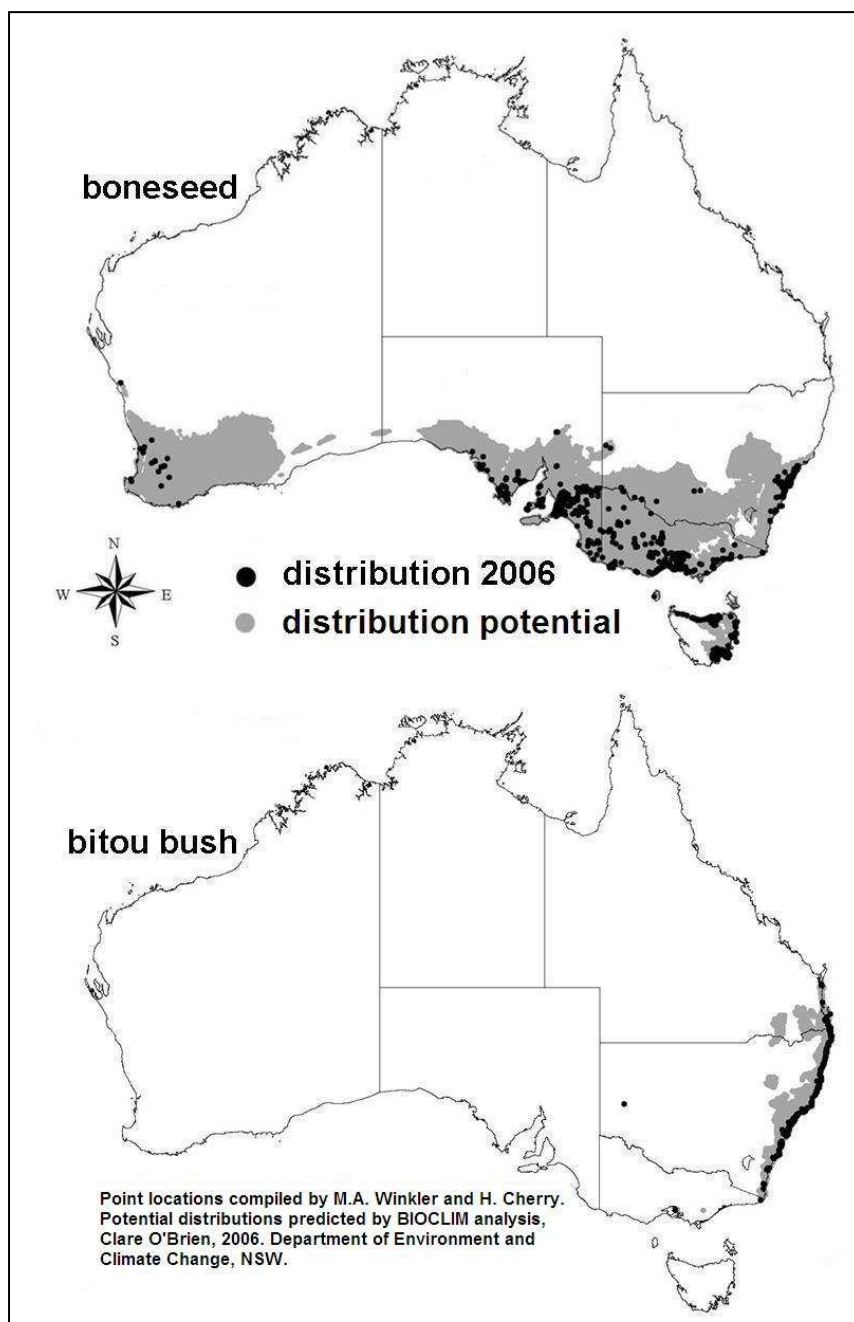


Figure 1. Australian distribution of *Chrysanthemoides monilifera* (boneseed and bitou bush). Information provided courtesy of the National Bitou Bush and Boneseed Management Group.

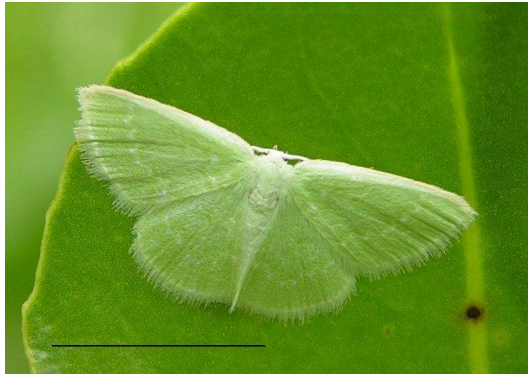


Figure 2. The bitou tip moth *Comostolopsis germana*. Scale bar 10 mm. (Photo, T Morley, Victorian Government).

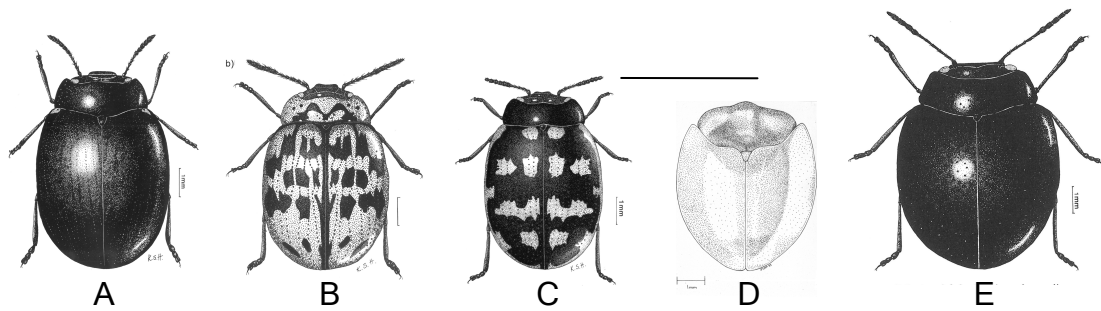


Figure 3. Chrysomelid beetles tested as biological control agents for *C. monilifera*. A–*Chrysolina scotti*, B–*Chrysolina* sp. B, C–*Chrysolina picturata*, D–*Cassida* sp. 3, E–*Ageniosa electoralis*. Scale bar 5 mm. Drawings A, B, C, E, KS Harmer; D, JGD Morrison.

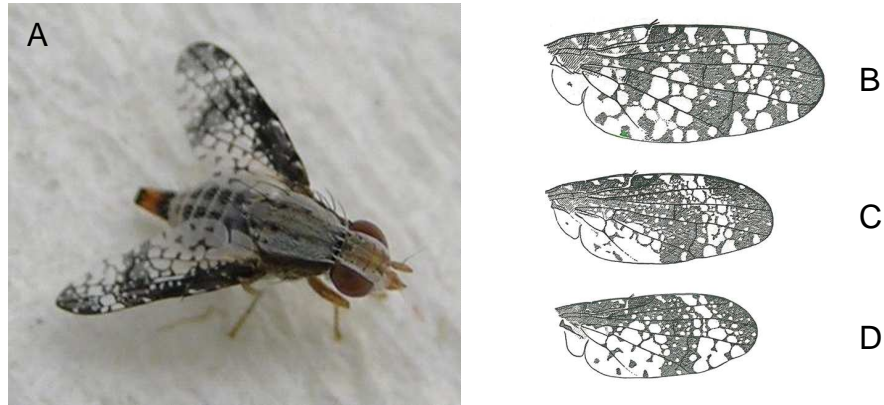


Figure 4. Seed flies of *Chrysanthemoides monilifera*. A; *Mesoclanis polana* female (Photo, T Morley, Victorian Government). B, C and D; wing pigmentation patterns of *Mesoclanis magnipalpis*, *dubia* and *polana*, respectively. Drawings adapted from Munro (1950).