Effects of soil disturbance and weed removal on germination within woodlands infested by boneseed (*Chrysanthemoides monilifera* ssp. *monilifera*)

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Summary
The effects of controlling the environmental weed boneseed (*Chrysanthemoides monilifera* (L.) Norl. ssp. *monilifera* (DC.) Norl.) on subsequent regeneration within two open woodlands in the Mount Lofty Ranges were investigated. The techniques used to control boneseed involved combinations of three levels of soil disturbance; minimum, low and high, and two levels of mulching; removing the cut/uprooted plants or stacking them in the centre of the quadrat. The germination of all plant species were unaffected by an interaction between these factors, or by mulching. The emergence of two native geophytes, *Arthropodium* sp. and *Lagenifera stipitata* (Labill.) Druce decreased with increasing levels of soil disturbance. Fewer *Stipa setacea* R.Br., *Freesia* sp., *Homeria flaccida* Sweet, *Caesia vittata* R.Br. and orchid plants emerged within areas infested by boneseed.

Introduction
Boneseed (*Chrysanthemoides monilifera* (L.) Norl. ssp. *monilifera* (DC.) Norl.) is a serious environmental weed because it invades undisturbed native vegetation, and there is evidence that it displaces native vegetation. It is a perennial shrub from the South African fynbos that was introduced to Australia, as a garden ornamental, over 100 years ago (Dodkin and Gilmore 1984). It has since spread throughout much of southern Australia, including the Mount Lofty Ranges, South Australia. Boneseed was widely established throughout these Ranges by 1909.

The relative success of boneseed in Australia is evident from the difference in plant and seed densities. South African boneseed populations consists of scattered plants with an occasional low density cluster of about one plant to every ten square meters (Adair, personal communication 1996). Very few seedlings are produced by boneseed in South Africa. In stark contrast, the principle author (unpublished data) found over 100 mature boneseed plants per square meter at an infestation within the Mount Lofty Ranges. Also at this site, densities of boneseed seedlings up to 200 m^{-2} were found to persist beneath dense boneseed canopies. In South Africa, boneseed forms a seed pool of about 100 to 300 m^{-2} (Milton 1980). In Australia viable seed pools of between 800 and 2500 m^{-2} have been found (Lane 1976) and boneseed was found to produce a mean of up to 50 000 seeds per plant over a 12 month period (Weiss 1984).

Boneseed has been controlled using a variety of techniques including hand-pulling, slashing and stump swabbing, herbicide spraying, burning, biological control and various combinations of these treatments. Various factors associated with these control techniques may affect the subsequent regeneration. For example soil disturbance caused when removing this weed and the smothering and allelopathic effects of mulching the cut or uprooted weed in treated areas.

Removal of adult boneseed plants has been found to stimulate germination of its seed (Parsons and Cuthbertson 1992) and soil disturbance has also been found to enhance the establishment of introduced annual plants within a eucalypt woodland (Hobbs and Atkins 1988). In contrast, the native vegetation of Mediterranean Australia has not evolved with, and has little response to, soil disturbance (Trémont and McIntyre 1994). It appears probable that the production of gaps and the creation of soil disturbance whilst removing boneseed will favour the colonization of the area by this and other weeds.

There is anecdotal evidence that boneseed has an allelopathic effect; its leaf litter and fruit leachates appear to inhibit the germination and growth of some native species (Parsons and Cuthbertson 1992). Such an effect should be evident when boneseed is mulched in a treated area.

This paper investigates the regeneration that occurred following the control of boneseed, and the effects that both the soil disturbance produced when removing boneseed, and that mulching the boneseed on site as compared to removing it, had on this regeneration.

Study site locations, climate, soils and history
The study sites are within the west of Belair National Park and the west of Morialta Conservation Park, both of which are on the western face of the Mount Lofty Ranges in the Adelaide region. This region has a Mediterranean climate, with mild, wet winters and hot, dry summers. The two hottest months are January and February, when average monthly maximum temperatures of over 28°C occur. The two coldest months are June and July, when average minimum temperatures fall below 8°C. Average annual rainfall at the Belair and Morialta study sites are 769 and 636 mm respectively. The soils at both sites are clay to clay loam. The pH was between 6.5 and 7 at Belair and between 7.1 and 8.5 at Morialta. The concentration of phosphorous in two soil samples was 4 and 5 mg kg^{-1} at Belair and 6 mg kg^{-1} and 11 mg kg^{-1} at Morialta. The total nitrogen concentration in these samples was 2.7 and 3.1 g kg^{-1} respectively at Belair and 3.1 and 4.7 g kg^{-1} respectively at Morialta.

The area containing the Belair study site was disturbed for a period of over 100 years by tree felling, scrub clearing, bark harvesting and horse, cattle and sheep grazing, all of which declined in intensity after 1945. The boneseed infestation at the study site has established over about the last 50 years (E. Robertson, personal communication 1996).

The area containing the Morialta study site was cleared of much overstorey vegetation to enhance the growth of grass fodder. Stock have grazed this area since the late 1840s until less than 20 years ago when it was acquired by the National Park (K. Brewer, personal communication 1996). Grazing may well have prevented the establishment of both *Olea europaea* L. and boneseed as their proliferation coincided with the removal of stock (ibid.).

Study site vegetation associations
The Belair study site is within a *Eucalyptus microcarpa* (Maiden) Maiden woodland association. The upper canopy is dominated by 10–12 m tall *E. microcarpa* and scattered *Pinus radiata* D.Don. The mid-canopy stratum is comprised of scattered shrubs including *Acacia* spp., *Pultenaea* spp., *Bursaria spinosa* Cav., and is dominated by boneseed. The third canopy stratum is dominated by low spreading shrubs, particularly *Hibbertia exutiacies* Wakef. Various grasses, sedges and rushes and the common raspwort *Gonocarpus tetragynus* Labill. exist within and between the undershrubs. Plants of the families Liliaceae, Iridaceae and Orchidaceae, which emerge and grow over winter and spring, contribute significantly to the lowest stratum over these seasons.

The Morialta study site is within a low woodland formation. The upper canopy stratum is formed by 8–10 m tall *Eucalyptus porosa* F.Muell. ex Miq. *Acacia pycnantha* Benth., *Casuarina stricta* Aiton and the invasive weed, *Olea europaea*, form the next canopy tier. The native shrubs present were *Acacia dodonaeifolia* (Pers.) Balb. and a few *Olearia ramulosa* (Labill.) Benth. A heavy boneseed infestation abuts the woodland; it appears to form medium density stands on the periphery, grading to low density stands in the centre of the site. During the drier season, much of the ground was bare or occupied by sparse dry grass. By mid-winter, the majority of the understorey plants appeared to consist of introduced annual grasses, including *Briza maxima* L. and *B. minor* L. and introduced forbs, including *Medicago* spp. and *Anagallis arvensis* L. Understorey plants were estimated to cover 30–50% of the ground at the beginning of September.

Materials and methods

During early March 1996, 5 × 5 m quadrats were marked out within the study areas. Twenty-three boneseed infested and four interspersed uninfested quadrats were marked out at Belair, and 22 infested and five interspersed uninfested quadrats were marked out at Morialta. The infested quadrats were randomly assigned one of seven different treatments (Table 1).

Minimum soil disturbance

Slashing boneseed does not involve breaking the soil crust, hence, a minimum level of soil disturbance was produced when using this control technique. Boneseed was slashed about 10 cm above ground level and the stalks swabbed, generally within 5 minutes and always within 20 minutes, with the undiluted herbicide glyphosate.

Low level of soil disturbance

A low level of soil disturbance was created when the boneseed plants were pulled at the same angle and direction as the bulk of the root system was oriented. Soil movement was low, and any disturbed soil was compacted by foot immediately after each plant was uprooted.

High level of soil disturbance

A higher level of soil disturbance was created when the boneseed plants were pulled more rapidly and at an angle slightly greater than that at which the root system was oriented. These quadrats were weeded from the centre outwards so that the disturbed soil would not be compacted underfoot during the process.

The cut or uprooted boneseed plants were either stacked in the centre of the treated quadrat (mulched) or taken away from the site. The treatments were also imposed upon a meter wide strip around each quadrat to allow access without disturbing the soil or the vegetation within the quadrat, and to lessen any edge effects.

Timing of treatments

All of the treatments were imposed by the end of April 1996 except for three quadrats at the Morialta site. The boneseed plants in these three quadrats could not be completely uprooted until after soaking rains had softened the soil. They were removed in the first week of June.

Assessment of germination

The sites were visited and each quadrat visually inspected at least once a month. The number of germinants altered little between early September and mid-October, hence we conclude that the germination of most of these plants had occurred by the first week of September. The number and species of plant that germinated within each quadrat at Belair was assessed within the first two weeks of September 1996. The germination at Morialta was assessed during early October 1996. The number of boneseed seedlings were also assessed at Morialta during May and August 1997 and April 1999, and at Belair during May 1997, January and November 1998 and April 1999.

Statistical analysis

The effect that the two main factors (soil disturbance and mulching) had on the emergence of a particular species was investigated using a Regression Analysis.

ANOVAs, assuming a Completely Randomized Design, have been used to determine if the eight treatment factors had any effect on germination. The ANOVAs were performed in GENSTAT, and the data were log (x+1) transformed when the plot of residuals indicated that there was a relationship between the mean and the variance.

The number of each species that germinated within the treated quadrats were pooled and compared with the number that germinated within the control and uninfested quadrats. This was done because the interaction between soil disturbance and mulching was not significant, and because killing of the boneseed is likely to be of major importance in determining the regeneration that occurs within such areas. The number of *Arthropodium* sp. and *Lagenifera stipitata* (Labill.) Druce were not investigated because the effect of soil disturbance had significantly influenced the germination of these two species. Caution must be used when interpreting the effect of 'killing boneseed' because of the influence of the different techniques used.

Where the data satisfied the assumptions required of an ANOVA, this test was used to compare the number of each species germinating in the uninfested, treated and control quadrats. Where the assumptions of ANOVA could not be satisfied using log (x+1) and $\sqrt{(x+0.5)}$ transformations, Mann-Whitney 'U' Tests and Kruskal-Wallis 'H' Tests (Kruskal and Wallis 1952) were used.

Results

Forty-one taxa across 16 families were noted at the Belair site (Tables 2 and 4) and 31 taxa from 21 families were recorded at the Morialta site (Tables 3 and 5). The greatest number of germinants at both sites were within the family Poaceae; *Microlaena stipoides* (Labill.) R.Br and introduced grass were predominant at Belair and Morialta respectively. Boneseed seedlings were among the poorly represented taxa germinating during this first post-treatment flush at both sites however three years later they are one of the most frequently occurring taxa at both Belair (Table 4) and Morialta (Table 5).

A very large increase in the number of boneseed seedlings occurred between October 1996 and May 1997 and again before August 1997 at Morialta. A large decrease occurred between August 1997 and April 1999, such that there were a similar number of boneseed seedlings present during May 1997 and April 1999. At Belair, there was a small increase in the number of boneseed seedlings between September 1996 and May 1997, followed by a very large increase before January 1998. There have been a similar number of boneseed seedlings present during January 1998, November 1998 and April 1999. Neither the numerical increases, nor the percentage increase over the original

Table 1. Treatments assigned to quadrats at Belair and Morialta.

Treatment	Level of soil disturbance [and number of quadrats]			
	Belair		Morialta	
Uninfested	none	[4]	none	[5]
Control	none	[4]	none	[4]
Slash and mulch	minimum	[3]	minimum	[3]
Slash and remove trash	minimum	[3]	minimum	[3]
Pull, compact soil and mulch	low	[3]	low	[3]
Pull, compact soil and remove trash	low	[4]	low	[3]
Pull, disturb soil and mulch	high	[3]	high	[3]
Pull, disturb soil and remove trash	high	[3]	high	[3]

Table 2. Mean [and standard error] numbers of germinants (other than boneseed) per plot at Belair.

Family	Scientific Name	Common Name	uninfested		minimum^A and mulched	
Adiantaceae	*Cheilanthes austrotenuifolia*	Rock fern				
Asteraceae	*Lagenifera stipitata*	Common bottle-daisy	4.0	[2.0]	5.0	[2.3]
	Leptorhynchos squamatus	Scaly buttons	0.3	[0.3]		
	Senecio pterophorus	African daisy	0.3	[0.3]	0.3	[0.3]
	Sonchus oleraceus *	Common sow-thistle	0.3	[0.3]	1.0	[0.6]
Cyperaceae		Sedge	43.8	[38.0]	19.0	[18.5]
Droseraceae	*Drosera auriculata*	Tall sundew	2.0	[2.0]		
	Drosera whittakeri	Scented sundew	1.5	[1.5]	1.0	[1.0]
Goodeniaceae	*Goodenia* sp.	Goodenia	0.5	[0.5]		
Poaceae	*Stipa* sp.	Spear-grass	291.5	[128.9]	20.7	[5.9]
	Microlaena stipoides	Weeping rice-grass	627.5	[515.8]	120.7	[44.8]
	introduced grass*		113.3	[71.6]	68.7	[68.2]
Iridaceae	*Freesia* sp.*	Freesia	3939.8	[1538.3]	38.3	[26.6]
	*Homeria flaccida**	One-leaved cape tulip	57.3	[29.3]	60.3	[55.9]
	Romulea sp.*	Guildford grass				
Liliaceae	*Arthropodium* sp.	Vanilla-lily	162.8	[54.2]	565.0	[126.5]
	Bulbine bulbosa	Bulbine lily	7.3	[4.2]	52.3	[24.4]
	Burchardia umbellata	Milkmaids	3.0	[3.0]		
	Caesia vittata	Blue grass-lily	329.0	[185.5]	298.7	[244.9]
	Chamaescilla corymbosa	Blue squill	63.3	[60.3]	2.0	[2.0]
	Dichopogon strictus ?	Chocolate lily	50.3	[28.3]	2.7	[2.7]
	*Myrsiphyllum asparagoides**	Bridal creeper				
	Thysanotus patersonii	Twinning fringe-lily	18.5	[11.3]	3.0	[2.5]
	Unidentified lily		4.3	[1.7]		
	Wurmbea dioica	Early Nancy; Bulls eye	1.0	[0.6]	0.7	[0.7]
Linaceae	*Linum marginale*	Native flax	8.5	[7.5]	0.3	[0.3]
Orchidaceae	*Acianthus exsertus*	Mosquito orchid			4.0	[4.0]
	Corybas sp.	Helmet-orchid	4.8	[3.8]		
	Diuris longifolia	Bulldogs				
	Pterosylis nana	Dwarf greenhood				
	Pterostylis pedunculata	Maroon hood				
	Pterostylis robusta	Larger striped greenhood				
	Thelymitra sp.	Sun-orchid	7.3	[6.3]	0.3	[0.3]
Oxalidaceae	*Oxalis perennans*	Native oxalis	51.0	[47.7]	6.3	[3.5]
	*Oxalis pes-caprae**					
Plantaginaceae	*Plantago lanceolata*	Ribgrass	49.5	[46.9]		
Primulaceae	*Anagallis arvensis* *	Scarlet pimpernel				
Rosaceae	*Acaena echinata*	Sheeps burr	0.8	[0.8]	3.7	[3.7]
Rubiaceae	*Asperula conferta*	Common woodruff				
Thymelaeaceae	*Pimelea humilis*	Common riceflower	2.5	[2.5]		

Treatment (^A = level of soil disturbance).
* = exotic.

number of seedlings varied across the treatments at either site.

Effects of soil disturbance and mulching on germination

There were no significant (P>0.05) interactions between the soil disturbance and mulching factors for any species at either site. The mean numbers of the native plants *Arthropodium* sp. and *Lagenifera stipitata* emerging at the Belair site (Table 2) were significantly (P=0.016 and P=0.026) decreased by soil disturbance but not by mulching. The mean number of these two species within the treated quadrats was greater than within uninfested quadrats only when minimal soil disturbance had been imposed. Also, their mean number was greater than within the control quadrats only when either a minimum, or a low level of soil disturbance was imposed (Figures 1 and 2 respectively).

The number of *Stipa setacea* R.Br. emerging at the Belair site was significantly greater (P=0.025) within the uninfested quadrats than within the treatment or control quadrats (Table 2), (Figure 3). The numbers of families and native and exotic taxa represented were not affected by the treatments imposed at either site.

The effect of treating boneseed, irrespective of the technique used

The majority of plants that germinated at the Morialta site were small annual exotic plants. The numbers of each species that germinated in sufficient numbers for statistical analysis did not differ within the uninfested, treated and control quadrats. The data indicates that the germination of native species was not affected by the boneseed.

At Belair, a significantly greater (P=0.0016) number of *Stipa setacea* were found within the uninfested quadrats; the number within the treated and control quadrants were not significantly different from each other. The number of *Freesia* sp. plants within the uninfested quadrats was also found to be significantly greater (P=0.006) than that within the treated and control quadrants. Also, the number of

minimum[A] and removed		low[A] and mulched		low[A] and removed		high[A] and mulched		high[A] and removed		control	
		122.0	[122.0]			9.7	[9.7]				
20.7	[10.3]	4.3	[2.4]	1.3	[1.3]			0.7	[0.3]	0.3	[0.3]
				0.5	[0.3]	0.3	[0.3]			0.3	[0.3]
1.0	[1.0]	0.3	[0.3]	1.8	[1.4]	0.3	[0.3]	0.3	[0.3]	0.5	[0.5]
37.0	[7.2]	21.0	[4.4]	51.0	[22.5]	35.3	[8.0]	63.7	[35.2]	12.3	[5.6]
0.3	[0.3]	7.0	[7.0]			2.0	[2.0]			0.5	[0.5]
48.7	[10.9]	23.0	[9.8]	30.8	[9.6]	53.7	[36.3]	13.0	[7.0]	19.0	[9.7]
908.0	[572.4]	348.7	[290.4]	1260.5	[489.8]	909.0	[222.7]	1192.7	[410.6]	458.3	[225.5]
3.7	[3.7]	0.3	[0.3]	64.5	[49.9]	42.3	[21.4]	879.7	[550.6]	263.8	[119.1]
1496.7	[627.9]	27.3	[13.2]	1135.5	[979.3]	995.3	[364.1]	678.7	[550.7]	160.3	[154.9]
13.3	[11.9]			16.3	[10.3]	1.7	[0.9]	16.0	[8.0]		
		0.3	[0.3]								
264.3	[127.8]	250.3	[122.5]	156.0	[60.9]	34.7	[31.7]	141.7	[75.6]	97.5	[76.6]
109.3	[49.8]	26.7	[22.7]	11.5	[7.2]	31.7	[20.9]	139.7	[77.0]	41.0	[37.1]
						0.3	[0.3]				
113.0	[69.3]	252.0	[212.1]	235.5	[86.3]	149.3	[149.3]	70.0	[69.0]	25.0	[25.0]
		3.0	[3.0]								
8.7	[8.7]	27.3	[22.5]	10.5	[10.5]	1.3	[1.3]	12.3	[12.3]	0.5	[0.5]
2.0	[1.0]	0.7	[0.7]	16.5	[15.2]			5.7	[3.0]	4.8	[4.1]
3.7	[3.7]	2.3	[2.3]								
				4.8	[4.8]l						
										0.5	[0.5]
1.7	[1.2]	0.3	[0.3]								
				1.0	[1.0]			0.3	[0.3]	23.5	[23.5]
14.7	[14.7]	510.0	[509.5]	0.3	[0.3]						
		0.7	[0.7]								
										0.5	[0.5]
2.3	[2.3]	22.7	[17.0]					2.7	[2.7]	33.8	[33.8]
										0.3	[0.3]
1.0	[0.6]	1.3	[1.3]	1.5	[1.0]						
40.3	[28.3]	6.7	[3.7]	29.8	[15.8]	6.7	[3.5]	39.3	[39.3]	17.8	[9.7]
0.7	[0.7]										
2.3	[2.3]	0.3	[0.3]	3.5	[3.2]					2.8	[1.9]
								2.7	[2.7]		
5.0	[5.0]	0.7	[0.3]	0.3	[0.3]	2.7	[0.9]	1.7	[0.7]	0.5	[0.3]
								12.0	[12.0]	2.3	[2.3]

Freesia sp. within the treated quadrats was greater than within the control quadrats (P=0.05) (Figure 4). Although no significant difference between the numbers of sun-orchid (*Thelymitra* sp.) was found between treatments, they were present in 75% of the uninfested quadrats, 32% of the treated quadrats, and not in any of the control quadrats.

There was no *Homeria flaccida* Sweet within any of the control quadrats. Neither native plants of the family Orchidaceae, nor any *Caesia vittata* R.Br. plants were found within three of the four control quadrats. The level of light and the biomass of native vegetation below this lightly infested exceptional quadrat appeared to be substantially greater than that below the other, more heavily infested control quadrats. No significant difference was found between the numbers of *H. flaccida*, *C. vittata*, or orchids within the uninfested and treated quadrats.

Discussion

The effect of the technique used to remove boneseed

There was no significant interaction between the effects of soil disturbance and mulching on the germination of any species at either site. The technique used to manually remove boneseed did not significantly influence the subsequent number of each plant species germinating, except for two species at the Belair site. A decrease in the number of *Arthropodium* sp. and *Lagenifera stipitata* that emerged at Belair was associated with an increase in soil disturbance. The environment within the quadrats from which boneseed had been removed using the minimum soil disturbance technique may be more conducive to the emergence of both these species than the environment within the uninfested quadrats. Resources such as light, water and nutrients may be more available within treated quadrats, and this has probably contributed to the observed response. In contrast, despite the probable increase in these resources, the environment within the quadrats in which a high level of soil disturbance had been imposed was no more conducive to the emergence of *Arthropodium* sp. or *Lagenifera stipitata*

Table 3. Mean [and standard error] numbers of germinants (other than boneseed) at Morialta per plot

Family	Scientific name	Common name	uninfested		minimum[A] and mulched	
Asclepiadaceae	*Asclepias rotundifolia**	Broad-leaved cotton-bush	0.2	[0.2]		
Asteraceae	*Senecio hypoleucus**	African daisy	2.4	[1.3]	6.7	[2.6]
	*Sonchus oleraceus**	Common sow-thistle	0.8	[0.4]	2.0	[2.0]
		Thistle sp.	8.2	[8.2]	0.3	[0.3]
Cyperaceae		Sedge				
Convolvulaceae	*Convolvulus remotus*	Australian bindweed				
	*Dichondra repens**	Tom Thumb				
Poaceae	Introduced grass spp.*		716.6	[109.3]	631.7	[150.0]
	Stipa sp.		7.2	[6.3]		
Goodeniaceae	*Scaevola albida*	Small-fruited fan-flower	0.8	[0.4]	0.7	[0.3]
Iridaceae	*Romulea* sp.*	Guildford grass	4.0	[2.9]		
Fabaceae	*Medicago** and *Trifolium**		165.6	[70.2]	94.0	[33.2]
	Vicia sp.*	Vetch	43.2	[20.8]	46.3	[46.4]
Liliaceae	*Bulbine bulbosa*	Bulbine lily	14.8	[12.7]	0.3	[0.3]
	*Myrsiphyllum asparagoides**	Bridal creeper				
Myrtaceae	*Eucalyptus porosa*		0.2	[0.2]		
Oleaceae	*Olea europaea**	Olive	0.8	[1.8]	0.3	[0.3]
Oxalidaceae	*Oxalis pes-caprae**	Sour-sob	1.8	[2.0]		
Plantaginaceae	*Plantago* sp.*	Plantain	13.4	[11.3]	1.3	[0.9
	Geranium solanderi	Native geranium				
Polygonaceae	*Rumex* sp.*	Dock				
Primulaceae	*Anagallis arvensis**	Blue pimpernel	66.4	[25.1]	103.3	[9.4]
Rosaceae	*Acaena echinata*	Sheeps burr	2.0	[2.0]		
Rubiaceae	*Asperula conferta*	Common woodruff				
	*Sherardia arvensis**	Field madder	36.2	[25.6]	8.3	[7.9]
Sapindaceae	*Dodonaea viscosa*	Sticky hop-bush	0.2	[0.2]	0.3	[0.3]
Solanaceae	*Solanum nigrum**	Blackberry nightshade				
Lythraceae	*Lythrum hyssopifolia*	Lesser loosestrife	42.8	[26.1]	38.3	[36.4]
Caryophyllaceae	*Cerastium glomeratum**	Broad-leaved chicken weed			0.3	[0.3]

Treatment ([A] = level of soil disturbance).
* = exotic.

Table 4. Mean [and standard error] germination over time of boneseed seedlings per plot at Belair.

Time	uninfested		minimum[A]		low[A]		high[A]		control	
Sep 1996	3.3	[1.2]	8.7	[3.0]	14.8	[8.3]	13.0	[5.4]	not assessed	
May 1997	7.8	[3.2]	21.8	[2.9]	34.7	[16.6]	25.3	[10.6]	8.3	[5.0]
Jan 1998	12.5	[5.0]	255.0	[51.0]	365.1	[89.2]	179.3	[76.2]	47.8	[34.7]
Nov 1998	11.0	[4.5]	265.0	[52.1]	337.4	[77.3]	176.5	[77.2]	39.3	[20.4]
Apr 1999	4.0	[1.7]	202.5	[40.7]	256.3	[54.5]	149.2	[65.3]	14.8	[8.0]

Treatment ([A] = level of soil disturbance).

Table 5. Mean [and standard error] germination over time of boneseed seedlings per plot at Morialta.

Time	uninfested		minimum[A]		low[A]		high[A]		control	
Oct 1996	10.8	[1.9]	14.0	[4.4]	27.7	[10.9]	not assessed		not assessed	
May 1997	46.4	[8.0]	192.8	[62.8]	364.0	[140.6]	299.7	[118.4]	271.0	[71.9]
Aug 1997	124.0	[29.0]	773.2	[232.2]	1390.3	[697.8]	1660.0	[743.1]	598.3	[86.6]
Apr 1999	33.0	[6.4]	190.3	[38.2]	299.5	[119.9]	183.2	[70.3]	153.3	[32.7]

Treatment ([A] = level of soil disturbance).

than that within the control quadrats. This indicates that the effects of soil disturbance are large and detrimental to the emergence of these species.

The effect of the presence and removal of boneseed

The removal of mature boneseed plants resulted in a large increase in the number of seedlings of this species at both sites. This increase appears to have peaked by the end of the next spring following the treatment (1997). The germination of boneseed at the Morialta site was very high during the 1997 spring, and inter-specific competition has probably contributed to the reduction in the density of these seedlings. The effect of factors such as season and yearly climatic variation is

minimum[A] and removed		low[A] and mulched		low[A] and removed		high[A] and mulched		high[A] and removed		control	
				1.0	[1.0]						
1.0	[1.0]	15.0	[6.1]	20.0	[20.0]	1.0	[1.0]	2.3	[1.8]	2.0	[1.1]
1.7	[0.9]	5.3	[2.9]	11.3	[9.9]	2.0	[1.0]	8.3	[3.4]	1.0	[1.0]
		2.7	[1.2]								
										1.5	[1.5]
								0.3	[0.3]	0.8	[0.8]
1.3	[1.3]	2.0	[2.0]	1.7	[1.2]	41.7	[20.8]			11.8	[11.8]
1300.0	[259.1]	1224.3	[499.8]	905.0	[167.0]	831.7	[213.0]	1347.3	[458.2]	619.0	[181.8]
0.7	[0.7]			2.3	[2.3]	5.3	[5.3]	8.7	[8.7]	1.8	[1.8]
1.0				4.3	[2.9]			0.3	[0.3]	0.8	[0.8]
0.7	[0.7]			7.0	[7.0]			0.7	[0.7]		
130.7	[65.5]	135.7	[71.6]	46.0	[6.1]	64.3	[14.3]	256.7	[104.3]	175.3	[80.8]
21.3	[9.2]	24.3	[12.8]	18.0	[12.1]	23.3	[17.0]	3.3	[2.8]	4.3	[2.6]
1.7	[1.7]					1.0	[1.0]				
						0.3	[0.3]				
1.7	[0.3]	0.7	[0.7]	0.3	[0.3]	0.7	[0.3]			0.5	[0.3]
		0.3	[0.3]			241.7	[159.6]	323.7	[323.7]	29.5	[29.5]
6.7	[6.6]	7.7	[6.7]	11.3	[10.3]	5.3	[2.9]	5.3	[5.3]	3.8	[1.7]
37.3	[24.3]			10.7	[10.7]	28.3	[28.3]	2.7	[2.7]	1.3	[1.3]
		4.3	[4.3]								
39.0	[20.3]	200.0	[69.6]	82.7	[43.2]	39.0	[21.4]	337.0	[92.7]	24.3	[22.0]
										0.8	[0.8]
				19.0	[19.0]						
18.7	[18.6]			0.7	[0.7]			6.7	[6.6]	3.3	[2.7]
		2.0	[2.0]			1.0	[1.0]			3.0	[3.0]
		0.3	[0.3]								
5.0	[3.2]	89.3	[84.4]	2.0	[1.2]	20.0	[17.0]	153.3	[72.2]	16.0	[16.0]
		4.7	[4.7]								

evident in the changes in the density of boneseed seedlings in the uninfested and control quadrats. However, such population dynamics are superimposed on the very large and sustained increase in density that has occurred following the removal of adult boneseed plants at both sites.

At Morialta, there was no obvious effect of boneseed removal on the germination of species other than boneseed. This was possibly because the species present in the seed bank do not respond differently to the treatments imposed, or that such a differential response either has a time lag or requires different climatic conditions than occurred in 1996 to be expressed.

At Belair, the emergence of the geophytes *Freesia* sp., *Homeria flaccida* and *Caesia vittata* from beneath heavy boneseed infestations was inhibited. Also, fewer *Freesia* sp. emerged from the treated quadrats than from the uninfested quadrats. This may indicate that the number of propagules of this species has been reduced because of the boneseed infestation. The probable lower level of resources due to competition from boneseed may have reduced the survival and/or reproductive rate of this species within such infestations.

Caesia vittata, a native lily, was commonly encountered across the entire Belair study site, hence its absence from all of the control quadrats except one lightly infested quadrat is salient. This species tends to grow in the shade rather than the open (Vanderpeer, personal communication 1996). It is probably a good tolerator as it grows well underneath native shrub canopies and within areas of dense native understorey species (ibid.). The propagules of *C. vittata* were not limiting within this site as a large number of this species emerged following the removal of boneseed. It is probable that this species was not emerging below the dense boneseed infestations either because of competition for resources from boneseed and/or because boneseed was producing allelopathic substances that suppressed its germination.

Plants in the Orchidaceae family were not found within any of the control quadrats apart from the lightly infested quadrat which contained a high density of *Pterostylis pedunculata* R.Br. and *Corybas* sp., species that flower under shade (Brewer, personal communication 1996). A reduction in light associated with the presence of boneseed is not likely to have inhibited the germination of orchid seed, as continuous darkness is recommended for terrestrial Australian orchids, 'at least until germination has commenced' (Hadley 1982). Light availability may have influenced the distribution of the sun-orchid *Thelymitra* sp. which was present at highest density in uninfested quadrats, decreased in treated quadrats and was not present in any control quadrats. If orchids are emerging from within dense boneseed infestations, the level of light and/or other resources may be too low to allow them to develop and reproduce there.

Long-term effects of boneseed

Many of the orchids that emerged from the treated quadrats were too large to have germinated from seed. Low numbers of orchids emerged from the quadrats that were previously densely infested. This

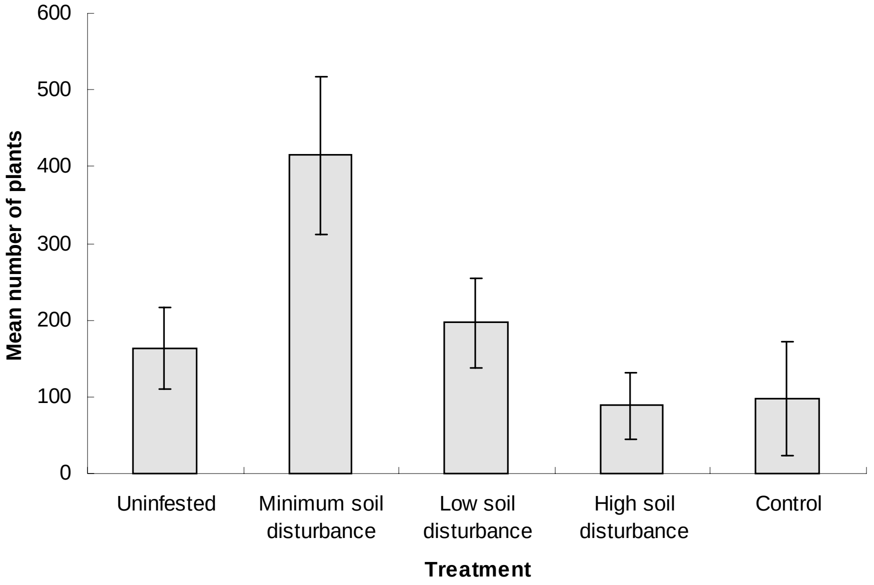

Figure 1. Mean number of *Arthropodium* sp. emerging per plot in uninfested, soil disturbed and control quadrats ± standard error.

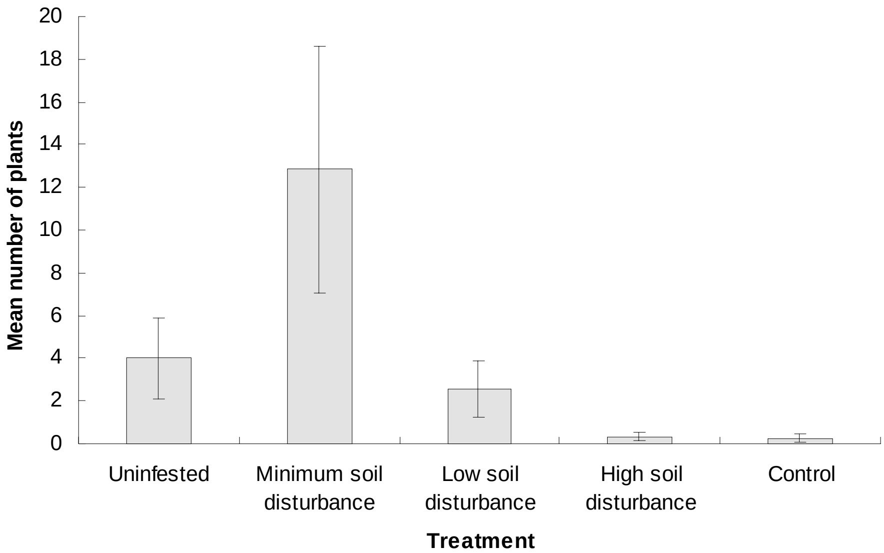

Figure 2. Mean number of *Lagenifera stipitata* emerging per plot in uninfested, soil disturbed and control quadrats ± standard error.

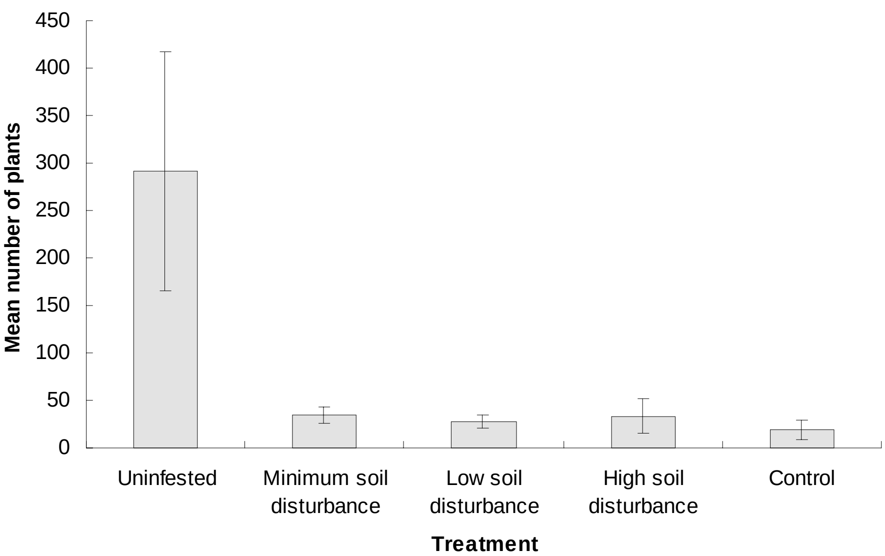

Figure 3. Mean number of *Stipa setacea* resprouting per plot in uninfested, soil disturbed and control quadrats ± standard error.

suggests that the time over which bulbs of orchids will persist is short relative to the time the boneseed has been present at high density. When a dense cover of boneseed has been removed, the regeneration of the orchid populations may require seeds to be blown into the area to supplement the seed production of any plants that do survive.

The number of *Stipa setacea* was greatly reduced within the infested quadrats. Most of the plants of this perennial species probably resprouted from their rootstock and thus their numbers are more indicative of their tolerance of stress within a boneseed infestation than their response to boneseed removal.

The effect of mulching

Mulching did not have a significant effect on the germination of any species at either study site. At both study sites, plants were seen to grow within the boneseed mulch, wherever light penetrated through to the ground. These plants were predominantly grasses that grew with an etiolated habit toward the light. As no species were notably absent under or near the mulch, an allelopathic effect from substances that may have leached from the boneseed mulch was not apparent. Any effect of leachates, though, may have diminished between the time of mulching and the time when germination occurred.

Soil disturbance and plant life-history

Classical successional theory (Grime 1977) predicts that a certain type of plant will possess a suite of morphological, physiological and / or phenomenological traits, that makes it suited (Grubb 1985) to pioneer disturbed areas. These traits include seed germination that is inhibited by darkness, thus allowing a species to accumulate a seed store under an established canopy, and a large number of small seeds that are widely dispersed and readily lodge in disturbed soil and hence are more likely to be present at any given site, particularly at a disturbed one. The propagules of such species germinate and grow rapidly following disturbance, hence they are able to utilize the resources that disturbance makes available. Such plants have been termed fugitive, ruderal (Grime 1977), or r-selected (MacArthur and Wilson 1967).

The prediction that fugitive species would be present within the treated quadrats, and that their numbers would increase as the level of soil disturbance increased was not supported at either study site. Fugitive species were prevalent throughout the Morialta site, indicating that the area has been so highly disturbed in the past that the added soil disturbance associated with the treatments was of little consequence. The absence of an increase in fugitive species associated with

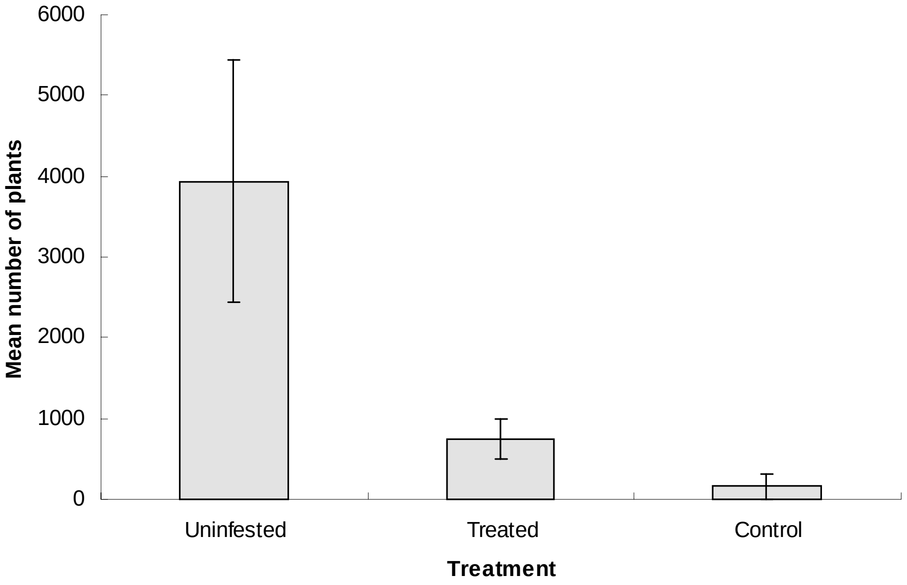

Figure 2. Mean number of *Freesia* sp. emerging per plot in uninfested, soil disturbed and control quadrats ± standard error.

soil disturbance at the Belair site may indicate that there is no such seed bank present.

Conclusions

The different techniques used in this study to control boneseed had no effect on the subsequent emergence of the seedlings of this species. Therefore, with regards the control of the boneseed soil seed bank, there is no difference between these techniques. An increase in soil disturbance was associated with a reduction in the germination of *Arthropodium* sp. and *Lagenifera stipitata*. Also, the germination of no native species responded positively to increasing soil disturbance. The findings of this study indicate that the effect of soil disturbance on subsequent regeneration needs to be considered when controlling environmental weeds. In an area with a species composition that reflects the high level of disturbance it has experienced, a primary aim may be to reduce the spread of the environmental weeds. A technique that results in the removal of these weeds from a larger area per unit time may then be preferable despite the associated higher level of soil disturbance. In areas where the native vegetation is reasonably intact, it may be appropriate to assume that its regeneration will be optimal when the environmental weeds are removed using a technique that produces a low level of soil disturbance. An assessment of how to optimize the regeneration of the native ecosystem may have to be made on a case by case basis, and may be time dependent, but such assessments should not be neglected.

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