Effects of boneseed (*Chrysanthemoides monilifera* (L.) Norl. ssp. *monilifera*) on the composition of the vegetation and the soil seed bank of an open eucalypt woodland

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Summary

The effects of the environmental weed boneseed (*Chrysanthemoides monilifera* (L.) Norl. ssp. *monilifera*) on the vegetation, and the soil seed bank, of an open woodland in the Mount Lofty Ranges were investigated. The vegetation and soil seed bank within infested and interspersed uninfested quadrats were assessed and compared. The most notable difference was a decrease in the abundance of two understorey dominants *Gonocarpus tetragynus* Labill. and *Hibbertia exutiacies* Wakef. within the infested quadrats. Also, the density of *G. tetragynus* and *H. exutiacies* decreased with increasing boneseed density. The understorey within the uninfested quadrats is dominated in terms of number, cover, and biomass by these two species, so their reduction represents a substantial community change. There were fewer *G. tetragynus* and *H. exutiacies* seeds, probably due to lower levels of productivity, in the infested quadrats. Seeds of these species had low levels of viability in the presence and absence of boneseed. There was a marginally significant (P = 0.057) reduction in *G. tetragynus* viable seed density in the infested quadrats. Boneseed seeds were present in uninfested areas, but at lower density. Diversity of both above-ground vegetation and the soil seedbank was reduced in infested areas. Changes in vegetation and viable seed densities may well comprise a long-term impact at this site, as regeneration might not restore the original species composition, and regeneration may take a long time to occur.

Introduction

Weed invasions in natural ecosystems have been found to be associated with a decline in native species richness or diversity in nearly all studies, both in Australia and overseas (Adair and Groves 1997). Environmental weeds are considered to be one of the greatest threats to nature conservation, and have been implicated in the extinction of four Australian plant species (Groves and Willis 1999). Few Australian studies have measured the impact of environmental weeds on native species and ecological processes (Humphries *et al*. 1991, Adair and Groves 1997), although negative correlations between weed invasion and native species diversity (McIntyre 1993) or the cover of an ecological analogue (Weiss and Noble 1984) have been demonstrated. In southern Australian open eucalypt woodlands, boneseed (*Chrysanthemoides monilifera* (L.) Norl. ssp. *monilifera*), an understorey shrub from the South African fynbos forms dense infestations, excluding the native ground flora and reducing the establishment of trees and shrubs (Lane 1979). Dense, continuous canopy cover has been recorded in areas of the You Yang Ranges (Adair and Holtkamp 1995), and the extinction of some 40 indigenous plant species within these Ranges has been largely attributed to their colonization by boneseed (Blood 1987).

The success of boneseed is probably associated with its release from heavy predation (Adair and Holtkamp 1995) that, in South Africa, can be very destructive to various parts of a plant and curtail its seed production (Neser and Morris 1984). In South Africa, boneseed forms a seed pool of about 100 to 300 m^{-2} (Milton 1980), while viable seed pools of between 800 and 2500 m^{-2} have been found in infested areas of Australia (Lane 1976). In Australia, boneseed was found to produce a mean of 3000 viable seeds per square meter of plant, and up to 50000 seeds per plant over a 12 month period (Weiss 1984). Boneseed seed remains dormant in the soil for more than 10 years (Parsons and Cuthbertson 1992), with a mean viability of 13% after three years (Weiss 1986), thus spreading the time for germination and establishment.

Boneseed seedlings are able to establish under poor conditions such as infertile soil, moisture stress and heavy shade (Lane 1981). The principle author found up to 200 boneseed seedlings per square meter persisting beneath dense boneseed canopies at an infestation within the Mount Lofty Ranges (unpublished data). The principle author also found that the canopy of boneseed infestations reduced the amount of light reaching the ground by up to 70% (unpublished data), which is favourable for the shade tolerant boneseed seedlings, but detrimental to the survival of seedlings not adapted to such low light conditions (Trigger 1981). A major portion of the plant species of Southern Australia has seedlings with low relative growth rates and seeds with very small amounts of resources in them (Panetta and Hopkins 1991). Revegetation trials indicate that weeds are likely to disadvantage species with these characteristics (ibid.).

Weed invasion requires both propagule supply and excess resources (Davis *et al*. 2000). Boneseed probably has a low resource requirement because the high level of resource removal by natural enemies would constitute strong selective pressure to obtain and/or utilize resources very effectively. An intrinsic low resource requirement, coupled with the release from heavy predation, may mean that unutilized resources within undisturbed native vegetation are sufficient for the establishment of boneseed. These factors have probably allowed boneseed plants to recruit until resources are at a very low level, thus forming dense monocultures. Plants that have a lower resource requirement and that reduce the resource base to this low level are superior competitors (Tilman 1982, 1988).

The aim of this study is to quantify the effect of boneseed on the vegetation within a *Eucalypus microcarpa* (Maiden) Maiden woodland at Belair, within the Mount Lofty Ranges, using a multi-site comparison. The changes in the vegetation associated with the presence of boneseed infestations have been quantified by comparing the numbers of, or area occupied by each species of plant within infested and interspersed, uninfested quadrats. The numbers of, and the percentage viability of the seed within these areas have also been compared. This is the first time that these environmental changes, caused by boneseed colonization, have been quantified. Such data form the basis for rational debate about the environmental impact of the plant.

Methods

Assessment of vegetation

The study site, its history, and the quadrats used in this study have been outlined in Thomas *et al.* (2000). The vegetation was assessed within thirteen infested and four interspersed, uninfested 5 × 5 m quadrats. This vegetation assessment consisted of counting all the plants that were distinguishable as individuals and measuring the area covered by the low spreading shrubs. For these undershrubs, the coverage area was calculated as the longest axis and the next longest axis perpendicular to it, multiplied together. Where there was any doubt about whether a shoot was a part of a larger shrub, this shoot was recorded as a separate individual. The percentage cover of dry grass and moss was visually estimated.

The vegetation within the quadrats was assessed between mid-April and mid-May 1996.

Assessment of soil seed bank

Soil was sampled in early June when only a small number of seedlings appear to have recently emerged, and about a month before a major germination event. The seeds within the soil samples, therefore, probably were representative of the available seed bank during the germination period. Blocks of soil were removed from just outside the four corner pegs of all four uninfested quadrats and four randomly chosen infested quadrats. A total of 16 soil samples each were removed, therefore, adjacent from infested and uninfested quadrats. Obvious micro-depressions or rises were avoided. At each block, the soil was removed over a surface area of 18 cm^2 and a depth of 3 cm using a ruler and spade. Only the top 3 cm of soil was sampled because the majority of the seed within woodlands are contained within this depth (Carrol and Ashton 1965, Howard and Ashton 1967, Hodgkinson *et al*. 1980). Such a distribution can be expected for soils that are non-cracking and not easily moved by wind or water (Hodgkinson *et al.* 1980), as is the case with our study site.

Seed was extracted from the soil using the technique that Malone (1967) describes as being typically 100% efficient and as having no affect on seed viability. A magnesium sulphate solution was used to produce dispersion of the soil, and flotation of the organic matter. The floating organic matter was scooped from the surface and washed through a set of sieves of 2, 1, 0.5 and 0.2 mm mesh size. The organic matter was then allowed to dry in the air and/or in an oven set at 35°C. A scrubbing brush was used to push out any organic matter that was embedded within the mesh and the matter was placed in clear plastic counting trays.

The counting trays had a continuous channel in which the viewed material for sorting was contained. The organic matter was viewed under a dissecting microscope set at 10X magnification. A pair of forceps was used to push just enough organic matter as to form a single layer into the field of view. Any matter that looked as though it may be an intact seed was removed. These seeds were later identified by a propagator of native plants, Kieren Brewer, and unidentified seeds were referred to by numbers, e.g. sp. 1. The seed of one *Wahlenburgia* species was not removed due to the damage inflicted during this process; these seeds were counted in the trays. The seeds of another *Wahlenburgia* species were sub-sampled; the number of seeds of this species was counted in part of the tray, and the total number derived by multiplying by the inverse of the fraction of the area assessed. A subsample of these seeds was removed from the litter for viability analysis. The matter was also inspected by a fellow honours student, and very few seeds and no species were found to have been missed. It should, however, be noted that any seeds with a diameter smaller than 0.2 mm would not have been collected. Also, light coloured seeds are difficult to distinguish from the background material and so their numbers will not be accurately assessed using this method (Gross and Renner 1989). It is possible that species with small, light coloured seeds, e.g. some *Eucalyptus* species, may have been missed altogether. Due to the large amount of organic debris, the process of extracting seed from the soil was very time-consuming and took about 12 hours per block.

The viability of the seeds of many species was tested using the tetrazolium test (Lakon 1948). Seeds with hard coats were pierced so that all seeds could be preliminarily moistened, as recommended by Moore (1973). Seed viability was assessed within 24 hours. The viability of each seed was apparent after it was sliced in half under a compound microscope at 20X magnification. A seed was determined to be viable if its embryo was stained pink and non-viable if it was white. Staining of the embryo was found to co-occur with the pigment being present within the endosperm.

The viability of boneseed was assessed by placing seeds on moist filter paper in Petri dishes on a windowsill and measuring their germination.

Statistical analysis

The vegetation and seed data from the uninfested and infested quadrats were analysed using ANOVAs. When required, the data were transformed to satisfy the requirements of this test (Fisher 1966). If the data were not normally distributed after transformation, then the data sets were compared using the non-parametric Mann-Whitney 'U' Test. The vegetation data sets were also compared after being pooled across families, life form and native or introduced categories. The null hypothesis was that there is no difference, at the 5% significance level, between the number or area covered by a species or class of vegetation, or number of seeds of a species, or number of viable seeds of a species, or number of seeds of all species other than boneseed between boneseed-infested and uninfested sites.

Correlations between the number of boneseed plants and other species in eight infested quadrats were also calculated.

Species diversity, defined by both the number of species present (species richness) and the abundance (frequency with which particular species were encountered) of these species was evaluated using two diversity indices for both above ground vegetation (excluding boneseed and the large *Eucalyptus* and *Pinus radiata* D.Don plants), and the soil seedbank (excluding bulbs, because different species were not distinguished, and boneseed). Species diversity was estimated for each quadrat, and an average for infested and uninfested areas was calculated.

Shannon's diversity index was used as an index of species diversity in which all species are given equal weight regardless of the relative abundance of species in the sampling unit, and was estimated for each quadrat as:

$$\hat{H}' = -\sum_{i=1}^{s} [(n_i / n) \ln (n_i / n)]$$

where n_i is the number of individuals belonging to the i^{th} of S species in the sample and n is the total number of individuals in the sample. The Shannon diversity index is a measure of the average degree of uncertainty in predicting to what species an individual chosen at random from a collection of S species and N individuals will belong. The average uncertainty increases as the number of species increases and as the distribution of individuals among the species becomes even (Shannon and Weaver 1949).

Simpson's diversity index weighs more-abundant species in the sampling unit more heavily than less-abundant species, and was used as an index of the diversity of the most predominant species in the sampling unit; it was estimated for each quadrat as:

$$\hat{\lambda} = \sum_{i=1}^{s} n_i(n_i - 1)) / n(n - 1)$$

where n_i is the number of individuals belonging to the i^{th} of S species in the sample and n is the total number of individuals in the sample. The Simpson diversity index varies from 0 to 1 and is the probability that two individuals drawn at random from a population belong to the same species. If the index is high, then the probability that two individuals are from the same species is high, and the diversity is low (Simpson 1949).

Results

Impact of boneseed on the vegetation

Species that were significantly more abundant (numbers) within the uninfested quadrats were *Briza maxima* L. ($P < 0.001$), *Gonocarpus tetragynus* Labill. ($P < 0.001$), *Bossiaea prostrata* R.Br. ($P = 0.004$), *Burchardia umbellata* R.Br. ($P = 0.023$), *Hibbertia exutiacies* Wakef. (number of – $P = 0.035$; area covered by – $P = 0.002$), *H. riparia* (R.Br. ex DC.) Hoogland ($P = 0.011$), and moss ($P = 0.020$) (Table 1). Plant categories that were more abundant in uninfested sites were the number of plants within the families Dillenaceae and Liliaceae ($P = 0.007$ and $P = 0.017$ respectively); and the number of ($P = 0.041$), and area occupied by ($P = 0.002$) native undershrubs (pooled plants of the families Dilleniaceae and Epacridaceae).

There was no significant difference between the number of adult 'introduced shrubs and trees' (pooled plants of the families Oleaceae, Pinaceae, Pittosporaceae, Protaeceae and Rhamnaceae), or adult *Eucalypus microcarpa* trees. There was however a greater number of young introduced shrubs and trees ($P = 0.03$) but fewer *E. microcarpa* recruits within the infested quadrats ($P < 0.05$) (Table 1).

The numbers of each species, and the groups of plants that were not found to be significantly different were *Lomandra dura* (F.Muell.), *L. glauca* (R.Br.) Ewart, *Hibbertia riparia*, *Lissanthe strigosa* (Sm.) R.Br., *Pultenaea largiflorens* F.Muell. ex Benth., adult, juvenile and seedling *Acacia pycnantha* Benth., plants within the families Epacridaceae and Juncaceae, the numbers of adult and young plants of the family Fabaceae (where 'young' is the pooled group of seedlings and juveniles), the number of adult native shrubs (pooled adults of the families Leguminosae and Pittosporaceae), and the number of native herbs (pooled *Acaena echinata* Nees, *Linum marginale* A.Cunn. ex Planch., *Opercularia ovata* Hook.f., *Oxalis perennans* Haw. and *Thysanotus patersonii* R.Br.) (Table 1).

The number of *Gonocarpus tetragynus* and *Hibbertia exutiacies* plants were negatively associated with the number of boneseed plants ($r = 0.81$, 0.77 respectively, $P < 0.05$, $df = 6$).

Both diversity indices indicated a reduction in above ground diversity within infested areas. Shannon's index ranged from 1.23 to 1.81 in uninfested areas and from a low 0.52 to 2.42 in infested areas. The average index was 1.74 (SE 0.23) in uninfested areas and 1.49 (SE 0.14) in infested areas. Simpson's index ranged from 0.12 to 0.40 in uninfested areas and from 0.11 to a high 0.81 in infested areas. The average index was 0.28 (SE 0.07) in uninfested areas and 0.38 (SE 0.05) in infested areas.

Impact of boneseed on the soil seed bank

There were three times as many seeds of all species other than boneseed in uninfested than infested areas ($P = 0.014$) (Table 2). A significantly greater number of bulbs ($P < 0.01$), *Gonocarpus* sp. ($P = 0.01$), *Hibbertia exutiacies* ($P < 0.01$), *Oxalis* sp. ($P = 0.049$), and *Wahlenbergia* sp. 1. ($P = 0.02$) seeds were found in the uninfested quadrats (Table 2). There was no significant difference between the number of *Phyllanthus* sp. (L.), sp. 2, sp. 4, sp. 5 and *Wahlenbergia* sp 2 seeds in the uninfested and infested quadrats.

A large percentage, generally >50%, of these seeds were hollow. This percentage does not appear to vary across infested and uninfested quadrats (Table 3). Of the seeds that were found to be full (Table 3), 14–100% were determined to be viable using the tetrazolium test (Table 3). Percentage viability of full seeds was not different between the uninfested and infested quadrats.

A significantly greater ($P = 0.014$) number of viable sp. 5 seeds, and a marginally significantly greater ($P = 0.057$) number of viable *Gonocarpus tetragynus* seeds were found within the uninfested quadrats. There was no difference between the number of viable *Hibbertia exutiacies* seeds within the uninfested and infested quadrats.

Both diversity indices indicated a reduction in soil seedbank diversity within infested areas. Shannon's index ranged from 1.52 to 2.11 in uninfested areas and from a low 0.88 to 2.12 in infested areas. The average index was 1.89 (SE 0.13) in uninfested areas and 1.57 (SE 0.31) in infested areas. Simpson's index ranged from 0.16 to 0.31 in uninfested areas and from 0.15 to a high 0.66 in infested areas. The average index was 0.21 (SE 0.03) in uninfested areas and 0.39 (SE 0.13) in infested areas.

Despite absence of reproductive boneseed plants, an average of 439 boneseed seeds m^{-2} were present in uninfested quadrats. A greater number of boneseed seeds were recorded in the infested quadrats (1172 m^{-2}), and the rate and percentage germination was very similar across uninfested and infested quadrats (Table 4).

Discussion

The abundance of the undershrubs, grasses, herbs, mosses and seeds at the study site were found to decrease within the boneseed infested areas. Also, the density of the two dominant undershrubs decreased with increasing boneseed density. Diversity of both above-ground vegetation and the soil seedbank was lower within the boneseed infested areas. The lowest levels of diversity of the above ground plants, as determined using both indices, was within the more densely infested quadrats (9–12 plants m^{-2}). These findings are reflected in the general appearance of the site; infested areas were greatly denuded of other plants, particularly within dense infestations. A decrease in the numbers of, or area occupied by a species of plant within boneseed infested areas, and a negative correlation between the density of boneseed and another plant is consistent with boneseed causing the displacement of that plant.

We assume that the sole reason for differences between the infested and uninfested areas is that the weed infestation simply has not yet completely saturated the site. We assume that any differences between the infested and uninfested areas are associated with the presence of boneseed. We assumed that the uninfested areas are not intrinsically different from the infested areas, that factors such as the presence of perching sites for bird dispersers could determine initial sites of infestation (Dodkin and Gilmore 1984). Therefore, we assume that the vegetation and soil seed bank within the uninfested quadrats is representative of the vegetation and soil seed bank of the area prior to boneseed infestation. The fact that the native vegetation within areas that are lightly infested by boneseed appears to be identical to that within adjacent areas that are not infested supports this assumption. Also, there is no reason to suspect that grazing by introduced herbivores, which is likely to have been a major disturbance at this site, would not have been of a uniform level of across the study site. Relatively unpalatable undershrubs, which are indicative of this disturbance, are prevalent within the uninfested areas. We also assume that boneseed has never been present in the uninfested areas, and information from the Park Rangers strongly suggests that this is so.

Competition for resources

Possible reasons for the reduction in the presence of the understorey species is that the rate of their germination, survival, and/or reproduction is reduced within a boneseed infestation. This reduction may be due to competition from boneseed for light, water, and/or nutrient resources. Boneseed caused a reduction in the amount of light reaching the ground beneath an infestation (unpublished data). The above ground competition for light may well affect competition for resources within the soil via a number of mechanisms (e.g. Jackson and Caldwell 1992). Also, the interactions between root and shoot competition may well be more than additive (Donald 1958). Boneseed infestations are probably imposing perpetual stress (*sensu* Grime 1979) upon the plants below, and so causing the decline in their abundance.

Table 1. Mean (and standard error) number and/or area covered by plants within four boneseed infested and thirteen uninfested quadrats.

Family	Scientific name	Common name	Variable	Uninfested plots		Infested plots	
				mean	standard error	mean	standard error
Asteraceae	*Chrysanthemoides monilifera* ssp. *monilifera**	Boneseed	>1.5m tall	0.00	0.00	17.63	0.64
			>1m tall	0.00	0.00	118.38	3.41
			>0.5m tall	1.25	0.50	53.75	1.81
			>0.05m tall	8.50	3.13	3.63	0.22
			seedling	3.25	0.94	11.23	1.17
	Lagenifera stipitata	Common bottle-daisy	number	36.50	14.47	0.08	0.02
Casuarinaceae	*Allocasuarina verticillata*	Drooping sheoak	number	0.00	0.00	0.08	0.02
Cyperaceae		Rush sp.	number	27.75	8.68	7.85	0.71
Dilleniaceae	*Hibbertia exutiacies*	Guinea-flower	number[a]	509.75	77.97	172.31	11.38
			area (m^2)[b]	8.53	1.24	1.94	0.12
	Hibbertia riparia	Erect Guinea-flower	number	11.75	3.07	2.38	0.32
			area (m^2)	0.59	0.09	0.08	0.02
Epacridaceae	*Astroloma humifusum*	Native cranberry	number	15.25	5.57	3.92	0.39
			area (m^2)	0.07	0.02	0.02	0.00
	Astroloma conostephioides	Flame heath	number	19.25	4.76	4.15	1.07
			area (m^2)	0.21	0.06	0.00	0.00
	Acrotriche serrulata	Honeypots	area (m^2)	0.00	0.00	0.03	0.01
	Lissanthe stringosa	Peach heath	number	6.75	1.89	66.69	5.40
Fabaceae	*Acacia paradoxa*	Kangaroo thorn	number	0.00	0.00	0.38	0.10
	Acacia pycnantha	Golden wattle	adult	7.25	1.76	1.69	0.14
			juvenile	5.75	1.46	1.69	0.16
			seedling	7.75	2.09	4.00	0.45
	Acacia rotundifolia	Round-leaved wattle	adult	2.00	0.67	1.31	0.24
			seedling	0.00	0.00	0.85	0.22
	Bossiaea prostrata	Creeping bossiaea	number	101.75	15.60	9.23	1.02
	Pultenaea daphnoides	Large-leaved bush-pea	adult	3.00	1.20	0.31	0.05
			juvenile	1.50	0.60	0.08	0.02
			seedling	0.00	0.00	0.38	0.10
	Pultenaea largiflorens	Twiggy bush-pea	adult	1.75	0.34	4.92	0.38
			seedling	0.00	0.00	8.00	0.78
Haloragaceae	*Gonocarpus tetragynus*	Common raspwort	number	669.25	126.90	14.46	1.59
Liliaceae	*Bulbine bulbosa*	Bulbine lily	number	0.00	0.00	11.92	2.09
	Dianella revoluta	Black-anther flax-lily	number	46.00	7.08	14.15	0.95
	Lomandra dura	Stiff iron-grass	number	72.75	10.96	48.85	4.16
	Lomandra glauca	Pale iron-grass	number	150.75	44.05	14.69	2.03
	Lomandra sororia	Small iron-grass	number	3.00	0.77	4.31	0.59
	*Myriphyllum asparagoides**	Bridal creeper	number	0.00	0.00	0.31	0.06
	Thysanotus patersonii	Twinning fringe-lily	number	40.00	11.46	0.31	0.05
Linaceae	*Linum marginale*	Native flax	number	2.50	0.62	0.08	0.02
Myrtaceae	*Eucalyptus microcarpa*	Grey box	adult	0.50	0.20	1.31	0.09
			juvenile	3.25	0.34	0.69	0.10
			seedling	0.25	0.10	0.38	0.05
	Eucalyptus leucoxylon	South Australian blue gum	number	0.25	0.10	0.00	0.00
Oleaceae	*Olea europea**	Olive	juvenile	0.00	0.00	3.85	0.89
			seedling	0.00	0.00	1.69	0.16
Oxalidaceae	*Oxalis perennans*	Native oxalis	number	0.50	0.20	0.54	0.12
Pinaceae	*Pinus radiata*	Radiata pine	adult	0.25	0.10	0.54	0.06
			juvenile	0.75	0.19	0.38	0.06
			seedling	2.50	0.87	1.00	0.12
Pittospoaceae	*Bursaria spinosa*	Sweet bursaria, Christmas bush	adult	0.00	0.00	0.23	0.06
			seedling	4.50	1.54	3.08	0.73
	*Pittosporum undulatum**	Sweet pittosporum	adult	0.00	0.00	0.23	0.03
			seedling	0.00	0.00	0.54	0.09
Plantaginaceae	*Plantago lanceolata**	Rib grass	number	5.25	1.84	1.31	0.23
Poaceae	*Briza maxima**	Quaking grass	number	328.00	29.41	10.00	1.46
		Dry grass	% cover	2.75	0.30	0.85	0.10
Proteaceae	*Hakea laurina**	Pincushion hakea	adult	0.25	0.10	0.00	0.00
			seedling	1.00	0.40	0.00	0.00
Rhamnaceae	*Rhamnus alaternus**	Blow-fly bush, buckthorn	juvenile	0.00	0.00	0.54	0.06
			seedling	0.00	0.00	8.15	0.64
Rosaceae	*Acaena echinata*	Sheeps burr	number	0.00	0.00	0.92	0.12
Rubiaceae	*Opercularia ovata*	Broad-leaved stinkweed	number	0.00	0.00	9.62	2.48
n/a		moss	% cover	44.50	7.20	12.54	1.19
n/a		unidentified herb seedling	number	0.00	0.00	3.62	0.38

* exotic.

[a] number of individual plants distinguished.

[b] individual plants not distinguished within this area.

Table 2. Mean number of seeds within four 18 cm^2 × 3 cm deep blocks of soil from boneseed infested and uninfested quadrats.

Species	Number of seeds			
	Uninfested		Infested	
	Mean	Standard error	Mean	Standard error
Eutaxia. sp	0.6	0.4	0.1	0.1
Gonocarpus tetragynus	25.0	7.1	2.9	1.3
Hibbertia exutiacies	31.8	6.5	5.2	2.2
Linum marginale	0.5	0.2	0.3	0.1
Phyllanthus sp.	8.8	2.5	4.2	1.1
Romulea sp.	0.6	0.2	1.2	0.7
Wahlenbergia stricta	1.3	0.4	0.6	0.2
sp.1	0.8	0.5	0.4	0.2
sp. 2	7.8	2.5	4.6	1.8
sp. 3	0.6	0.3	0.5	0.2
sp. 4	4.8	1.4	3.5	0.8
sp. 5	7.9	2.7	1.1	0.4
sp. 6	0.4	0.2	0.2	0.1
sp. 7	3.0	1.4	0.9	0.3
sp. 9			0.3	0.1
sp. 10			0.3	0.2
sp. 11	0.3	0.2	0.1	0.1
Acaena echinata			0.1	0.1
Arthropodium strictum	0.3	0.1	0.1	0.1
bulbs	8.8	1.4	2.7	0.8
Burchardia umbellata	0.1	0.1		
Exocarpos cupressiformis	0.4	0.2	0.3	0.1
Freesia hybrid	0.2	0.2		
Lagenifera stipitata	0.4	0.4		
Oxalis sp.	53.4	13.6	23.1	5.6
Wahlenbergia sp. 1	44.4	22.3	18.1	10.8
Wahlenbergia sp. 2	9.0	2.9	1.3	0.5
sp. 8	0.2	0.1	0.1	0.1
sp. 12			0.6	0.4
sp. 13	0.2	0.1	0.1	0.1
sp. 14	0.2	0.1		
sp. 15	0.1	0.1	0.1	0.1
sp. 16	0.1	0.1		
sp. 17	0.1	0.1		
sp. 18	0.1	0.1		
sp 19	0.1	0.1	0.1	0.1
sp. 20			0.1	0.1
sp 21			0.1	0.1
sp. 22	0.1	0.1		
sp. 23			0.1	0.1
sp. 24	0.1	0.1		
sp. 25	0.1	0.1	0.1	0.1
sp. 26	0.1	0.1		
sp. 27	0.1	0.1		
sp. 28			0.1	0.1
sp. 29			0.1	0.1
sp. 30	0.1	0.1		
sp. 31	0.1	0.1		
sp. 33			0.1	0.1
sp. 34	0.1	0.1	0.1	0.1
sp. 35			0.1	0.1
sp. 36			0.1	0.1
sp. 37			0.1	0.1
sp. 38			0.1	0.1
sp. 39	0.1	0.1		
sp. 40			0.1	0.1

The alterations of the environment within the boneseed-infested areas of the study site appear to have caused a substantial decrease in the presence of many small native species. Evidence from the current study strongly suggests that the infestation will spread and continue to displace native species if the spread of boneseed is left unchecked. It is likely that boneseed is a superior competitor, and if increasing boneseed density is associated with increasing age of the infestation patch, then other species will be eliminated over time. Also, boneseed seed was present in uninfested areas, and was of equal quality across infested and uninfested areas. Adult boneseed plants greatly reduced boneseed germination (Thomas *et al*. 2000), and native plants may also reduced germination of this weed. The relatively low level of boneseed germination in uninfested areas (Thomas *et al*. 2000) may have been due not just to fewer seeds, but also to the presence of native plants. Native plants probably slow the rate of, but do not prevent infestation. The recovery of the native species is likely to be greatly influenced by the density of their *in situ* seed bank, and on properties such as the dispersal, longevity, and germination requirements of their seed.

Regeneration and the soil seed bank

Regeneration of the native vegetation community that was present before infestation by an environmental weed is the ultimate aim of weed management. As the regeneration that occurs following the removal of boneseed will probably be largely determined by the amount and type of viable seed that is present within the treated area, any changes to the seed bank associated with this weed is of great ecological significance.

Diversity of the soil seedbank was lower in infested areas, as determined using both indices. Also, overall density of seed of species other than boneseed was much lower within infested areas. A significantly greater number of viable sp. 5 seeds and a marginally significantly greater number of viable *Gonocarpus tetragynus* seeds were found within the uninfested quadrats. A reduction in the density of a plant species within a boneseed infestation may well result in a reduction in the density of its soil seed bank. This is because there are fewer plants to produce seed, and because the species may produce fewer seeds per unit biomass. This reduction in the amount of resources allocated to reproduction may occur because boneseed has caused a reduction in the amount of resources available to the plant, and because plants that are adapted to resource-limited environments tend to devote a greater proportion of whatever resources are limiting to ends that maximize individual survival rather than fecundity (Harper 1977).

Table 3. Mean and standard error (SE) for percentage of hollow seeds, number of full seeds, and per cent viability of full seeds within four 18 cm^2 × 3 cm deep blocks of soil from boneseed infested and uninfested quadrats.

Species	Percentage hollow seeds				Average number of full seeds				% viability of full seeds			
	Uninfested		Infested		Uninfested		Infested		Uninfested		Infested	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Eutaxia. sp	[A]		100	0.0	2	2.0			100	0.0		
Gonocarpus tetragynus	75	9.0	77	0.0	24	11.6	3	2.4	34	5.9	30	0.0
Hibbertia exutiacies	84	9.6	74	3.7	11	5.7	5	3.2	42	9.1	79	0.0
Linum marginale	93	7.1	75	25.0	0.3	0.3	0.3	0.3	100	0.0	100	0.0
Phyllanthus sp.	92	5.7	96	4.2	5	3.8	0.3	0.3	16	3.8		
Romulea sp.	100	0.0	100	0.0	0.3	0.3	1	1.3	100	0.0	100	0.0
Wahlenbergia stricta	71	35.0	79	21.4	2	1.7	1	0.7	14	0.0	83	16.7
sp.1	84	3.8			0.5	0.3	1	0.8			100	0.0
sp. 2					1	0.5	2	1.8			64	35.7
sp. 3	100	0.0	100	0.0	0.3	0.3	1	1.0	100	0.0	58	8.3
sp. 4	79	15.8	83	11.8	3	1.5	2	1.7	42	8.3		
sp. 5	26	1.1	89	11.1	28	16.0	1	0.8	55	10.4		
sp. 6	60	0.0	100	0.0	1	1.3	0.5	0.5	60	0.0		
sp. 7	100	0.0	100	0.0	0.3	0.3			100	0.0		
sp. 9							1	0.8				
sp. 10			75	0.0			0.3	0.3				
sp. 11					1	0.7	0.3	0.3	100	0.0		

[A] blank cells = not determined.

Table 4. Mean number of boneseed seeds within four 18 cm^2 × 3 cm deep blocks of soil from boneseed infested and uninfested quadrats, and the rate and percentage germination of these seeds on a window sill.

	Number of seeds		% of germination within		% germination	
	Mean	SE	First three weeks	Next two weeks	Mean	SE
Uninfested	79	40.6	91.5	8.5	10	7.5
Infested	211	38.8	85.7	14.3	8	2.5

The number of *Hibbertia exutiacies* and *Gonocarpus tetragynus* plants were much greater within the uninfested quadrats than the infested quadrats, and their numbers decreased with increasing boneseed density. As the seeds of these species appear to have poor dispersal potential, the greater number found within the uninfested quadrats probably reflects the greater number of parent plants present. High numbers of seeds were found to be non-viable or empty in both infested and uninfested areas, therefore boneseed itself did not appear to affect the factor(s) responsible for this phenomenon. Factor(s) other than boneseed had a greater impact on the density of viable seed.

The absence of *Hibbertia exutiacies* or *Gonocarpus tetragynus* seedlings within the study quadrats, the predominance of shoot production by *H. exutiacies*, and the apparent low longevity and dispersal potential of their seeds indicate that the persistence of these species is more dependent on continuous insitu seed production by adult plants than on the presence of a well dispersed or persistent seed bank. Regeneration of these two species may then be limited by seed availability. Many other factors, including the germination requirements of their seed, the rate of shoot production by *H exutiacies*, predation, competition and the time required for these species to reach reproductive maturity will influence their rate of recolonization.

There were fewer bulbs within the infested quadrats. These bulbs were probably *Arthropodium* sp., *Caesia vittata* R.Br., and *Freesia* hybrid, the three most common geophytic plants to emerge over winter. Fewer plants of these three species emerged from quadrats from which boneseed had been removed, compared with their numbers in uninfested quadrats (Thomas *et al.* 2000). Fewer bulbs and fewer emergents is consistent with boneseed having caused propagule availability to be a factor that limited the emergence of geophytic plants. The fewer number of bulbs found within the infested quadrats may indicate that the rate of germination, assimilation and/or reproduction of these geophytic plants is decreased by the boneseed infestation.

Conclusions

Boneseed is probably the most important causal factor producing the difference in plant and seed numbers found within the infested and uninfested quadrats. This change has probably resulted in a decline in the quality of native animal habitat as resources such as nectar, seed, pollen and foliage of native plants species are reduced (Dodkin and Gilmore 1984, Weiss 1986). On the basis of the evidence within this study, it is reasonable to presume that if this infestation is left unchecked, the density of boneseed will increase and the number and density of native plants, the prospects for regeneration, and the habitat quality in this area will continue to decrease.

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