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Biotic resistance to *Chrysanthemoides monilifera* ssp. *monilifera* in Tasmania

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Abstract Boneseed, *Chrysanthemoides monilifera* ssp. *monilifera* (Asteraceae) is concentrated in and near cities and towns on the north and east coasts of Tasmania. Its absence from intervening rural and bushland areas cannot be attributed to environmental conditions or a lack of time for dispersal from introduction points. The hypothesis tested in the present paper is that the range of boneseed in Tasmania is limited by biotic resistance through herbivory. Cafeteria experiments and field observations showed that sheep (*Ovis aries*), cattle (*Bos taurus*), Tasmanian pademelons (*Thylogale billardierii*), Bennett's wallabies (*Macropus rufogriseus*), garden weevils (*Phlyctinus callosus*) and native invertebrates all consumed boneseed, while common brushtail possums (*Trichosurus vulpecula*) did not. A boneseed population subjected to sheep grazing for 168 days suffered high mortality, while an adjacent ungrazed population survived intact. A replicated exclosure experiment showed that 75 days of grazing by cattle reduced the size of boneseed plants. Observations of a population subject to Bennett's wallaby and Tasmanian pademelon grazing over 1 year and 2 months showed consistently high leaf damage to foliage within pademelon reach and a decline in population, with high mortality rates in the driest and coldest times. Leaf loss attributable to invertebrates did not prevent a nearby population without wallabies from growing. The distributions of the taxa were consistent with biotic resistance, with those demonstrating no severe effect on boneseed individuals widespread, while those with evidence of severe effects more common in rural areas than in urban areas. Boneseed seemed unlikely to survive for very long at normal stocking levels. Macropod grazing, particularly that of *T. billardierii*, may also inhibit the invasion of boneseed. Thus, the recent introduction of foxes to Tasmania may not only cause the extinction of species such as *T. billardierii*, but also may cause an expansion of the range of boneseed.

Key words: biotic resistance, *Chrysanthemoides monilifera*, herbivory, invasion.

INTRODUCTION

The biotic resistance hypothesis (Elton 1958) proposes that interactions with native plant, fungi, animal and viral species limit the establishment and spread of many exotics (Crawley 1987; Maron & Vilà 2001; Mitchell & Power 2003). A meta-analysis found that native herbivores and competition with the native vegetation play equally strong roles in biotic resistance to invasion of exotics (Levine *et al.* 2003). A reduction in the number of herbivore species feeding on a plant in newly colonized parts of the world does not always result in the plant suffering less herbivore damage (Maron & Vilà 2001). In fact, several studies have found that exotic plants actually suffered more leaf herbivory from arthropods, insects and molluscs than native plants (Agrawal & Kotanen 2003; Parker & Hay 2005).

Boneseed, *Chrysanthemoides monilifera* ssp. *monilifera* (Asteraceae), is a woody environmental weed introduced to Australia from South Africa. It is one of two subspecies of *C. monilifera* present in Australia, the other being bitou bush (*C. monilifera* ssp. *rotundata*), which is only present in mainland Australia.

Chrysanthemoides monilifera is listed as one of the 20 Weeds of National Significance in Australia due to its negative impact on biodiversity, economic and environmental costs, potential for spread and invasion of many vegetation communities in south-eastern Australia (ARM Council of Australia and New Zealand 2000; Rudman 2001; Department of Environment and Heritage 2003). Within Australia, boneseed is highly invasive in South Australia, Victoria and southern New South Wales (Weiss *et al.* 1998). Boneseed is also highly invasive in both New Zealand (Syret 2002) and southern continental France (Brunel & Tison 2006). In a global context, *C. monilifera* has also been identified as one of seven priority weeds for the development of predictive modelling (Underwood *et al.* 2006).

Chrysanthemoides monilifera can displace native species in both disturbed and undisturbed native vegetation by forming dense monospecific stands (Gray 1976; Paterson & Volframs 1976; Copeland 1984; Dodkin & Gilmore 1984; Weiss & Noble 1984a,b; Kirkpatrick 1986; Parks and Wildlife Service Tasmania 2003).

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Chrysanthemoides monilifera ssp. *monilifera* was first recorded in Australia in Sydney in 1852, and Melbourne in 1858. The first records in Tasmania were at Ulverstone on the North West coast in 1931 (Gray 1976), followed by Sandy Bay in 1943 and Huonville in 1947 (Rudman 2001).

Despite its long history in Tasmania, boneseed is largely confined to urban and periurban areas (Fig. 1). This pattern suggests the possibility of biotic resistance, especially given that the species is dispersed by native and exotic birds, sets seed within a year or two of germination, does not require disturbance for invasion, and has a climatic and edaphic range in Tasmania that is much wider than its present distribution. Weiss *et al.* (1998) and Cother (2000) hypothesized that *C. monilifera* could be controlled by stock grazing, on the basis of its restriction to non-agricultural areas. However, this hypothesis has not been tested by either observation or experiment.

Observations of damage to boneseed from the activities of Australian native species are few. Nikandrow *et al.* (1996) found a scattered dieback due to native fungi in 48 populations of *C. monilifera* along the NSW coast. Less frequent occurrences of a more damaging fungal pathogen were also found on bitou bush in NSW (Cother *et al.* 1996; Cother 2000). One Australian study (Adair & Scott 1991) documented the presence of a small number of invertebrate herbivores on *C. monilifera* and, although the invertebrate damage was not quantified, concluded that the impact was minimal. We know of no observations of boneseed consumption by native vertebrate herbivores, although another Australian woody weed species in the Asteraceae, *Ageratina riparia*, has been shown to be consumed by the red-necked pademelon (*Thylogale thetis*) (Zancola *et al.* 2000).

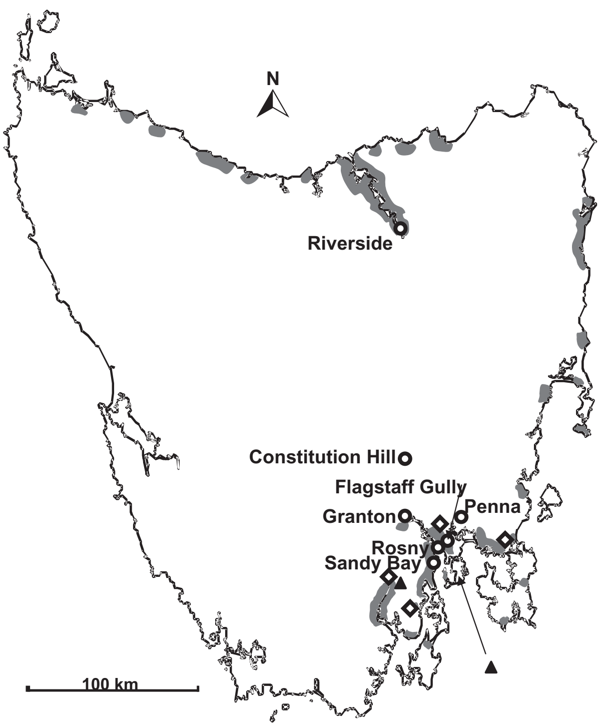

Fig. 1. Grey-shaded areas indicate distribution of *Chrysanthemoides monilifera* ssp. *monilifera* in Tasmania (Ireson *et al.* 2002). Open circles indicate boneseed observation sites. Solid triangles indicate periurban vertebrate herbivore observation areas. Open diamonds indicate natural bushland vertebrate herbivore observation areas.

We test the hypothesis that biotic resistance from herbivores is responsible for the limited range of boneseed in Tasmania. We try to validate this hypothesis by testing whether there are herbivores that could prevent boneseed from invading non-urban areas. The first step in this process is to look for evidence that particular species do or do not eat boneseed. The second step is to test whether any consumer of boneseed is associated with boneseed decline in field conditions. If such an association is shown, the validation of the biotic resistance hypothesis then requires a demonstration that the species apparently causing mortality are concentrated in the areas from which boneseed is absent. In undertaking these tests we consider invertebrates, Tasmanian pademelons (*Thylogale billardierii*), Bennett's wallabies (*Macropus rufogriseus*), common brushtail possums (*Trichosurus vulpecula*), sheep (*Ovis aries*) and cattle (*Bos taurus*).

METHODS

Testing willingness to consume

Populations of boneseed at Riverside, Constitution Hill, Granton, Sandy Bay, Rosny and Flagstaff Gully (Fig. 1) were examined periodically between September 2004 and March 2006 and invertebrate species associated with leaf damage collected for identification. Where possible, live specimens were taken. These were reared on transplanted boneseed seedlings.

After observing distinctive insect damage at several sites, the source of this damage was identified as the garden weevil (*Phlyctinus callosus*), an introduced agricultural pest. To assess the maximum current impact due to garden weevil herbivory, mean leaf area loss in a boneseed population heavily infested with garden weevils was quantified. Twelve fully expanded leaves were randomly picked from each of 10 mature boneseed plants at Constitution Hill. The upper side of each leaf was scanned to enable quantification of the level of defoliation. To quantify daily consumption, a boneseed leaf was placed in a 5 × 5 cm container with a single weevil for 24 h, and then the leaf was scanned. Twenty replicates were performed in all; four each day

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for 5 days. The Scion Image program was used to analyse the scans of the leaves, to determine the amount of surface area removed from each leaf.

Sheep and cattle in paddocks at Penna (Fig. 1) were observed to determine whether they ate boneseed. The boneseed had invaded in periods in which stock were absent (see below).

Cafeteria trials involving common brushtail possums (*T. vulpecula*), Tasmanian pademelons (*T. billardierii*) and Bennett's wallabies (*M. rufogriseus*) were conducted at Bonorong Wildlife Park near Hobart. Sixteen transplanted seedlings 15–45 cm tall were placed in enclosures with each species for 24 h. Damage to bark (present/absent), and defoliation was recorded in classes (0 = no damage, 1 = 1–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–99% and 6 = 100%). After 24 h the undamaged plants from the common brushtail possum enclosure were moved to an area frequented nightly by wild common brushtail possums, and only accessible to them. Measurements were repeated after 14 days, and the percentage of stems eaten was estimated using the same classes.

Testing relationships between consumers and stand characteristics

Four sites (Fig. 1) were used to observe the temporal and spatial relationships between boneseed consumption by herbivores and boneseed stand characteristics.

Flagstaff Gully

This site was located within *Eucalyptus viminalis* grassy woodland, on the edge of a large area of native vegetation with few houses nearby, on shallow soils formed on dolerite. Bennett's wallabies, Tasmanian pademelons and common brushtail possums were all frequently observed and were profuse in their production of scats. Five 10 × 10 m quadrats were subjectively placed around groups of boneseed plants in mid October 2004. Each boneseed plant was numbered, and the location of each plant recorded. For each individual boneseed plant in each of these quadrats, plant height and minimum and maximum heights of foliage damage were measured, and average leaf area loss was estimated for the whole plant (using the scale above), and for the damaged area (the area between minimum and maximum damage heights). Scats were collected from each quadrat and counted. All vertebrate scats were removed on 22 October before data collection began. Bennett's wallaby and Tasmanian pademelon scats were counted conjointly as wallaby scats. The term 'wallabies' hereafter refers to both species. The measurements of boneseed individuals and counting of scats took place every 2 months for 14 months.

Rosny Hill

This site was located within a vegetation remnant on shallow dolerite soils bounded by roads and housing and the Derwent Estuary. The vegetation consisted of sparse *Eucalyptus viminalis* trees over an open-scrub of *Allocasuarina verticillata* over tussock grassland. Common brushtail possums were present, but there was no evidence of other native vertebrate herbivores. The methods used to sample and measure the attributes of boneseed individuals and count scats were the same as for Flagstaff Gully. The level of invertebrate damage, and presence of invertebrate herbivores on the boneseed plants were also recorded. The presence or absence of garden weevil damage was recorded at each census. The first measurement was in mid November followed by a second measurement in February 2005 (2.5 months after the initial measurements). Subsequent measurement dates were April, June, August, October and December 2005.

Old orchard at Penna

This site at Penna was an orchard until the 1950s when the fruit trees were removed, and sheep grazing commenced. Sheep were removed from the paddock in 2000 in the hope of promoting regeneration of native vegetation. However, the only woody plant regeneration that occurred consisted of boneseed. In November 2004 the land owner stocked the 19 ha paddock with 80 DSE (1 dry sheep equivalent (DSE) = merino wether of 45 kg live weight), which were removed after 216 days, on 18 July 2005. Thirty-two live boneseed plants were randomly selected from the paddock, including recently dead individuals. Twenty-six plants were selected using the same procedure in the adjacent paddock, which was not grazed by either stock and only lightly grazed by wallabies during the period of measurement. Measurements of the boneseed individuals commenced 60 days after the onset of sheep grazing in the old orchard and were repeated at 102, 146 and 186 days. Defoliation, in the damage classes noted above was recorded at each measurement time.

Penna degraded bush

This site had been subjected to woodcutting and grazing until around 1960. At this time the property was subdivided, grazing and woodcutting ceased, and the land was left unmanaged. At the time of the trial, tens of thousands of boneseed plants, ranging from seedlings to large 3-m-tall mature plants were present. Twelve randomly located paired 4 × 4 m plots (i.e. 24 plots in all) were used to compare grazed against ungrazed boneseed. The paired plots were located no more than

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10 m apart, and had the same slope, aspect, parent rock and surrounding vegetation characteristics. The ungrazed plots were fenced with three strands of barbed wire. This prevented access by cattle, but ensured that the low population of wallabies was free to access both the ungrazed and grazed plots. The first measurements were made the day before cattle grazing commenced. The 28 ha site was stocked with 37 head of 2-year-old cows for 75 days, from 4 June to 6 August 2005. The height, width at the widest part of the crown and the defoliation level in the classes described above were recorded fortnightly during this period.

Testing for the ranges of herbivores

In order to test the assumption that boneseeds main native vertebrate herbivores were more common in natural bushland than in areas of the urban fringe, nocturnal spotlight surveys were conducted at 92 sites on private property in two parts of the periurban fringe of Hobart (Fig. 1) and in four control sites in corresponding areas of natural bush well-removed (>500 m) from urban development. The surveys were focussed on recording the presence of common brushtail possums, Tasmanian pademelons and Bennett's wallabies, three species easily detected by spotlight in a variety of habitat types (Driessen & Hocking 1992). Between October 2006 and March, 2008, 510 periurban and 87 natural bushland spotlight surveys were conducted. Spotlight surveys were carried out on foot with a hand-held one million candle power spotlight. Spotlight surveys were conducted along tracks, roads and fire-breaks whenever possible. In areas of open forest lacking these established paths, spotlighting was conducted along paths of least resistance/disturbance. If an area of dense bush lacked established paths then the spotlighting was conducted along its perimeter, as encroaching into areas of dense bush created unacceptable disturbance. Following Southwell and Fletcher (1985); Driessen and Hocking (1992), all spotlight surveys were carried out within 4 h of sunset, on fine, dark (i.e. not a full moon, unless heavy cloud cover was present) nights with little to no wind or rain.

The collection data attached to specimens of garden weevil held in the collections of the Department of Primary Industry and Water, Hobart and the Biogeography Laboratory, University of Tasmania were classified into urban (including rural towns) and non-urban locations (mostly orchards and vineyards).

Data analysis

Chi-square tests were used to test the significance of relationships between class variables, with adjacent classes being combined when expected values were less than 5 in one of them. The Kruskal–Wallis test was used to test whether classes significantly differed in relation to continuous variables, rather than ANOVA because of difficulty in satisfying the requirement of normality in the residuals. Pearson's correlation coefficient was used to measure the strength of linear relationships between continuous variables.

RESULTS

Willingness to consume

Of the 11 native and 3 exotic invertebrate species observed consuming boneseed only the garden weevil was found at all sites (Table 1). The larvae of the native geometrid moth *Capusa cuculloides* were observed to feed on the widest range of plant parts, including stems, leaves, flowers, fruits and seeds. It was the only species which damaged fruits or seeds. The garden weevil was the only other species to feed on more than one type of plant part, consuming leaves, stems and roots. The nigra scale *Parasaissetia nigra* was found several times in association with an unidentified black sooty mould. This combination caused partial or whole plant dieback of boneseed plants at Riverside, Flagstaff Gully and two other sites (New Norfolk and Bruny Island). Garden weevils had removed 20.7 ± 2.9% of leaf area at Constitution Hill. In the cafeteria experiment they consumed 6.82 ± 0.55 mm^2 per day.

Both sheep and cattle were observed eating boneseed foliage, stems and inflorescences. In the cafeteria experiment, Tasmanian pademelons caused significantly greater damage to the foliage ($\chi^2 = 48.00$, d.f. = 6, $P < 0.001$) and bark ($\chi^2 = 48.00$, d.f. = 2, $P < 0.001$) after 24 h, and to foliage ($\chi^2 = 52.76$, d.f. = 4, $P < 0.001$) and stems ($\chi^2 = 63.247$, d.f. = 4, $P < 0.001$) after 14 days, than the other species. After 24 h the Tasmanian pademelons removed more than 75% of the foliage from 13 of 16 plants, with a minimum damage level of 25–50%. Tasmanian pademelons also stripped bark from every plant after 24 h, while the other animals left the bark intact. After 24 h the Bennett's wallabies damaged only one plant, and the common brushtail possums did no damage to the boneseed. After 14 days Tasmanian pademelons had completely consumed the above ground plant tissue of every boneseed plant. Bennett's wallabies consumed parts of some plants. Common brushtail possums occasionally broke off leaves and stems but did not eat them.

Relationships between consumers and stand characteristics

Boneseed mortality varied markedly between sites, with 16 out of 32 measured live plants dying between

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Table 1. Insects found feeding on boneseed (*Chrysanthemoides monilifera* ssp. *monilifera*) at several sites in Tasmania between September 2004 and March 2006

Scientific name	Common name	Site	Date	Eats
Acarina				
*Tetranychus urticae**	Red spider mite	Ro	Oct	Chlorophyll
Coleoptera				
*Phlyctinus callosus**	Garden weevil	Ri, Gr, Sa, Fl, Ro, Co	Sept–Jun	L, St, R
Tribe Tychiini	Tychiine weevil	Ro	Oct–Nov	L
Hemiptera				
Agonoscelis rutilis	Horehound bug	Ro	Dec	Sap
Amorbus sp.	Grey stinkbug	Ri	Oct–Nov	Sap
Dindymus versicolor	Harlequin bug	Ri	Sept	Sap
*Parasaissetia nigra**	Nigra scale	Ri, Fl, Ro	All year	Sap
Family Pentatomidae	Green stinkbug	Ri, Ro	Nov	Sap
Family Pseudococcidae	Pink root scale	Ri, Gr, Sa	Sept–Dec	Sap via roots
Lepidoptera				
Capusa cuculloides	Geometrid moth	Ro	Oct–Nov	Fr, St, L, Fl, Se
Epiphyas postvittana	Light brown apple moth	Ri, Gr, Fl, Ro	Sept–Dec	L
Spilosoma glatignyi	Glatigny's tiger moth	Ri, Gr	Sept–Oct	L
Undet. larva	Moth caterpillar	Ri	Nov	St
Orthoptera				
Caedecia simplex	Katydid nymph	Ri	Sept–Oct	Fl

The sites were Riverside (Ri), Granton (Gr), Flagstaff Gully (Fl), Sandy Bay (Sa), Rosny Hill (Ro) and Constitution Hill (Co). Date, months in either or both years that observations were made; Eats, plant parts eaten; L, leaves; Fl, flowers; Fr, fruit; St, stems; Se, seed; R, roots; sap, sap.; * = Exotic species.

Table 2. Wallaby scats per 100 m^2 per 2 months, and boneseed numbers, establishment, mortality and mortality rate (%) at Flagstaff and Rosny

	Oct	Dec	Feb	Apr	Jun	Aug	Oct	Dec
Flagstaff								
No. of individuals	189	183	166	160	155	137	127	n.a.
No. established	n.a.	5	3	2	2	0	3	n.a.
No. dead	n.a.	11	20	8	7	18	13	n.a.
Mortality rate	n.a.	5.7	10.8	4.8	4.3	11.6	9.3	n.a.
Wallaby scats	n.a.	15	25	19	20	28	5	n.a.
Rosny								
No. of individuals	n.a.	120	127	126	128	124	126	126
No. established	n.a.	n.a.	10	1	3	0	3	3
No. dead	n.a.	n.a.	3	2	1	4	1	3
Mortality rate	n.a.	n.a.	2.3	2.0	0.7	3.1	0.8	2.3
Wallaby scats	n.a.	n.a.	0	0	0	0	0	0

n.a., not applicable.

60 and 186 days after sheep were placed in the old orchard at Penna, while no measured plant died in the adjacent paddock. Nor did any plants die in the fenced and unfenced plots at the other site at Penna in the 75 days of measurement after cattle were introduced. Over 365 days at Flagstaff, 77 individuals out of 204 died. Over 365 days at Rosny 12 out of 140 individuals died (Table 2).

Variation in percentage mortality at Flagstaff was more strongly correlated with variation in the percentage mortality of boneseed at Rosny in the five coincident 2-month periods ($r = 0.591$, $P = 0.294$) than with wallaby scat numbers in six 2-month periods ($r = 0.277$, $P = 0.595$). Mortality at both sites was highest in mid-winter and lowest in autumn and spring, although there was little absolute variation in mortality at Rosny (Table 2).

Morbidity was also highly variable between sites. By 60 days after sheep were placed in the old orchard at Penna there were no fully expanded leaves on all measured boneseed plants, which were only known to be alive from resprouting shoots and the greenness of their stems. None of the measured plants in the adjacent paddock was recorded in a foliage damage class

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of greater than 6–25% at any of the measurement times.

In the cattle grazing experiment all of the plants protected from grazing and six of the 12 grazed plants showed no change in foliage damage class during the trial. The maximum foliage damage class recorded for the grazed plants was 26–50%. Plants unprotected from cattle grazing lost width over the 75 days while those within the fences did not (fenced *vs.* unfenced, Kruskal–Wallis, $H = 8.49$, $P < 0.01$).

At Flagstaff Gully, grazing damage was evident on an average of 91% of plants, and this figure varied little between measurement times. On average, 40% and 50% of plants respectively had between 76–100% and 51–75% of their foliage removed. The maximum height at which foliage damage consistently occurred at Flagstaff was around 65–70 cm, with an extreme value of 130 cm. At Rosny, 74.8% of plants had 1–5% of their foliage removed, and 18.6% had no foliage removed. Damage to foliage at Rosny was almost exclusively caused by the garden weevil. The frequency of plants with invertebrate damage increased from 67% to 93% over the observation period.

The total number of boneseed plants in the quadrats decreased from 183 to 127 at Flagstaff, while increasing from 120 to 126 at Rosny during the coincident monitoring time (Table 2).

The ranges of herbivores

Bennett's wallabies were observed 5.6 times more than expected in bushland than in periurbia ($\chi^2 = 70.132$, d.f. = 1, $P < 0.001$). Tasmanian pademelons were observed 1.5 times more frequently than expected in bushland than periurbia ($\chi^2 = 5.171$, d.f. = 1, $P < 0.025$). Overall common brushtail possums were observed 1.3 times more than expected in bushland than in periurbia (chi-square = 6.065, d.f. = 1, $P < 0.025$), however, in the dry open forests most susceptible to boneseed invasion, the frequency of observation did not significantly vary between periurbia and natural bushland.

Records for the garden weevil were concentrated in cities and towns (23 records) rather than rural areas (13 records). There were no records in national parks, although many of them are well-collected for invertebrates.

DISCUSSION

Consumers of boneseed

We have conclusively shown that sheep, cattle, Tasmanian pademelons, Bennett's wallabies, garden weevils and several other species of invertebrate consume boneseed in Tasmania. The hypothesis that stock eat boneseed (Weiss *et al.* 1998; Cother 2000) has been confirmed, and two native marsupials have been shown for the first time to consume boneseed. We have also shown that common brushtail possums do not consume boneseed.

In contrast to our results, Adair and Scott (1991) found very few invertebrate leaf herbivores on *C. monilifera* in Australia. They suggested that the foliage of *C. monilifera* was an underutilized resource. Attempts to introduce invertebrates for biological control have not met with great success (Ireson *et al.* 2002). However, the garden weevil, an earlier accidental introduction from South Africa, and native invertebrates now feed on all plant parts, from roots to flowers and seeds. Among the natives, *C. cuculloides* larvae have previously been found only on *Eucalyptus* species (Herbison-Evans *et al.* 2005) and peas (*Pisum sativum*). The tiger moth, *Spilosoma glatignyi,* has several recorded hosts in the Asteraceae (Herbison-Evans *et al.* 2005) and is likely to have been pre-adapted to the anti-herbivore chemicals of boneseed. A similar pre-adaptation is highly likely for the light brown apple moth, *Epiphyas postvittata*, a generalist with over 70 host plants (Danthanarayana 1975).

The magnitude of grazing effects

Our data strongly indicate that the presence of sheep is unlikely to be compatible with the survival of boneseed. While the comparison between sheep grazing and its absence is not replicated, two adjacent paddocks in the same environment had similar infestations of boneseed before the sheep were introduced into one of them, with a spectacular decline in boneseed numbers where sheep were present and constancy where they were not. The complete defoliation of boneseed by sheep in less than 2 months is consistent with the 80–90% defoliation within 6–13 days previously reported for sheep-grazed *C. monilifera* ssp. *pisifera* (Barnard *et al.* 1992). Sheep have long been noted to be effective in suppressing the establishment of many species of woody plant (Crawley 1990; Kirkpatrick 2007). Cattle also seem highly likely to have the capacity to eliminate boneseed within a few years. Our results contrast strongly with cattle-grazing facilitation of the spread of the invasive shrub *Mimosa pigra* in northern Australia (Buckley *et al.* 2004) and the generalization of Hobbs (2001) that stock promote weed invasion in Western Australia. It seems that the effects of stock on weeds in Australia are variable, depending on weed and context.

We were not able to introduce macropods to an area already infested by boneseed. However, we were able to demonstrate that, in one area with high numbers

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of macropods, boneseed leaves were substantially damaged to the height that a Tasmanian pademelon could reach, and that the boneseed population was declining, despite ongoing recruitment. Variation in the numbers of wallabies at the site, as indicated by the abundance of their scats, was not likely to have been primarily responsible for temporal variations in boneseed mortality, as this mirrored the lesser mortality at the Rosny site more than scat numbers, with most boneseed mortality occurring in the coldest and driest times of the year.

The complete consumption of plant stems by Tasmanian pademelons in the cafeteria trial was consistent with damage and mortality data from Flagstaff Gully. The identification of the Tasmanian pademelon as the main native vertebrate browser of boneseed was also consistent with the results of Statham (1983); Driessen (1992) and Sprent and McArthur (2002) who found that Tasmanian pademelons preferentially ate softer broad leaved forbs and shrubs, while Bennett's wallabies preferentially ate grasses. The red-necked pademelon (*Thylogale thetis*) has been shown to consume another weedy composite shrub, *A. riparia* (Zancola *et al.* 2000). *Thylogale thetis* has also been shown to browse vines, shrubs and trees on a rainforest–grassland interface in southeast Queensland (Wahungu *et al.* 1999).

The levels of leaf damage caused by invertebrates in the present study were similar to those found in monospecific stands in its native South Africa, where there was a range of 5.4–19.1%, with a maximum of 10% of the current year's growth being consumed by herbivores (Scott 1996). Low levels of consumption of boneseed by invertebrates in Australia were observed by Adair and Scott (1991). This difference from the results of the present study may be attributable to differences in environmental conditions or observation techniques, but could also be explained by a subsequent higher adaptation by invertebrates to the availability of boneseed as a resource. Newly established exotic plants often rapidly accumulate a native herbivore fauna (Strong *et al.* 1977). Natural selection for the utilization of exotic hosts can be rapid (Singer *et al.* 1993; Thompson 1998). This phenomenon has resulted in the evolution of preference for an introduced host in *Rhagoletis* flies and *Euphydryas* butterflies in less than 100 years, and for *Papilio* butterflies in approximately a century (Thompson 1998).

The frequency of boneseed plants subjected to herbivory at Rosny was also greater than the maximum frequencies of 65–76% found in a survey of 27 native plant species in near coastal scrub vegetation on Wilson's Promontory (Ashton & Chappill 1989). The mean defoliation levels of 10% (Ohmart *et al.* 1983) and 15% (Fox & Morrow 1983) found for several eucalypt species growing in natural environments in temperate areas of Eastern Australia were similar to the insect damage to boneseed at Rosny Hill and less than the level of damage observed at Constitution Hill. This suggests that boneseed is experiencing little or no release from invertebrate herbivory relative to its native competitors in Australia. Agrawal and Kotanen (2003) suggested that this is the case with many other invasive species. Equally, our data suggest that invertebrate herbivory, in itself, is not enough to prevent the survival and growth of boneseed populations.

While sheep, cattle and wallabies appear to be primarily responsible for losses of boneseed foliage at the sites at which they were abundant, other herbivores would have contributed to the total grazing pressure at all of these sites, as witness the losses of foliage at the stock-free sites at Penna. It is normal in the Tasmanian countryside to have both sheep and wallabies, or all of cattle, sheep and wallabies in grassy vegetation dominated by native plant species (Kirkpatrick *et al.* 2007).

Distribution of boneseed herbivores

The herbivore species that we have considered are distributed in a way that is consistent with the biotic resistance hypothesis. Common brushtail possums are ubiquitous in lowland Tasmania, from the centres of cities and towns to the most remote forest country (Rounsevell *et al.* 1991). Gardeners in Hobart are well aware of the consequences of their herbivory (Zagorski *et al.* 2004), which do not include the consumption of boneseed. If common brushtail possums ate boneseed it would not be a weed problem in and around towns and cities in Tasmania.

Our results, and the distribution maps of Rounsevell *et al.* (1991) show that Bennett's wallabies and Tasmanian pademelons survive in low numbers at the edges of cities and towns. However, they do not penetrate to their midst, usually being absent from remnant patches of native vegetation surrounded by suburbia, as in the case of Rosny Hill and the Queens Domain (Kirkpatrick 2004). Mortality from domestic dogs (*Canis lupus familiaris*) and traffic probably combine to cause their absence within, and relative rarity around, cities and towns. There is evidence that the wallaby populations that build up in the absence of high levels of mortality exclude many exotic plant taxa other than boneseed through preferential grazing (Zancola *et al.* 2000; Kirkpatrick 2007).

In rural lowland eastern and northern Tasmania those parts of the landscape that do not have substantial populations of wallabies tend to be grazed by sheep and/or cattle, low numbers of wallabies being due to culling (Kirkpatrick *et al.* 2007). While stock are occasionally raised on some small acre periurban properties, they are not found in vegetation remnants within cities and towns. Where boneseed is occasionally found

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in the countryside, as at Constitution Hill, it is in road reserves that cannot be grazed by stock because of traffic hazard.

The distribution of the well-named garden weevil is not consistent with the hypothesis that it is an agent of biotic resistance.

Wider implications

The failure of expensively obtained, tested and disseminated invertebrates from South Africa to affect boneseed populations suggests that biotic resistance might be a cheap alternative to biological control for this species, and should be automatically investigated for other invasive plants of concern.

The potential of sheep and cattle as control agents for boneseed has relevance outside of Tasmania, possibly for both the subspecies. The use of stock grazing regimes to control other weeds is well established (Friend & Kemp 2000). It may be possible to use stock grazing as a means to eliminate boneseed from areas not normally stocked, such as coastal reserves and urban parks. In vegetation dominated by scleromorphic shrubs and sedges boneseed is likely to be among the most palatable species. Most native species in vegetation dominated by native grasses and herbs have survived stock grazing, although other means of eliminating boneseed should be used where native species that have been eliminated by stock grazing over most of their original ranges survive.

The potential to use Tasmanian pademelons as a management tool to control boneseed exists, but is inhibited on mainland Australia by high populations of foxes (*Vulpes vulpes*), which have rendered the species locally extinct. In 1979, an attempt was made to reintroduce Tasmanian pademelons to Tower Hill in western Victoria. The animals were taken by foxes (Mansergh & Seebeck 2006). More recently Tasmanian pademelons have been successfully reintroduced to Victoria in Little River Earth Sanctuary where fox proof fencing was constructed before the introduction of pademelons and other small mammals. Further fox proofing and introductions of Tasmanian pademelons could be strategically located in areas with boneseed infestations. The recent establishment of a population of foxes in Tasmania may not only threaten animals, such as the Tasmanian pademelon, but also may cause an explosion of the populations of at least one exotic shrub, currently kept under control by their browsing.

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