Bone-seed (*Chrysanthemoides monilifera* ssp. *monilifera*) invasion effects on native regeneration in New Zealand coastal plant communities

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Abstract: Bone-seed, *Chrysanthemoides monilifera* ssp. *monilifera* (L.), is an environmental weed of coastal vegetation communities scattered throughout New Zealand. To assess the long-term implications for native forest regeneration in sites where bone-seed is present, we selected four study sites around Wellington, New Zealand, where bone-seed was abundant. We compared seed bank composition in bone-seed-invaded sites with nearby native forest patches, and monitored bone-seed and native seedling recruitment with and without control of mature bone-seed plants. We also tested the potential effects of fire on bone-seed recruitment in these communities by heating seeds prior to germination. Bone-seed, gorse (*Ulex europaeus*), and native species emerged from seed bank samples taken from bone-seed-invaded sites, but only native species and (less) gorse emerged from seed bank samples taken from native forest patches. Gorse germination was strongly promoted by heat but bone-seed germination was less affected by heat. Bone-seed seedling abundance increased dramatically following canopy removal, whereas native seedling abundance decreased dramatically. This suggests that disturbance of any form is likely to favour recruitment of bone-seed (and gorse) over native species, although in the long term, native seedlings can establish beneath the canopy of mature bone-seed plants. It is not yet known if, in the absence of further disturbance, regenerating native vegetation will eventually replace bone-seed in New Zealand.

Keywords: fire; germination; gorse; invasive species; seed bank; seedling recruitment; succession; weed invasion

Introduction

Bone-seed, *Chrysanthemoides monilifera* ssp. *monilifera* (L.) T. Norl. (Asteraceae)[1], is an environmental weed found in scattered coastal locations throughout New Zealand. It is an erect shrub 1–3 m high that originates from the southern coast and adjacent mountains of South Africa. It was first recorded in New Zealand (Auckland) in 1870 (Webb et al. 1988), most likely introduced as an ornamental plant. Since then, it has spread throughout New Zealand from Northland to Otago, establishing along coastlines and in forest and woodland communities up to 20 km inland (Department of Conservation 2007). It tolerates a wide range of soil types, moisture levels, disturbance levels, and light environments (Weiss et al. 1988). Seeds are dispersed by gravity and birds, and possibly also possums and cattle (Weiss et al. 1988; Williams et al. 2000; Parsons & Cuthbertson 2001). Bone-seed is also considered an environmental weed in Australia, occurring in a range of vegetation types including coastal dune scrub, coastal woodlands, heathland, riparian vegetation, mallee scrub, dry and wet sclerophyll forest (Blood 2001). Another subspecies, *Chrysanthemoides monilifera* ssp. *rotundata* (bitou bush), is also highly invasive, and detrimental to native plants and animals in Australia (Parsons & Cuthbertson 2001; Gosper 2004), but, to our knowledge, does not occur in New Zealand.

In New Zealand, bone-seed is subject to control by the Department of Conservation in eight out of 13 conservancies, and is included in 12 out of 16 regional council pest management strategies. In 2001, bone-seed was declared an unwanted organism under Sections 52 and 53 of the Biosecurity Act 1993, which means it is illegal to propagate, sell, or distribute it in New Zealand.

Despite being widely considered a serious environmental weed in New Zealand, there is little empirical evidence on which to judge the potential long-term impacts of bone-seed. Studies in Australia have

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[1] Nomenclature follows Webb et al. (1988).

shown that bone-seed can invade intact native vegetation, displace native species, and reduce biodiversity (Dodkin & Gilmore 1985; Weiss et al. 1988; Thomas et al. 2000). Anecdotally, bone-seed may also have a detrimental effect on faunal carrying capacities in Australia, by reducing nectar resources, seed, pollen, and foliage of native plant species (Weiss et al. 1988). Bitou bush is more widely studied, and has been shown to displace and possibly reduce seed production, germination, and seedling growth of the Australian native coastal wattle, *Acacia sophorae* (Weiss & Noble 1984a,b; Vranjic et al. 2000). Bitou bush may also reduce the abundance and diversity of plant-feeding birds (French & Zubovic 1997) and litter invertebrates (French & Eardley 1997; Lindsay & French 2006; Wilkie et al. 2007), displace important food sources for migratory birds (Parsons & Cuthbertson 2001), and alter rates of litter decomposition and nutrient cycling (Lindsay & French 2004). In New Zealand, bone-seed may have some, or all, of the effects that bone-seed and bitou bush have in Australia.

The potential impact of weed invasions may be lessened if the invaded site has native seed propagules present, either at the site, or within dispersal distance (Bakker et al. 1996; Turner & Corlett 1996; Chazdon 2003). In this situation, providing that seed dispersal vectors are present, native seeds will be continually arriving at the invaded site, with the potential to germinate and establish and compete with the weeds. However, whether natives or exotics establish depends on a range of interacting factors, including seed viability, germination requirements, environmental conditions, and competitive relationships with other species present (Watt 1947; Levine 2001; Seabloom et al. 2003). Seed viability, longevity, and dormancy characteristics vary among woody native species in New Zealand, but in general most species have seeds that germinate soon after ripening, and relatively few have seeds that remain viable in the soil for more than one year (Burrows 1994; Sem & Enright 1996). Data on the seed viability of bone-seed in New Zealand are lacking, but in Australia bone-seed seeds are thought to retain 'high viability' in the soil for at least 4 or 5 years (Parsons & Cuthbertson 2001). However, other studies have shown that only 6–13% of seeds remain viable after 3 years (Weiss 1984), and that deeply buried seeds can remain viable for more than 10 years (Adair & Ainsworth 2000). In its native range, bone-seed has a relatively low-density seed bank (estimates include 3–85 seeds m^{-2} and 100–300 seeds m^{-2}), and produces few seedlings (Scott 1996; Thomas et al. 2000). However, in Australia, plants can produce ten times more seed than they do in South Africa (Scott 1996), and seed bank densities of 2500 seeds m^{-2} and seedling densities of 200 seeds m^{-2} have been reported (Lane 1976 in Thomas et al. 2000).

Native species recruitment at bone-seed-invaded sites may also be influenced by another, frequently co-dominant, invasive species, gorse *Ulex europaeus* (L.) (Fabaceae). Gorse is a spiny shrub up to 4 m tall, and is the most widespread weed in New Zealand (Department of Conservation 2007). Gorse seed viability is high in New Zealand: 80–100% in one study where seeds were extracted from the soil (Zabkiewicz & Gaskin 1978), and more than 99% in another study where seeds had been stored in the laboratory for up to 10 years (Hill et al. 2001). Gorse seed is thought to remain viable in the soil for several decades at least (Moss 1959; Partridge 1989; Hill et al. 2001), and can build up to densities of 10 000 seeds m^{-2} (Ivens 1978). Not surprisingly, very high densities of gorse seedlings have also been recorded in New Zealand following disturbance (up to 350 seedlings m^{-2} in one study) (Ivens 1978).

Human-induced disturbance often facilitates invasion by exotic species (Hobbs 1991; Hobbs & Huenneke 1992; D'Antonio et al. 1999), particularly when there are few early-successional species in the native flora, as is the case in New Zealand (Healy 1961; Wardle 1991; Craine et al. 2006). However, providing no further disturbance occurs, their presence is frequently ephemeral, and is eventually replaced by native regeneration (Allan 1936; D'Antonio et al. 1999; Kotanen 2004). In New Zealand, for example, gorse is eventually overtopped by native species (Lee et al. 1986; Wilson 1994), and is widely considered to be a useful shelter crop that facilitates native regeneration. Recent research, however, adds a cautionary note to this assertion; the composition of forest that regenerates through gorse is not necessarily the same as the composition of forest that regenerates through native species (Sullivan et al. 2007). It is not known whether native succession through bone-seed proceeds in a similar way to that through gorse. Weed control can result in significant disturbance if the methods employed involve canopy removal or displacement of soil. Conversely, weed control can also reduce both above- and below-ground competition, and (as is frequently the intention of such control measures) can facilitate native seedling recruitment (Masters et al. 1996; Sweeney et al. 2002; Baer & Groninger 2004).

Fire is another form of disturbance that may play an important role in bone-seed recruitment and competition with natives and other exotic species. Fire promotes seed germination in some species, usually because heat breaks physical dormancy imposed by the seed coat (Baskin & Baskin 1998; Fenner & Thompson 2005). However, other fire-related cues can also promote germination, e.g. smoke, charcoal and nitrate (Keeley et al. 1985; Bell et al. 1999; Kenny 2000; Enright & Kintrup 2001). Exactly what combination of temperature and duration of exposure optimises germination can vary between species (e.g. Auld & O'Connell 1991; Herranz et al. 1999), so fires of different intensity and durations can affect competitive relationships, and thus result in different regeneration patterns. Bone-seed plants can be killed by even low intensity fires (Weiss 1984), but bone-seed germination and seedling establishment is promoted by

fire (Weiss 1984; Adair & Ainsworth 2000). Similarly, gorse germination is promoted by fire (Zabkiewicz & Gaskin 1978). In New Zealand, very few native plants display specific adaptations to fire (Basher et al. 1990; Ogden et al. 1998), so fire can have devastating effects on the native vegetation. Furthermore, fire often provides conditions favourable for the establishment of exotic weeds (Milberg & Lamont 1995; Harrod & Reichard 2001; Lesica & Martin 2003). In New Zealand it is often gorse that dominates a site following fire, but bone-seed can sometimes be the dominant species following fire, despite the likely presence of gorse in the seed bank (KGM & SMT pers. obs.).

To assess the long-term implications for native forest regeneration in sites where bone-seed is present, we conducted a series of experiments designed to answer the following questions: (a) what is the composition of the seed bank in bone-seed-invaded sites and nearby native forest patches, (b) what are the patterns of bone-seed and native seedling recruitment in bone-seed-invaded sites, with and without canopy disturbance, and (c) what is the potential effect of fire on bone-seed recruitment in these communities?

Materials and methods

Study sites

In October 2001 we identified four coastal sites in the Wellington Region where mature bone-seed was abundant within a mixed community of native and exotic shrub, tree, grass, and herb species. All sites were within 200 m of a patch of secondary forest (disturbed in the past, but now dominated by regenerating native forest). In New Zealand, these secondary forest patches typically contain a mix of ferns, perennial herbs, shrubs, and broadleaved and podocarp trees (Wardle 1991). Sites 1 and 2 were on the west-facing slopes of the rolling hills above the suburb of Seaview, approximately 250 m apart (Site 1, 41°14′ S 174°55′ E; Site 2, 41°14′ S 174°54′ E). Site 3 was on the north-facing slopes of similar hill country in the suburb of Happy Valley (41°19′ S 174°45′ E). Site 4 was on the north-facing coastal scree slopes of Pukerua Bay, 35 km north of Wellington (41°02′ S 174°51′ E). Underlying soils at all sites were either yellow-grey or yellow-brown earths (NZ Soil Bureau 1968). Mean annual rainfall in Wellington is 1249 mm and mean annual temperature is 12.8°C (National Institute of Water and Atmospheric Research 2007).

Regeneration following bone-seed control

In October 2001 we subjectively selected 10 discrete, mature bone-seed plants at each of the four bone-seed-invaded study sites, giving a total of 40 plants. Selected plants were a minimum of 5 m apart. To prepare the sites, we cut these bone-seed plants off at ground level and marked out a 1-m^2 plot centred on the bone-seed stump. We also removed all gorse plants from the plots by cutting them off at ground level. To examine the effect of bone-seed control on bone-seed and native regeneration, we counted all native and exotic seedlings in these 40 plots at the time of canopy removal in October 2001, then again in February 2002. Part-way through the experiment (December 2001) plots were divided in half in order to add another treatment: weeding. One half was randomly allocated the weeding treatment, and was hand-cleared of exotic grasses, bracken fern (*Pteridium esculentum*), and resprouting gorse. The other half was left uncleared.

To further assess the potential for native seedling recruitment under bone-seed, in February 2002 we noted whether native seedlings (up to 100 cm tall) were present beneath 25 mature bone-seed plants scattered throughout study sites 2, 3, and 4, and beneath an additional 10 mature bone-seed plants at Raumati Beach, on the west coast 50 km north of Wellington (40°56′ S 174°58′ E). The vegetation at Raumati Beach was similar to that of our other four study sites: mature bone-seed abundant within a mixed community of native and exotic shrub, tree, grass, and herb species.

Germination from the seed bank

To examine seed bank composition at bone-seed sites and nearby native forest patches, we extracted 320 soil cores (each 51 mm in diameter and 51 mm deep) in November 2001. Half of the soil cores were taken from the four bone-seed-invaded study sites, and half were taken from the nearby native forest patches. At the bone-seed-invaded sites, one core was taken from each corner of each 1-m^2 plot where a mature bone-seed plant had been removed (see regeneration experiment above) (40 plots × 4 cores = 160 cores). In each of the four nearby native forest patches, one core was taken from each corner of 10 1-m^2 plots randomly located within each patch (4 native patches × 10 plots × 4 cores = 160 cores). Site 4 was different to the other sites, because it was dominated by low-growing native vegetation, with mature bone-seed plants scattered throughout. Accordingly, the 'native' cores were taken from 10 subjectively selected 1-m^2 plots located directly beneath native vegetation, a minimum of 20 m from any bone-seed plant.

The four cores from each plot were mixed, sieved through 10-mm^2 mesh to remove large stones and roots, and spread out to a depth of 1–5 mm on a 20-mm layer of peat moss in a perforated plastic tray (320 mm × 265 mm × 60 mm). In order to detect any seed contamination from either the surrounding area or the peat moss, five control trays containing sterilised soil and five containing peat moss were included in this study. No bone-seed, gorse, or native seedlings germinated from these trays. Trays were randomly distributed in the outdoor area of the Wellington City Council plant nursery where they were exposed to natural conditions and kept moist with frequent watering.

Bone-seed, gorse, and native seedlings were counted and removed monthly from December 2001 to May 2002, by which time germination had ceased.

Germination following exposure to heat

To examine the germination response of bone-seed and gorse to the heat of fire, we exposed seeds to a range of treatments in a domestic oven, comprising various combinations of temperatures (°C) and duration of exposure: 60°, 80°, 100°, and 120° for 0.5, 1, 5, and 10 min, 140° and 160° for 0.5, 1, and 5 min, and 180° for 0.5 and 1 min. At the higher temperatures, we exposed seeds to only the shorter durations because we assumed that seeds would not survive the highest temperatures for long durations. Fruits were collected in June 2002, after which the bone-seed putaminas (seeds contained within the hard, shell-like seed covering, or 'bones') were cleaned of fruit flesh, and the gorse seeds were extracted from pods. Bone-seed putaminas and gorse seeds were then stored dry until July 2002 when we conducted the heating experiment. Three replicates per species were heated separately for each treatment: 3×40 seeds for bone-seed and 3×30 seeds for gorse. Fewer gorse seeds were available for collection because it was early in the season for gorse seed development (Moss 1959), but also because a large proportion of seeds on each plant had been damaged by seed-feeding invertebrates. Bone-seed putaminas are c. 6–7 mm in diameter (Parsons & Cuthbertson 2001), whereas gorse seeds are c. 3 mm long (Weiss 1986). Before each replicate was heated, we checked the oven temperature using a CHY k-type thermometer (CHY Firemate Co., Taiwan) with a 500-mm stainless-steel-encased temperature probe attached (PCWI Precision Instrumentation, Australia). Following heating, each replicate of seeds was spread out on sterile soil in a perforated aluminium tray (90 mm in diameter and 25 mm high). Trays were randomly distributed within a shaded glasshouse, and kept moist with frequent watering. Germinated seeds were counted and removed weekly for 14 weeks, at which point germination appeared to have ceased. During the course of the experiment, the average weekly maximum temperature in the glasshouse was 32.9°C and average weekly minimum temperature was 11.7°C.

Analysis

To examine the effect of weeding on bone-seed and native seedling regeneration after bone-seed clearance, we used a Poisson generalised linear model with final number of seedlings as response variable, and site and weeding treatment as predictors. Bone-seed and native data were analysed separately. There were no significant interactions, so all were removed from the model, using a stepwise process.

To test whether germination from the seed bank differed between native and bone-seed-invaded sites, we applied a permutation test of bone-seed invasion status

for the eight averages of site × bone-seed invasion. The data exhibited strong non-normality with big differences between sites, and this made it difficult to find valid models using seedling count data at within-site level. Results for the permutation tests are presented on a two-sided basis, without any assumption that seeds of bone-seed and gorse would be more numerous in soil cores taken from bone-seed-invaded sites, or that seeds of native species would be more numerous in soil cores taken from native sites.

To examine the effect of heat on seed germination of bone-seed and gorse, we used three-way ANOVA with arcsin-transformed percent germination as response variable, and species, temperature, and duration as predictors. Interactions between all three variables were examined, and the model was simplified using an F-test to successively remove non-significant factors in higher order interactions. Species, temperature and duration were all treated as categories. A loess local smoother (Cleveland & Devlin 1988) was added to scatter plots to highlight the trends shown by the data.

Statistical analyses were performed using R statistical software (R Development Core Team 2007).

Results

## Regeneration following bone-seed control

In general, removing mature bone-seed plants had a positive effect on bone-seed regeneration, and a negative effect on native regeneration (Fig. 1). There were no bone-seed seedlings present in any of the 40 plots at time of initial canopy clearance in October 2001, but by February 2002 there were 64 bone-seed seedlings present (1.6 ± 0.4 per plot; mean ± SE; data summed across weeding treatments). Conversely, the total number of native seedlings declined from 83 (2.1 ± 0.5 per plot) in October 2001 to 10 (0.3 ± 0.1 per plot) in February 2002. Gorse seedlings were not counted in this experiment because seedlings were mostly indistinguishable from resprouts at two of the sites where gorse was most abundant. Such gorse seedlings or resprouts were numerous by February 2002 in these sites, and likely outnumbered seedlings of all other species combined.

Weeding had no significant effect on the final number of seedlings recorded for either bone-seed ($P = 0.53$) or native species ($P = 0.52$). There was no difference among sites for the number of native seedlings ($P = 0.62$), but there was for bone-seed seedlings ($P < 0.001$), probably due to the comparatively high number of bone-seed seedlings present at Site 4 by February 2002 (Fig. 1).

Seventy percent of the 35 additional mature bone-seed plants we surveyed had native seedlings present beneath the canopy.

Germination from the seed bank

Very few bone-seed seedlings emerged from soil cores
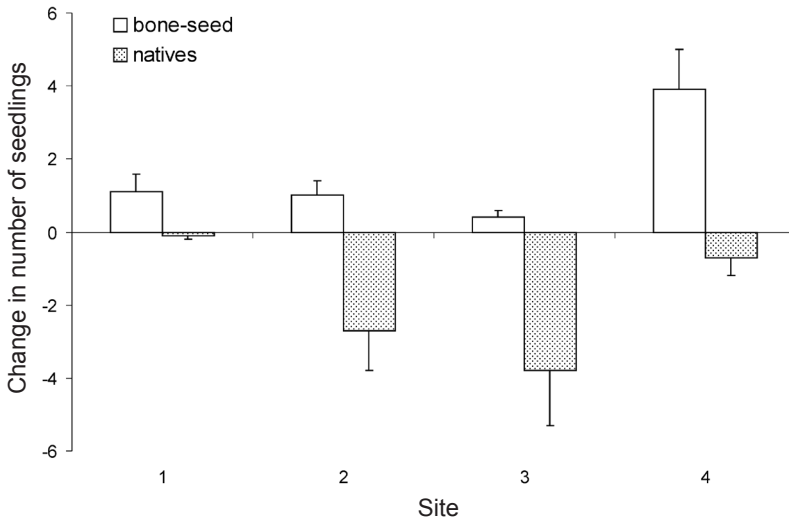
Figure 1. Change in number of bone-seed and native seedlings following control of mature bone-seed plants. Each bar represents the average (± SE) change in the number of seedlings in the 10 plots at each site.

taken from bone-seed-invaded sites (0.15 ± 0.07 per plot; mean ± SE), and none emerged from soil cores taken from native sites (Fig. 2). There was no significant difference between native and bone-seed-invaded sites for bone-seed seedlings ($P = 0.43$). Many more gorse seedlings emerged from soil cores taken from bone-seed-invaded sites (9.9 ± 1.72 per plot) than from native sites (0.03 ± 0.03 per plot) (Fig. 2) but this difference was not significant ($P = 0.14$). Many more native seedlings emerged from soil cores taken from native sites (3.33 ± 1.40 per plot) than from bone-seed-invaded sites (0.13 ± 0.06 per plot) (Fig. 2) but this difference was also not significant ($P = 0.09$). The lack of statistical significance is likely due to the large variation in the number of seedlings among the four sites.

**Germination following exposure to heat**

Germination of gorse increased dramatically as both temperature and duration increased, but may have been starting to decline at the maximum duration of exposure (10 min) (Fig. 3). Germination of bone-seed was much less variable across the range of temperatures and durations of exposure (Fig. 3). Gorse germination reached an observed maximum of 60% after exposure to 140°C for 5 min, whereas bone-seed germination reached an observed maximum of 22.5% after exposure to 100°C for 0.5 min.

The ANOVA confirmed that percent germination differed significantly between species, with different effects of temperature and duration between species (Table 1). However, there was no evidence of interaction between temperature and duration.

Discussion

Disturbance can promote weed invasion, largely because it can increase the amount of bare ground available for seedling recruitment (Grime 1979; Crawley 1987), reduce competition from native plants (Noble 1989; Jesson et al. 2000), alter resource availability (Wilson & Tilman 1993; Burke & Grime 1996), and/or facilitate weed seed dispersal or germination (Hobbs 1991; Parendes & Jones 2000). In our study, the disturbance created by removing mature bone-seed plants resulted in a dramatic increase in seedling numbers of both bone-seed and gorse, and a dramatic decrease in seedling numbers of native species (Fig. 1). Similarly, Thomas et al. (2000) demonstrated that increasing soil disturbance during removal of bone-seed in Australia was detrimental to the establishment of many native species. These results suggest that minimising both canopy and soil disturbance when controlling bone-seed and gorse in New Zealand, e.g. by leaving dead plants standing, may improve subsequent rates of native species regeneration. On the other hand, in the absence of disturbance (including bone-seed control), there does appear to be good potential for native regeneration beneath mature bone-seed. However, whether this means that bone-seed will eventually be replaced by native succession remains to be seen.

Fire is another type of disturbance that has been demonstrated to promote germination of both bone-seed (Weiss 1984) and gorse (Zabkiewicz & Gaskin 1978). In Australia, bone-seed seedling emergence has been shown to be up to 150 times higher in burnt compared with unburnt areas (Lane & Shaw 1978). In our study,
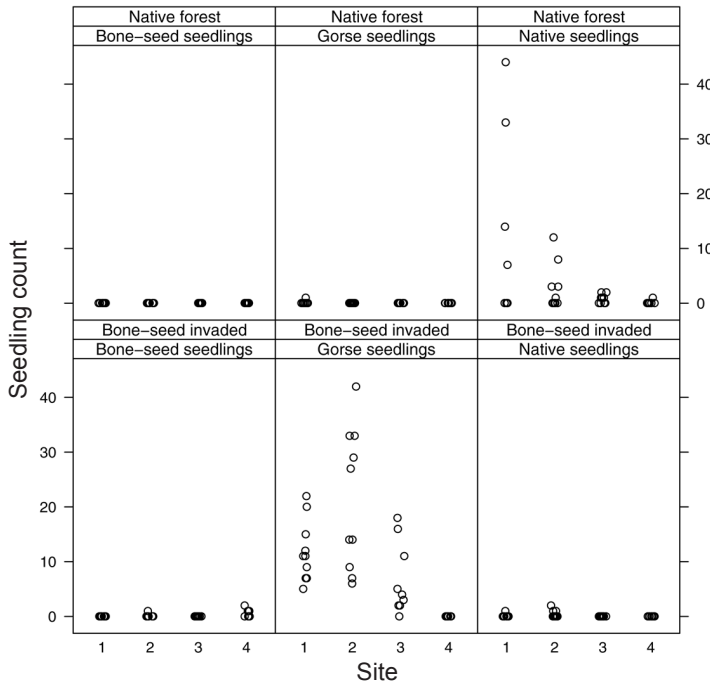
Figure 2. Germination of bone-seed, gorse, and native seeds from seed bank samples taken from native forest (top panels) and bone-seed-invaded sites (bottom panels). Each data point represents the number of seeds that germinated from four combined soil cores, taken from each corner of one plot. Data points are jittered to allow overlaid points to be seen.

Figure 3. Germination of gorse (top panels) and bone-seed (bottom panels) seeds following exposure to heat. Each data point represents the percentage germination of 30 (gorse) or 40 (bone-seed) seeds. Seeds were exposed to various combinations of temperature (60°, 80°, 100°, 120°, 140°, 160°, 180°C) and duration (0.5, 1, 5, 10 min). Note: 160°C was the maximum temperature used for the 5-min-duration trial, and 120°C the maximum temperature for the 10-min trial. Data points are jittered to allow overlaid points to be seen, and a loess local smoother line added to highlight the trends in the data.
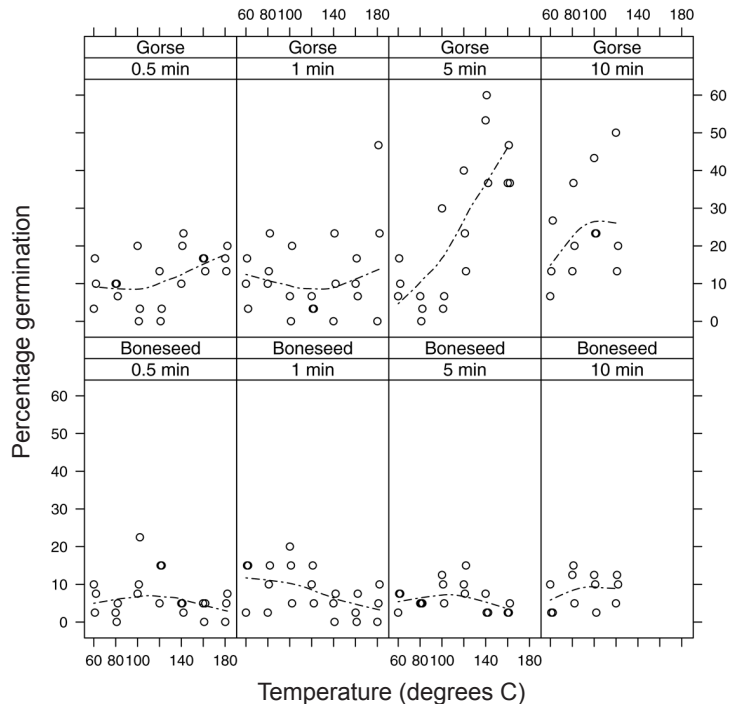
Table 1. ANOVA summary table of the effect of species, temperature, and duration (predictors) on percent germination (response variables, arcsin-transformed), showing degrees of freedom (d.f.), sum of squares (SS), variance ratios (F), and P values. Species, temperature and duration were all treated as categorical variables.

Predictors	d.f.	SS	F	P
Species	1	0.67205	32.5854	<0.001
Temperature	6	0.07010	0.5665	0.756
Duration	3	0.33648	5.4383	0.002
Species × temperature	6	0.48202	3.8952	0.001
Species × duration	3	0.40123	6.4847	<0.001
Residuals	124	2.55741		

however, germination of bone-seed was largely unaffected by exposure to heat, showing similar rates of germination across the range of temperatures we tested from 60°C to 180°C. It may be that heat alone is insufficient to promote a strong increase in germination, and that smoke is a key fire effect stimulating bone-seed germination, as has been found for other hard-seeded plant species (Morris 2000; Enright & Kintrup 2001). The chemical in smoke responsible for stimulating germination has been isolated (Flematti et al. 2004), and 'smoke-water', rather than heat, is often used to stimulate the germination of desired fire-responsive species for restoration (e.g. Tieu et al. 1999; Coates 2003).

By contrast, gorse germination was strongly promoted by heat; the highest rates of germination were from seeds exposed to 140°C for 5 min. Gorse germination appeared to decline only after exposure to 120°C for 10 min. Our results are similar to another study in which 84% of gorse seeds germinated after exposure to 100°C for 10 min, but only 4% germinated after exposure to 150°C for 10 min (Zabkiewicz & Gaskin 1978). Temperatures at the soil surface vary greatly during a wildfire, depending on meteorological conditions, fuel characteristics and local topography (Cheney 1981). In a study of three New Zealand fires, temperatures at the soil surface ranged from 100°C to 1000°C (Payton & Pearce 2001). Temperatures below the soil surface are likely to be significantly lower because of the insulating properties of soil (Bradstock & Auld 1995; Ferrandis et al. 1999). In the study of New Zealand fires (Payton & Pearce 2001), temperatures 2.5 cm below the soil surface never exceeded 69°C. Thus, seeds on the soil surface are more likely to be destroyed by fire than are buried seeds. Since small, persistent seeds are more likely to be deeply buried than large, less persistent seeds (Thompson et al. 1993; Bekker et al. 1998), it is likely that a lesser proportion of the gorse seed bank will be destroyed by fire compared with the seed bank of bone-seed. Where there are high numbers of gorse seeds present in the soil, any disturbance – and fire, in particular – is likely to result in a gorse-dominated site for several decades to come (Lee et al. 1986).

Soil seed banks can play a crucial role in determining

the composition of plant communities following disturbance (Skoglund 1992; Ferrandis et al. 1996; Pakeman & Small 2005). Prior knowledge of the species present in the seed bank can help managers predict the risk of post-disturbance weed invasion, and thus identify sites that may require management following such an event. We did not detect any bone-seed seedlings, and only very few gorse seedlings, in the seed bank samples taken from native forest patches. However, these results do not necessarily indicate that bone-seed is absent, and gorse uncommon, in the seed bank at these sites; they may just as well be attributed to a lack of power in our sampling design. This is a fundamental problem with measuring dispersal at a distance from the source, particularly when the events are relatively rare (Cain et al. 2000). Such seeds, at the 'tail-end' of the dispersal curve, occur at low densities, and so are extremely difficult to detect and require huge sampling effort (Dessaint et al. 1996; Nathan & Muller-Landau 2000). We also detected very few bone-seed seedlings in the seed bank at bone-seed-invaded sites, even though we sampled directly below the canopy of mature bone-seed plants where numerous bone-seed seeds were present; this also suggests that our sampling power was too low. Nevertheless, even if seed dispersal events occur only rarely, they can still play a major role in the invasion process by initiating new 'satellite' populations (Moody & Mack 1988; Kot et al. 1996; Clark et al. 1998).

In summary, while all forms of disturbance are likely to favour bone-seed and gorse recruitment over native species, it appears that there is good potential for native species to establish beneath the canopy of mature bone-seed. If bone-seed plants are removed in order to restore native vegetation, control methods that minimise disturbance are likely to be more favourable for native seedling recruitment. Follow-up control of bone-seed (and gorse, if present) seedlings is also likely to assist native seedling recruitment, and the addition of native seed may also be necessary if natural seed sources are absent. It is not yet known whether native regeneration (in the absence of disturbance) can eventually replace bone-seed in the same way that it can replace gorse.

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