MANAGEMENT OF BONESEED (*CHRYSANTHEMOIDES MONILIFERA* SSP. *MONILIFERA*) (L.) T. NORL. USING FIRE, HERBICIDES AND OTHER TECHNIQUES IN AUSTRALIAN WOODLANDS

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Abstract

Invasive plants cause ecosystem degradation throughout the world, including the reduction of native plant density and diversity, and changes in ecosystem structure and function. Woody weeds often grow faster than native species and in invaded habitats produce larger and/or more seed and outshade other mid- and under-storey species. Boneseed *Chrysanthemoides monilifera* ssp. *monilifera* (L.) T. Norl. has caused the degradation of many temperate woodlands in Australia and has not yet reached its full potential distribution in this country. The control of this weed is therefore a high priority in Australia. Biological control agents have not controlled boneseed populations to date and no detailed integrated control strategies exist for different densities of mature boneseed plants and soil seed banks in native vegetation of varying levels of degradation. Fire, herbicides and manual plant removal have previously been used to control boneseed; however, substantial landscape scale control has not yet been achieved.

Boneseed population control experiments were undertaken in two temperate woodlands in Victoria, Australia. In highly degraded temperate grassy woodlands at the You Yangs Regional Park west of Melbourne in Victoria and in a highly diverse native closed woodland at Arthurs Seat State Park in south-eastern Victoria. Several combinations of the weed control techniques of fire, herbicide application, hand-pulling of seedlings and distribution of competitive native grasses were found to control both mature boneseed populations and the large reserves of viable boneseed seeds in the soil. The efficacy of controlled burning, and the combination and timing of control techniques were found to vary according to differing densities of boneseed plants, viable soil seed banks and post-fire emergent seedlings.

Where sufficient fine fuel existed, a warm, even, autumn burn consumed above ground biomass, killed the majority of viable boneseed seed in the soil, and caused the remaining boneseed seed to germinate. Spraying with glyphosate herbicide was as effective as metsulfuron-methyl herbicide for killing boneseed seedlings along with the secondary climbing weed *Billardiera heterophylla* (Lindl.) L.W.Cayzer & Crisp after fire. However, the use of glyphosate also killed all native species, resulting in bare ground. After fire in species rich vegetation, boneseed was eliminated where seed of the native C3 grass *Poa sieberiana* Spreng. had been broadcast onto the post fire ash-bed, and seedlings had been sprayed five months after the burn or where seedlings had been sprayed 12 months after burning. Boneseed control occurred when seedlings were sprayed five months after the burn. In degraded vegetation few boneseed seedlings remained where seedlings were sprayed 17 months after fire. Where insufficient rainfall occurred, hand-pulling flowering boneseed seedlings prevented new seed fall for 6 to 12 months.

Suggestions are made for the integration of these methods with the establishment and proliferation of biological control agents. A new protocol for utilising several integrated control strategies for boneseed and other woody weeds in a mosaic at both the site and landscape scale is described. A mosaic would allow for a variety of native species responses to fire and other control methods and thus lead to heterogeneous ages and structures within the native vegetation following weed control.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being made available in all forms of media, now or hereafter known.

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Chapter 1: Introduction

Boneseed, *Chrysanthemoides monilifera* ssp. *monilifera,* (L.) T. Norl. (Asteraceae) is an aggressively invasive woody plant species originating from South Africa (Adair 1992) (Figure 1.1). The species was brought to Australia as a garden ornamental plant in the 1850"s and has since spread and created near monoculture conditions in many vegetation types in temperate Australia. Boneseed infestations create dense canopies with little light penetration and reduce the density and diversity of native species in invaded areas (Adair 1995; Adair and Groves 1996; Thomas et al. 2005). Boneseed has not reached its full potential distribution in southern Australia and continues to encroach on new areas of temperate Australian vegetation (Scott 1993). The need to restore degraded natural ecosystems (Vitousek et al. 1997) makes the control of boneseed an important conservation goal in Australia. While many successful weed control techniques and ideas can be adapted from cropping and pasture systems, there are unique limitations in natural ecosystems. The control of one, or perhaps a few, serious weeds must be achieved while protecting, or even promoting, a much larger number of native species (Lane 1981). To date the control methods for boneseed have been used in isolation and have not resulted in landscape scale control of boneseed populations.

Management of boneseed is currently a high priority in Australia (Brougham et al. 2006) due to its current and potential distribution, and the devastating impact of the species on native vegetation. Biological, herbicidal and physical control methods have been employed individually to control boneseed; however, as has been found for other woody weeds, including *Mimosa pigra* L. in the Northern Territory of Australia, individual control methods have not resulted in large scale, long term weed population control (Paynter and Flanagan 2004). The primary hindrance to boneseed population control in Australia is the large accumulated soil seed bank under boneseed populations in this country. Therefore, boneseed control measures must target the elimination or reduction of the boneseed seed bank.

Wildfire completely removes boneseed plants and the extensive store of boneseed seeds in the soil (pers. obs.). However, wildfire has the devastating effect of causing the rapid expansion of boneseed populations in Australia (Bray 2006). Effective methods of boneseed population control using herbicides currently exist for small areas of boneseed; however, there are no effective or practical solutions to the control of these species in large areas of native vegetation (Scott and Adair 1992). Boneseed seedlings that emerged after a slow cool fire were killed using the herbicide bromoxynil at a rate of 1:1600 (Lane 1981). Bromoxynil applied at this rate was found to not harm post-fire emergent Acacia or grass species (Lane 1981); however, this herbicide is now rarely used owing to its toxicity. Current weed control practice in Victorian native vegetation favours the use of glyphosate (a broad-spectrum, phloem translocated herbicide) over the use of metsulfuron-methyl (a broadleaf plant selective herbicide with residual activity in the soil), as the latter can kill mature trees if accidentally sprayed in the same area twice.

Manual pulling of boneseed plants and seedlings, usually undertaken by volunteer groups, is a commonly used and extremely effective method of weed management in small areas of native vegetation. Manually removed boneseed does not re-establish when left to dry in contact with the ground, and can be pulled and left to decompose *in situ*. This has the added benefit of preventing access to the pulled area by herbivorous animals, giving native species a chance to re-establish where boneseed has been removed. The „Bush for Life‟ organisation in South Australia recommend cutting boneseed plants that have been cut off at the base into small pieces and spreading them evenly across the ground to prevent smothering of native plant species (Tucker 2006). Many volunteers will not pull larger weed seedlings or mature plants in order to prevent soil disturbance and the consequent emergence of further weeds, preferring instead to cut boneseed near the base of the trunk and immediately swab with glyphosate. Weed emergence after soil or other disturbance could be a valid strategy where the disturbance is implemented prior to a planned application of herbicide to kill the seedlings that emerged after disturbance.

There is potential for the distribution of native grass seed onto the post-fire ash-bed to increase the density of native grasses and thereby outcompete emerging boneseed seedlings. However, it is unknown whether seed of native grasses would establish successfully when manually broadcast after fire. Moreover, after fire, seedlings of native plant and weed species begin germination, emergence and aboveground growth from the same point in time. Large tussocks of the dominant *Themeda triandra* Forsk. are highly competitive and established populations are resistant to weed invasion (Cole 2005). Populations of other perennial native grasses of southern Australia, such as *Poa sieberiana* Spreng., *Microlaena* spp., *Danthonia* spp., or *Stipa* spp., could be similarly competitive.

Many global temperate ecosystems are under threat from degradation by invasive plant species, often in combination with other degrading processes. There is therefore a need to bring all weed infestations under control in those ecosystems. To achieve effective landscape scale weed control it is necessary to undertake research into the most effective ways of combining known control methods for each weed and for groups of weeds that may occur together. It is also important to conserve and restore ecosystem integrity in areas that have been highly degraded by weed infestation. Therefore, „integrated" weed management should not only involve effective integration of weed control techniques, but also the integration of spatially appropriate restoration techniques. In this way, the restoration of natural ecosystem diversity, structure and function becomes the goal to be achieved by undertaking „integrated" weed management.

1.1 Aims of this thesis

This thesis aimed to assess whether boneseed could be eliminated by fire along with subsequent treatment of infested areas with a combination of herbicide application (glyphosate or metsulfuron-methyl), manual removal of emergent seedlings and broadcasting of grass native seed (*P. sieberiana* and/or *T. triandra*). The experiments sought to determine an integrated boneseed control strategy for two contrasting Australian temperate woodlands: one that had been highly degraded by long-term boneseed invasion; the other that contained high species diversity amongst the boneseed invasion.

The varying boneseed vegetation structures and sizes of the boneseed soil seed bank in degraded and species rich native vegetation were categorised and correlated to implications for boneseed population management (Chapters 3, 4 and 5). Measurements of fuel loads were taken in various densities and structures of each boneseed infestation (Chapter 3) in order to observe the fuel load characteristics of the boneseed infestation types that were most able to sustain a controlled burn (Chapter 4). This study also investigated, for differing plant structures and densities within each boneseed infestation (Chapter 3), whether a fire of a given temperature would effectively kill and/or stimulate the germination of boneseed seeds and from what portion of the soil seed bank (Chapter 4). The impact of metsulfuron-methyl and glyphosate herbicides, when applied in different growth seasons after fire, at different rates, and by different application methods, on boneseed seedlings (Chapter 5) secondary weeds and native species (Chapter 6) was investigated. The impact of hand pulling flowering boneseed seedlings, after fire, on the control of boneseed seedlings (Chapter 5), and secondary weeds

(Chapter 6), and on the establishment of native species (Chapter 6) was measured. At the species rich site, the ability of dense swards of *P. sieberiana* or *T. triandra* to outcompete emerging boneseed seedlings (Chapter 5) or seedlings of the secondary weed *Billardiera heterophylla* (Lindl.) L.W.Cayzer & Crisp (a climbing vine originating from Western Australia, Chapter 6) was investigated. The impact of the distribution of native grass seed on the diversity and abundance of native species that emerge naturally after fire was assessed for the species rich site (Chapter 6).

Chapter 2: Literature Review

2.1 Processes of native ecosystem degradation

There are few ecosystems in the world that have not been directly degraded in some way by human activity, and human activity is also responsible for changing the world"s climatic systems, which will directly or indirectly cause changes to every ecosystem on earth (Hobbs and Harris 2001; Hobbs and Yates 2003; Alley et al. 2007). Although global land masses, climate and species composition and distribution have changed continually over geological time, the current rate of human induced change is too fast for impacted species and native communities to evolve adaptations for survival (D'Antonio and Vitousek 1992; Mack et al. 2000; Lovei 2001; Flannery 2005; Hansen et al. 2005; Hansen et al. 2007). Based on natural background rates of species extinctions over geological time, only one species in the world should have become extinct in the last four hundred years. Instead, the rate of global extinctions since the 1600s is equivalent to being one of the six global mass extinction events that have occurred over geological time (Lovei 2001). Agriculture, mining and urbanisation often deplete, fragment, contaminate or devalue soil, water, atmospheric and plant resources in native ecosystems (Alston and Richardson 2006; Bennett et al. 2006). Forest ecosystems in particular have suffered from overuse by humans, with 90 percent of the 1.2 billion poorest people in the world depending directly on forests in some way (Hobley 2005). Human induced global climatic changes are also a cause of ecosystem degradation, for example in terrestrial ecosystems, where species cannot survive increasing water scarcity, or in the ocean, where rising temperature kills coral (Flannery 2005). The world"s changing climate also alters the potential distribution of current and future invasive species, once again impacting upon ecosystems that will already be undergoing changes in composition due to climate change (Kriticos et al. 2003; Flannery 2005; Kriticos et al. 2006; Buckley 2008). The study of invasive ecology (Catford et al. 2009), of which this thesis forms a contribution, can be defined as, „the study of human-mediated introduction of organisms, especially introductions to areas aoutside the potential range of given organisms as defined by their natural dispersal mechanisms and biogeographical barriers (Richardson 2008).

The transfer of invasive species from one locality to another around the world has been one of the most significant negative impacts that humans have had on the earth (Rejmanek 1996;

Vitousek et al. 1997; Mack et al. 2000; Mack and Lonsdale 2003). The global transportation and use of agricultural plants has been, and is, vital for sustaining human food resources (Pimental and Pimental 2000; Stephenson 2000). However, plants transported for agricultural, horticultural, aquacultural, ornamental, medicinal, recreational and amenities uses, amongst other reasons, have often become invasive and caused the degradation of natural ecosystems (McNeely 2005; Richardson 2008). Invasion of native ecosystems by animal, insect, fungal, algal, bacterial, viral or plant organisms can threaten biodiversity and therefore alter the structure and functioning of the whole ecosystem (Drake et al. 1989; Naeem et al. 1994; Luken 1997; Lonsdale 1999; Primack 2001). Due to the multiscalar ecological effects of weed invasion (Brown et al. 2008) weed management solutions need to be constructed at both a broad landscape scale and be adaptive over time (Buckley 2008). For example, landscapes of once scattered trees with a grassy understorey have become continuous shrub layers with bare soil underneath where *Cytisus scoparius* (L.) Link is invasive in southern Australia or where *Acacia nilotica* (L.) Willd. ex Del. and *M. pigra* are invasive in northern Australia (Downey and Smith 2000; Tiver et al. 2001; Paynter 2003; Paynter and Flanagan 2004). There is a plethora of examples of invasive species changing ecosystem functioning; in the Northern Territory of Australia invading *Andropogon gayanus* Kunth changes fire regimes into a self-perpetuating cycle of spreading grass and increasing fire intensity, and in South Africa water tables are lowered by invasive tree species (D'Antonio and Vitousek 1992; Mack et al. 2000; Rossiter et al. 2003; Holmes et al. 2005; Ferdinands et al. 2006).

2.2 Global plant invasions – ecosystem degrading processes

Invasion can be the direct human-mediated consequence of naturalisation of plants or other organisms purposefully introduced to an area, or the indirect product of organisms establishing in native vegetation from their intended location (Richardson 2008). Globally, higher numbers of weedy species are found amongst species rich plant communities, outside nature reserves and on islands (Lonsdale 1999). In Australia, weed invasion in National Parks and reserves increases with increasing visitor numbers (Lonsdale 1999). Anthropogenic disturbances can increase or allow introduction of invasive species. For example, wildfire or poorly designed restoration practices can increase weed population density or spatial presence (Melland 2002; Mansourian et al. 2005; Bray 2006; Cummings et al. 2007). In Montana, USA, more weeds were found where wildfires were hottest, while in Australia, roads provide a path for weed spread and feral animals can disperse viable weed seeds (Wace 1977; Lynes and Campbell 2000; Hunter et al. 2003).

Woody plant species have invaded and caused negative impacts on ecosystems in many parts of the world (Richardson and Rouget 2002). Woody weed species degrade the ecosystems that they invade by altering the dominant life-form, reducing structural diversity, changing hydrologic cycling, increasing vegetation biomass, disrupting the prevailing vegetation dynamics, changing existing nutrient cycling patterns and changing disturbance regimes (Adair 1995; Luken 1997; Richardson 1998; Prieur-Richard and Lavorel 2000; Darrouzet-Nardi et al. 2008). Typically, woody weeds reduce floristic diversity, with a consequential reduction in dependent fauna. For example, Australian Acacia species and other woody invasive species have established along South African waterways and are the greatest threat to the persistence of endemic dragonflies and damselflies (Odonata) in that country (Samways and Taylor 2004). However, some woody weed species, especially thorny species and species with growth habits close to the ground, can provide protection from predation for birds and other small fauna (Lawrie 2000; Lawrie 2002; Garden et al. 2007). As well in subtropical Australia, invasion of disused pastures by the *Cinnamomum camphora*, a tree with fleshy fruit, has been shown to provide habitat for rainforest birds, thereby facilitating the establishment of native rainforest plants that depend on those birds for seed dispersal (Neilan et al. 2006).

In South Africa, invasion by woody species threatens biodiversity and ecosystem structures of „fynbos" (native low shrubland) including riparian (stream bank) ecosystems (Holmes 2002; Holmes et al. 2005). In that country many of the most invasive woody weeds are of Australian origin and belong to the Eucalypt and Acacia families. Beneath dense infestations of Australian *A. saligna* (Labill.) Wendl. on sand plains, the seed bank density and richness of fynbos species were significantly reduced (Holmes 2002). After weed clearance, the area was expected to regenerate into a herbland, that is, into a different ecosystem from the pre-invasion shrubland (Holmes 2002). Similarly, *A. mearnsii* De Wild. and *A. longifolia* (Andrews) Willd. have a detrimental effect upon stream flow in riparian areas of mountain fynbos catchments in the Western Cape Province (Prinsloo and Scott 1999). Two Australian eucalypt species, *Eucalyptus camaldulensis* Dehnh. and flooded gum *E. grandis* W.Hill ex Maiden have recently been added to *E. lehmannii* (Schauer) Benth. already known to be invasive in South Africa. These eucalypts have invaded natural vegetation in South Africa, especially riparian areas, and have the ability to cause structural and functional changes to the ecosystems of invaded areas (Forsyth et al. 2004).

Ecosystem level changes have also occurred in Australia due to the presence of woody weeds. Species such as *M. pigra* (in the wetlands of the Northern Territory), *C. scoparius* (in the NSW highlands), *Tamarisk aphylla* (L.) H. Karst. (in riparian vegetation), *Pittosporum undulatum* Vent. and *Genista monspessulana* (L.) L.A.S. Johnson (in temperate woodlands), *Chrysanthemoides monilifera* ssp. *rotundata* (DC.) T. Norl. (bitou bush, hereafter referred to as bitou bush) (in coastal NSW), and boneseed (in southern states), are creating monoculture stands in place of native vegetation of various vegetation strata (Lonsdale and Miller 1993; Adair 1995; Lloyd 2000; Paynter et al. 2003). On the fore-dunes of the subtropical Queensland coast, 59% of the flora is weedy, predominantly from the Poaceae, Asteraceae and Fabaceae, and dominated by *Asparagus aethiopicus* L., *Bryophyllum* sp., bitou bush, *Gloriosa superba* L., *Lantana camara* L., *Panicum maximum* Jacq., *Schefflera actinophylla* Endl.) Harms, *Schinus terebinthifolius* Raddi*, Senna pendula* var. *glabrata* Vogel) H.S.Irwin & Barneby and *Wedelia trilobata* (L.) A.S. Hitchc. (Batianoff and Franks 1998). In Western Australia, *Lycium ferocissimum* Miers creates deciduous habitat in locations where populations of seals require the evergreen habitat provided by shrublands dominated by native *Nitraria billardieri* DC. (Keighery 1991). In Vietnam, Cambodia, Thailand and other parts of Asia, as well as in the Northern Territory of Australia, *M. pigra* creates a difficult to control monoculture that threatens subsistence farming and conservation values respectively (Shibayama et al. 1983; Julien et al. 2002; Nguyen Thi Lan Thi et al. 2002).

The most destructive environmental weeds in Europe include many examples of woody species. For example, in France there are 221 species of alien flora, with the most threatening to natural ecosystems being woody species, hydrophytes and polyploid taxa of varying lifeforms, and the ecosystems most under threat being the Mediterranean region, zones at low altitudes, wetlands and coastal habitats (Verlaque et al. 2002). On the British Isles, there are 2834 non-native plant species including 715 hybrid species. Seventy of those hybrids have formed on the British Isles between native and introduced species (Abbott 1992). Currently in the British Isles, garden ornamentals of the 19th century such as *Buddleja davidii* Franch., *Heracleum mantegazzianum* Sommier & Levier, *Impatiens glandulifera* Royle, *Fallopia japonica* (Houtt.) Ronse Decr. Syn: *Reynoutria japonica* Houtt. and *Rhododendron ponticum* L., invade both urban areas and natural ecosystems (Evans 2003). In areas of the Pyrenees, Spain, populated by *Pinus nigra* Arnold s.l. ssp. *nigra*, a recent reduction of the human population and their associated domestic grazing stock, has allowed populations of the woody *Genista scorpius* (L.) DC. to increase (Valderrabano and Torrano 2000). *G. scorpius* has a high ignition capacity and behaves invasively even though it is native to the region, consequently increasing fuel loads and fire risk in these areas (Valderrabano and Torrano 2000). Woody weeds therefore substantially degrade European ecosystems.

Weeds, including many woody species, impact negatively upon the diverse ecosystems of Asia, and North and South America. In Asia, the Americas and Oceania, vast areas of forest are destroyed by the invasion of exotic C4 grasses and the consequential build up of fine fuels, which lead to increases in fire frequency and temperature. The grasses also cause soil nutrient losses, inhibit the re-establishment of native woody species and „thus arrest ecological succession" (Sage and Kubien 2003). In the Americas, invasive plants cause a loss of approximately $27 billion/yr to the United States economy (Pimental and Greiner 1997; Pimentel et al. 2002). Over 50% of all plant introductions and 85% of woody plant introductions occurred for use as ornamental and landscape species (Li et al. 2004). Weeds are a problem in habitats ranging from the northern Rocky Mountains in Canada (Sutherland 2003), to New Mexico, in the south of the USA (Hunter et al. 2003). In riparian ecosystems of western North America, the displacement of native plant communities, degradation of wildlife habitat including that of many endangered species, increase in soil salinity and wildfire occurrence, and the lowering of water tables are ecosystem level changes caused by four saltcedar species: *Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. parviflora* DC., and *T. canariensis* Willd. and their hybrids (DeLoach et al. 2003). Forty species (mostly trees) have invaded the natural vegetation along roadsides in the rolling pampa grasslands of Argentina. In these grasslands, as well as in riparian corridors, the most common invasive species were *Gleditsia triacanthos* L., *Morus alba* L., and *Melia azedarach* L (Ghersa et al. 2002).

Therefore, negative environmental, economic and social impacts of woody weed invasions occur throughout a broad range of the world"s native ecosystems. The amelioration of those impacts requires continued improvement of biological and ecological knowledge of woody weed population dynamics, as well as woody weed management techniques.

2.3 The environmental weed problem in Australia

The many current threats to conservation due to the continuing spread of invasive plants in Australian native vegetation have been extensively reviewed in the last two decades (Fox and Fox 1986; Groves 1991; Humphries et al. 1991; Carr 1993; Adair 1995; Low 1999; Williams and West 2000; Australian Bureau of Statistics 2001; Lindenmayer and Burgman 2005). Of Australia"s approximately 25,000 species of flora, at least 10% are naturalised, with half of these being environmental weeds (Groves 1991; Williams and West 2000). Within Australia, humans have aided the dispersal of 90% of 233 noxious weed species (weeds that are detrimental in native and/or agricultural landscapes), and of these, humans were the sole dispersers of 21% (Panetta and Scanlan 1995). The extinction of four vascular plant species in Australia has been largely attributed to the presence of environmental weeds (Groves and Willis 1999); while an estimated 21 vascular plants are threatened with extinction within the next 20 years due to weed invasion (Burgman et al. unpublished data cited in (Lindenmayer and Burgman 2005)).

Australia"s temperate eucalypt woodlands are currently threatened by many disturbances, both natural and anthropogenic in nature (Yates and Hobbs 1997; Specht 2000; Yates et al. 2000b; Saunders et al. 2003), as are *T. triandra* dominated lowland temperate grasslands (Lunt 2003) and Poaceae dominated grassy woodlands of eastern and south-eastern Australia (Clarke and French 2005). Invasion by weeds is one of the threatening processes negatively impacting upon these systems. In the fragmented vegetation of temperate southeastern Australia, multi-species plant invasions are common (Humphries et al. 1991).

There are currently three important lists of damaging agricultural and environmental weeds in Australia: the „Weeds of National Significance" (WoNS) list, which includes boneseed (Department of Environment and Heritage Australian Government 1999); the „National Environmental Alert List" (Department of Environment and Heritage Australian Government); and the „Priority Sleeper Weeds" list (Department of Environment and Heritage Australian Government) (Appendix 1 a, b and c). Throughout southern Australia, in all types of conservation areas, the weeds with the highest priority for biological control in 1992 were deemed to be *Chrysanthemoides monilifera*, *Delairea odorata* Lem., *Ehrharta* sp., *Eragrostis curvula* (Schrad.) Nees, *L. ferocissimum*, *Melinis repens* (Willd.) Zizka, *Asparagus asparagoides* (L.) W.Wight, *Pennisetum macrourum* Trin., *Polygala* sp., *Asparagus africanus*

Lam., *Senecio pterophorus* DC., and *Watsonia* sp. (Scott and Delfosse 1992). In Victoria in 1909, 364 naturalised alien plants were recorded for environmental and agricultural areas (Ewart 1909), with fifty-three of these being members of the Asteraceae family. The list included useful agricultural species as well as „troublesome" species. Of these plants, 42 species had been proclaimed, „on account of their obnoxious or poisonous character", with 37 of these being introduced plants and the remaining five being native species (Ewart 1909). Of Australia"s native vegetation Ewart (1909) reported, „Our forests…are almost solely composed of native trees, although a few alien herbs and shrubs have crept into the undergrowth". In Victoria, natural grasslands are the most weed-invaded vegetation type, with 17% of plant species being introduced rather than indigenous. The second most invaded vegetation type in that state is coastal vegetation, which contains 11% introduced plant species (Gullan cited in (Groves 1991)). By 1992, in Victoria, there were 584 species of environmental weeds: 534 from other countries, 28 from other states of Australia, and 22 species that had expanded their pre-European distribution (Carr et al. 1992).

In the northern areas of Australia, the invasion of vast areas of land by a single weed species is common (Humphries et al. 1991). In the Northern Territory of Australia, the woody weeds *M. pigra*, *T. aphylla*, *Prosopis* sp. and *Annona glabra* L. are the most invasive woody plant species (Setter et al. 2002). Of south-eastern Queensland"s 200 invasive weed species, 75 species (37%) are woody weeds (Batianoff and Butler 2002). The ten most invasive weeds (most of which are woody) in south-east Queensland were *L. camara*, *Baccharis halimifolia L.*, *Bryophyllum delagoense* (Eckl. & Zeyh.) Schinz, *Macfadyena unguis-cati* (L.) A.H.Gentry, *Anredera cordifolia* (Ten.) Steenis, *A. africanus*, *Celtis sinensis* Pers., *Cinnamomum camphora* L.) T.Nees & C.H.Eberm., *S. terebinthifolius* and *Salvinia molesta* D.S.Mitch. (Batianoff and Butler 2002). In geographically isolated Western Australia, there are 800 significant weeds of agriculture, natural environments, gardens and horticulture (Hussey et al. 1997). Throughout all of Western Australia"s conservation areas there are 458 species of naturalised plants, 40 of which threaten the natural ecosystems in which they have naturalised (Keighery 1991). In Western Australia the woody weeds that pose the largest threat to conservation are native Australian species from the eastern side of the continent. Woody species that invade banksia woodlands include *Acacia dealbata* A.Cunn. [nom. illeg.], *A. decurrens* Willd., *A. longifolia* and *A. melanoxylon* R.Br. along with *Eucalyptus maculata* Hook. and *Brachychiton populneum* (Schott & Endl.) R.Br. (Keighery 1991).

Leptospermum laevigatum (Gaertn.) F.Muell. invades southern coastal areas and *L. ferocissimum* is common on offshore islands (Keighery 1991).

In Australia the conservation of many landscape types in a variety of climatic regions relies in part on the control of woody (and other) weeds. Economic and ecological analysis shows that environmental and social benefits can be gained by controlling weeds across the natural, agricultural and forestry landscapes of Australia (Sinden and Griffith 2007). The number and distribution of woody weeds in Australia has increased markedly over the last century. Therefore, in order to manage the conservation of Australian ecosystems an increased understanding of the population dynamics of woody weeds and the most effective control techniques, within the context of Australian native vegetation, are required.

2.4 Causes and processes of invasiveness

Prediction of weed species is not entirely possible, although plant species can be assessed for their weed potential (Scott and Panetta 1993; Rejmanek 1996; Rejmanek and Richardson 1996; Prieur-Richard and Lavorel 2000; Groves 2006; Grotkopp and Rejmanek 2007) and this can be combined with an assessment of the susceptibility of an ecological community to invasion (Richardson and Pysek 2006; Thomsen et al. 2006; Caley et al. 2008). Indeed weed risk assessment (WRA) is now a widely used tool for assessing the likely impact, potential distribution and invasibility of a plant is a given landuse system (Crossman and Bass 2008). Woody plants can become invasive in non-indigenous environments for a number of reasons (Callaway and Maron 2006); important plant attributes for invasiveness were outlined by Rejmanek (1996) for North American ecosystems:

> "At present, several limited generalizations are available for seed plants: (1) invasiveness of woody species in disturbed landscapes is significantly associated with small seed mass, short juvenile period, and short mean interval between large seed crops; (2) vertebrate dispersal is responsible for the success of many woody invaders in disturbed as well as 'undisturbed' habitats; (3) primary (native) latitudinal range of herbaceous Gramineae (Poaceae), Compositae (Asteraceae), and Fabaceae seems to be the best predictor of their invasiveness, at least for species introduced from Eurasia to North America; (4) low nuclear DNA content (genome size) seems to be a result of selection for short minimum generation time and, therefore, may be associated with plant invasiveness in disturbed landscapes; (5) analysis of exotic Gramineae and Compositae introduced from Europe to California supports Darwin's suggestion that alien species belonging to exotic genera are more likely to be invasive than alien species from genera represented in the native flora."

The control of invasive weeds requires the following three management objectives to be met: A: prevention/exclusion of the species; B: early detection/rapid assessment of the weed problem; and control/containment/eradication of the population, which Rejmanek (2000) describes can be achieved using the following research areas within the field of invasion ecology: "1. stochastic (roles of inoculum sizes and residence times), 2. empirical, taxon-specific (does a particular species invade elsewhere?) 3. evaluation of biological characters responsible for, or associated with, invasiveness, 4. evaluation of habitat compatibility, and 5. experiments."

Assessing the weed risk of a species often relies on prior experience of that species becoming weedy in other similar environments and where this is limited, investigation of the plasticity (the ability of a particular plant to vary an expressed trait/characteristic) of an invasive species is warranted (Hastwell and Panetta 2005; Hastwell 2008). The possession by a species of genetic plasticity and adaptive evolution (the changing of the genetic makeup of plants within a population over many generations) could contribute to the ability of invasive seedlings to establish in a wide range of climates (Sexton et al. 2002). When investigating the seedling growth morphology of *T. ramosissima,* a woody weed of North America, Sexton (2002) found genetic variation for growth traits, but not for gas exchange traits. Seedlings invested in root growth under cold growth conditions and shoot growth under warm growth conditions, possibly aiding their survival during the first season in a new environment (Sexton et al. 2002). In Australia, faster generation times and more rapid plant growth than native species are amongst the most common attributes of woody weeds. In sub-tropical Australia (south east Queensland) testing of aquatic plants against an increasing nutrient gradient showed a tendency towards an increase in photosynthetic surface area amongst weedy species but not amongst native species (Hastwell 2008).

Woody species can invade intact vegetation and vegetation that has been disturbed (Adair and Scott 1993; Lesica and Miles 1999; McAlpine and Drake 2003; Sanford et al. 2003). Disturbance can increase the incidence and extent of plant invasion (Hobbs and Huenneke 1992; Gleadow and Narayan 2007; Firn et al. 2008). The interactions between disturbance and fertility and extent of interactions between different trophic levels within a plant community are also thought to be important determinants of community susceptibility to invasion (Prieur-Richard and Lavorel 2000). Species richness can be a poor indicator of resistance to invasion; however, studies have also found that the presence of diverse functional groups, including those similar to the invading species, increases resistance to invasion (Higgins et al. 1999; Pokorny et al. 2005). The issue remains unresolved and is potentially scale dependent (Pokorny et al. 2005). In the Cape Peninsula region of South Africa, species richness, which is usually inversely related to degree of disturbance, was positively correlated with modelled invasibility by six woody weed species (*A. Cyclops* A.Cunn. ex G. Don*, A. longifolia*, *A. mearnsii*, *A. saligna*, *Pinus pinaster* Aiton and *P. radiata* D.Don)(Higgins et al. 1999). In a riparian ecosystem in north-central Montana, *Elaeagnus angustifolia* L. invades intact vegetation underneath mature *Populus fremontii* trees high on river bank terraces, as well as the more disturbed moist habitat on the lower river bank terraces (Lesica and Miles 1999).

2.4.1 Anthropogenic and natural disturbance events

Several types of disturbance can increase weed invasion (Buckley et al. 2007; Firn et al. 2008), for example, soil disturbance, wildfire or controlled burning, or natural climatic or disturbance events, such as violent storms, can increase weed distribution. In the El Palmar National Park in Argentina, an invasive tree species that normally reproduces by seed, *M. azedarach* L., has been found to reproduce clonally after disturbances such as fire and herbivory (Tourn et al. 1999). Human-induced climate and atmospheric change can also influence the spread of weeds. The distribution potential of *A. nilotica*, a woody weed in Australia, is likely to increase with the effects of global warming (Kriticos et al. 2003). An increase in atmospheric CO_2 will allow *A. nilotica* to increase its water-use efficiency and so colonise drier areas. Temperature increases are also predicted to enable *A. nilotica* to colonise areas south of its current distribution in Australia (Kriticos et al. 2003). In Californian shrublands (USA), increased atmospheric nitrogen deposition from vehicle emissions has favoured the growth of exotic grasses by up to 70% and, combined with increased fire frequency, contributed to a 76% reduction in native forb diversity (Allen 2005).

2.4.2 Climatic similarity

Weed species are often highly successful in regions of the world where the ecoclimatic conditions are similar to those in their country of origin. This is exacerbated where the weed species can also grow free from their natural predators, such as herbivorous and pathogenic species, that restrict population growth in their country of origin. For example, many plant species from the Mediterranean Basin are found as weedy populations in other mediterranean type climatic environments of the world: in central Chile; California in the USA; southern Australia; and the Cape Region of South Africa. Also, where natural fire regimes in Mediterranean type climatic regions around the world have been suppressed by human intervention across the landscape, plant species that originate from more mesic climatic areas are able to invade and persist (Gleadow and Narayan 2007).

The climatic similarities between mediterranean and sub-tropical parts of Australia and South Africa have meant that many South African species are able to grow well in Australia. Also, South Africa"s *en route* location (via sea) for immigrants to Australia from Europe, and the aesthetic, agricultural, horticultural uses and growth attributes of many species of Iridaceae and Asteraceae have led to many plants of these families being introduced to Australia (Scott and Delfosse 1992). Many plant species of South African origin (251) have established in (mostly southern) Australia and 68 of these species have become weeds (Scott and Delfosse 1992). Scott and Delfosse (1992) calculated that 20% of the established species from South Africa are from the Iridaceae family, 15% from the Asteraceae, and 13% from the Poaceae. However, the 20 most damaging weeds in Australia (Appendix 1a) come from wide ranging regions of the world.

2.4.3 Competitive ability in a novel environment

Woody weeds often have larger population densities and soil seed banks in the ecosystems they have invaded than in their country of origin. The population density of *C. scoparius* (scotch broom, a woody weed in Australia) has been found to be higher in weedy populations than in native stands (Paynter et al. 2003). However, the growth rate of weeds is often similar in weedy and native stands because high population densities lead to intraspecific competition, which reduces growth rates. Furthermore, mature plants within populations of *Ulex europaeus* L. and *C. scoparius* (woody weeds in Australia) have reduced longevity in their weedy habitat compared with their native habitat (Paynter et al. 2003). The number of woody weed seeds stored in the soil in temperate ecosystems is often far greater than the total number of seeds of native species (Ne'eman and Izhaki 1999; Enright 2001)(Table 2.1). For example, Enright (2001) recorded 59 native species in the Grampians National Park, Victoria, Australia (Table 2.1) as having a combined soil seed bank of 855-1080 seeds m^{-2}, which compares poorly with the up to 100,000 seeds m^{-2} found under *G. monspessulana* populations in similar ecosystems (Lloyd 2000) or the average of 2,500 seeds m^{-2} previously found in boneseed populations (Weiss 1986). The soil seed bank of some woody weed species, however, does not persist for many growth seasons. For example, the seed bank of *A. glabra* in tropical Queensland, Australia contained less than 3% of its original fresh viable seed pool after 12 months buried at either 2 or 10 cm deep in the soil (Setter et al. 2004). Even so, the greater number of woody weed seeds in Australian soil when compared with even high densities of native seed in the soil suggests a recruitment advantage to the invading species. There has been limited research into quantifying the degradation of the composition and size of seed banks in remnant woodlands after weed invasion (Thomas et al. 2005). Invasion of the South African fynbos by Australian *A. saligna* trees has reduced the density and diversity of species native to the fynbos (Holmes 2002). In Australia, anecdotal evidence suggests that the reintroduction of native species would be necessary in woodlands with degraded understorey diversity, due to the inability of depleted native seed banks to naturally re-establish native populations (Yates and Hobbs 1997).

Where woody weeds are competing with native woody species, increased soil nutrient status (commonly nitrogen or phosphorus) can influence weed species dominance (Thomson and Leishman 2005). Soils enriched with nutrients from agricultural and urban runoff and air pollution can provide a favourable environment for woody weed invasion (Bidwell et al. 2006). Increased soil nutrients cause increased survival, growth rates and biomass of exotic species (Leishman and Thomson 2005). Although Australian native plants are adapted to low nutrient soils, increased soil nutrients can also increase the competitive advantage of certain native species (Fogarty and Facelli 1999; Thomson and Leishman 2004). *C. scoparius* invades natural ecosystems in temperate Australia, often outcompeting native *Hakea rostrata* F Muell. Ex Meisn., *Acacia verniciflua* A.Cunn., and *A. myrtifolia* (SM.) Willd (Fogarty and Facelli 1999). *C. scoparius* has a higher relative growth rate than the native species, even though *C. scoparius* and the acacia species all grew better on soils containing higher organic carbon, nitrogen and soluble phosphorus. Where soil nutrients were higher (an effect that can be caused by *C. scoparius* itself), competition with acacia reduced the biomass of *C. scoparius*, while competition with *C. scoparius* reduced the biomass of *H. rostrata*. Where soil nutrients were low, no decrease in biomass due to competition was found for any of the species (Fogarty and Facelli 1999).

Table 2.1 Viable seeds stored in the soil for native temperate ecosystems.

Location	Vegetation type ± dominant native species	Estimated viable native seeds m^{-2} ***
Small seed bank		
Grampians National Park, Victoria, Australia*	*Eucalyptus baxteri* (Benth.) Maiden & Blakely ex J.M.Black heathy woodland	855 ± 70 to 1,080 ± 58, burned approx 25 yrs prior
Australia*	*E. baxteri* woodland	523 to 987, burned four years prior to study
Victoria, Australia*	*E. regnans* F. Muell. forest	61 ± 11 to 668 ± 101
Western Australia*	Kwongan	919 ± 159, burned, 1545 ± 189, unburned
Western Australia*	*E. marginata* Donn ex Sm. forest	377 to 1579
Mt.Carmel, Mediterranean region of Israel**	*Pinus halepensis* Mill. forest	300 to 1,300, in stands 6 to 55 years post fire
South Africa****	Fynbos, boneseed (*Chrysanthemoides monilifera* spp. *monilifera*)	100 to 300
Medium seed bank		
Wyperfeld National Park, Victoria, Aust.*	Heathlands	3,307 ± 146 to 3,521 ± 188
Ravensworth State Forest, NSW, Aust.*		2,887 to 7,578
South Africa*	fynbos	1,683 to 4,518
Large seed bank		
Grampians National Park, Victoria, Aust.*	*E. baxteri* heathy woodland	547 ± 449 smoke stimulated plus more stimulated by heat not smoke, 14 years post burn
United Kingdom*	Fire prone *Calluna* heathland	6,510 to 12,148
California*	Chaparral	8,000 to 25,000
Mt. Lofty Ranges, South Australia*****	*G. monspessulana*	Up to 100,000

*Data from Enright (2001) and references therein.
**Ne"eman (1999)
***Mean ± sd and range under a variety of management scenarios
**** (Milton 1980)
***** (Lloyd 2000).

2.4.4 Fire

In Mediterranean-type ecosystems, fire often plays a natural role in promoting species reproduction and in influencing the species and structural composition of the ecosystem

(Hanley and Fenner 1998). Conserving native populations in Mediterranean-type ecosystems involves understanding fire regimes that promote the persistence of fire-killed plant populations in these areas (Rokich and Dixon 2007; Groeneveld et al. 2008). In Banksia woodlands in Western Australia, optimal fire frequency required for ecosystem conservation is thought to be longer than occurred during pre- and early- European settlement periods of time. At the landscape scale, patchy fires could occur at both short and long frequencies, however, at the local dune scale fire frequency needed to be greater than 8 years in order for Banksia populations to persist (Groeneveld et al. 2008). In the absence of other disturbances or nutrient enrichment of soil, fire does not generally promote weed invasion in fire prone communities (Hester and Hobbs 1992; Thomson and Leishman 2005); however, fire disturbance can promote invasiveness of weeds in some environments (Gleadow and Narayan 2007). In Mediterranean-type ecosystems the heat shock of fire can influence seed germination and may influence seedling survival by advantageously changing the soil nutrient availability to seedlings, and by altering herbivory patterns across the area (Hanley and Fenner 1998). Where long-term (47yrs) annual burning has occurred in southern African savannas, hervibory patterns tended to be associated with clay and some soil micro- (but not macro-) nutrient levels, although the differences in savanna vegetation responses to fire, labelled the „savanna problem", remain unresolved (Mills and Fey 2005). Invasive species can establish after wildfire due to increased nutrient levels in the post fire ash-bed, increased light levels on the large expanses of bare ground and reduced plant competition (Sutherland 2003). In turn, native plant regeneration after wildfire can be inhibited by plant invasion (Hunter et al. 2003). In south-western Western Australia, the South Australian eucalypt species, *Eucalyptus cladocalyx* F. Muell., appears to have a greater resilience to frequent fires than do two indigenous eucalypts *E. gomphocephala* DC. and *E. marginata*. *E. cladocalyx* displays greater survival of post fire seedlings and faster recovery of the tree canopy after fire on mature trees, mechanisms which are thought to facilitate the invasiveness of the species into natural vegetation in Western Australia (Ruthrof et al. 2003).

Fire can increase the susceptibility of disturbed vegetation to invasion by weeds. When vegetation has been disturbed by road construction and maintenance, nutrient input from adjacent paddocks on stock trampling, then fire can render the vegetation more susceptible to invasion by exotic species. When vegetation has not been disturbed, fire can stimulate regeneration of native vegetation (Hobbs 1991). After a protracted period of weed invasion, a native soil seed bank may no longer contain seed of all seed bank stored species due to seed death. For example, in soils that have been artificially nutrient enriched, burning to remove invasive weeds resulted in the successful establishment of native species in schlerophyll vegetation on sandstone soils in the Sydney region of Australia. However, only some of the native species that were found growing in nearby (natural) lower nutrient containing soils were able to establish in the higher nutrient locations, even given the establishment cue of burning (Thomson and Leishman 2005). Therefore, the underlying causes of ecosystem degradation may need to be addressed prior to burning for weed control and native species restoration. However, native vegetation also often requires fire for regeneration, so fire suppression can promote weed invasion. In Illinois, USA, fire suppression and agriculture have caused the disappearance of most of the area‟s savannas (Bowles and McBride 1998), whilst in Washington, USA, *Quercus garryana* Dougl. ex Hook. woodlands have been invaded by non-native species since fire exclusion began in the early 1900‟s (Tveten and Fonda 1999).

A detailed understanding of the causes and processes by which woody weeds invaded native ecosystems is required for effective control techniques to be developed. Without such understanding, the implementation of control techniques, such as the use of fire, could cause an increase in the density or distribution of the weed population, or both. The response of a woody weed population to various types of disturbance, in varying climatic situations is essential prerequisite knowledge if effective long-term management of the weed or weeds is to occur. Likewise for effective weed control management to be able to be implemented it is essential to ascertain species responses to management, within a weed population, between populations of mixed weed species, and between weeds and native species.

2.5 A short history of fire/plant interactions in Australia

Grasslands and schlerophyll vegetation first developed in Australia during the Miocene and Pliocene prehistoric periods - that is, from the mid-Tertiary, 20 to 1.8 million years ago (Beadle 1981; Kemp 1981; Singh et al. 1981). The sclerophyllous (thickened) tissue found in the leaves of many Australian native woody species reduces transpiration and is an adaptation to mesic or xeric environments. The sclerification of the secondary walls of leaf parenchyma cells develop from either cell lignification, or the development of sclerophyllous cells directly from the apical meristem (Tootill 1984). The frequency of fires is also suggested to have increased as Australia became drier, the number of grasslands increased and as more areas of fire-sensitive rainforest species were replaced by sclerophyllous vegetation (Kemp 1981). The eucalyptus and myrtaceous tree and shrub species that now dominate temperate Australian ecosystems could themselves have arrived as post-fire „weeds" (Singh et al. 1981). The relationship between the dominance of schlerophyll vegetation and climatic fluctuations (nine cold periods in the last 700,000 years), overall climatic change (to a drier continent) and frequent cool burning by humans (from at least 32,000, if not 120,000 years ago) is unresolved (Singh et al. 1981). However, Jackson (1968 cited in (Singh et al. 1981)) has described Australian schlerophyll species as, „fire requirers" and „fire promoters" and the majority of the Australian flora now displays schlerophyllous characteristics (Singh et al. 1981).

Due to the history of interaction between fire and Australian ecosystems, any fire regime artificially imposed on an area should take account of the post-fire ecological responses of species inhabiting that area (Gill and Bradstock 1995). Ecological responses of Australian species to even a single fire are varied and not completely understood (Gill 1999). In fire-prone Australian environments, all flora and fauna achieve optimum population densities after different combinations of fire events, rather than in response to one fire (Gill 1981). The natural fire regime of a particular location is described by the annual and seasonal frequency, the intensity and the fire type; peat, ground or crown fire (Gill 1975). Inappropriate fire regimes cause a decline in indigenous flora and fauna diversity and abundance and can cause local extinction of species (Gill 1999) (Table 2.2). In Australia, knowledge of fire responses by particular species is incomplete; however, a database of known information has been commenced (Gill and Bradstock 1995). Fire regimes cannot consist of fires that are too frequent, as all species in the community need to re-establish their post-fire reproductive structures. For example, epicormic buds on tree stems require the growth of bark for protection. The frequency of major natural fires in the temperate region around Melbourne has been estimated to be every three to ten years. However, forested areas within this region are often burnt every five to nine years for fuel reduction or other purposes. Within this region the natural fire season is expected to occur over summer, between December and March (Gill 1981). Temperate eucalypt vegetation is highly flammable at most times of the year, as it is often dry and contains large amounts of leaf litter. Adding to vegetation flammability are the higher levels of volatile essential oils and the lower amounts of minerals in temperate eucalypt vegetation compared to those found in tropical plants (Vines 1981).

Therefore, the use of fire to manage woody weeds in native vegetation requires an understanding of the fire history of the area and ecosystem response to a single fire as well as to various fire regimes. Where weed management involves fire it is essential to understand the impact of the weed population on the natural fire fuel loads and burn characteristics of an area. The impact of fire on reducing the vigour and long-term soil seed reserves of the weed population, compared to impacts on native species in the invaded ecosystem, also needs to be ascertained.

Table 2.2 Changes in species richness in native Australian vegetation types after a single fire event (redrawn from Gill (1999) and references therein).

Vegetation type	Changes in species richness of different Australian vegetation types after fire
Vascular plant species in most communities	i) soon after fire the numbers of species rise to levels higher than those occurring immediately before the fire ii) numbers rise to a peak often within one year but sometimes after 2 or more years
Open eucalypt forests („dry sclerophyll forests") Forests with heathy understoreys	iii) changes appear most conservative, are possible exceptions
Heaths	iv) either no change in richness with time after fire, or decreases
Arid and semi-arid communities (especially in hummock grasslands and mallee)	v) rapid decreases soon after fire
Species rich rainforest Species poor rainforest	vi) sequences of species replacement after fire may increase species richness or decreases species richness

2.6 Boneseed as an invasive species in Australia

Two sub-species of the South African native plant species *Chrysanthemoides monilifera* are significant environmental woody weeds in eastern and south-eastern Australia – boneseed (Figure 2.1a) and bitou bush. The earliest record of boneseed in Australia is from 1852 from „MacLeay"s trädgård {garden}, nära {near} Sidney, Nova Hollandia", recorded by N. J. Anderson (Norlindh 1943). In 1858 the sub-species was introduced and used as a garden plant around Melbourne and presumably around Adelaide, where a specimen was recorded in 1892 (Parsons 1973). It was later recorded in Western Australia in 1948 and in Tasmania in 1931 (Weiss 1986). The earliest record of bitou bush is from 1908, in Stockton, N.S.W. (Gray 1976). Bitou bush was introduced later than boneseed where it was used for sand-dune stabilization along the N.S.W. coastline from 1946 to 1968 by the Soil Conservation Service and by mining companies (Mort and Hewitt 1953 cited in (Weiss 1986)).

The two sub-species appear not to have been distinguished as such in Australia until after the work of Norlindh (1943; Gray 1976). Prior to this, alarm regarding the incursion of populations of the species into native vegetation referred to both sub-species. Boneseed is not included in Ewart‟s (1909) census of naturalised alien plans in Australia; however, since that time, many authors have voiced concern regarding the incursion of boneseed into natural ecosystems (Gray 1976; Lane and Shaw 1978; Adair and Edwards 1996).

Boneseed and bitou bush are considered to have serious ecological impacts on invaded areas (Gray 1976; Dodkin and Gilmore 1985; Adair 1995; Groves 2008; Weiss et al. 2008). Both boneseed and bitou bush can become monocultures in areas of undisturbed native vegetation and reduce the density and diversity of native flora (Figure 2.1b)(Adair 1995; Thomas et al. 2000; Vranjic et al. 2000; Thomas et al. 2005; Ens and French 2008). This is of particular concern in areas where flora and fauna are already rare, endangered or of known susceptibility to woody weed invasion. Vegetation types most at risk are foredune grasslands, dune scrub, dune forest/woodland, headland grassy heaths and littoral rainforest (Dodkin and Gilmore 1985)(Table 2.3). Particularly threatened locations include the Bicheno area on the east coast of Tasmania and the vegetation of coastal N.S.W. Also at risk are already fragmented vegetation types and/or where invasion occurs at the limit of the distribution of a vegetation type (Dodkin and Gilmore 1985). Particular plant species threatened by boneseed and bitou bush include the *Pterostylis truncata* Fitzg. of the You Yangs range west of Melbourne in Victoria (Parsons 1973; Pescott 1995) and, in other areas of Australia, *Austromyrtus dulcis* (C.T.White) L.S.Sm., *Rulingia hermannifolia* (DC.) Endl., *Cryptocarya foetida* R.T.Baker and *Acianthus amplexicaulis* (F.M.Bailey) Rolfe (Dodkin and Gilmore 1985). Bitou bush growing on sand dunes can eliminate *Acacia longifolia* var. *sophorae* (Labill.), *Leucopogon parviflorus* (Andr.) Lindl. and *Correa alba* Andr. Var. *alba* from an area (Gray 1976). In boneseed-infested areas of the Mt. Lofty Ranges, adjacent to Adelaide, South Australia, less emergence of *Stipa setacea* R.Br., *Freesia* sp., *Homeria flaccida* Sweet, *Caesia vittate* R.Br. and orchid plants occurred, compared to uninfested areas (Thomas et al. 2000). *C. monilifera* also has a wider negative ecological effect through its negative impact on populations of migratory fauna (Dodkin and Gilmore 1985).

a)

b)

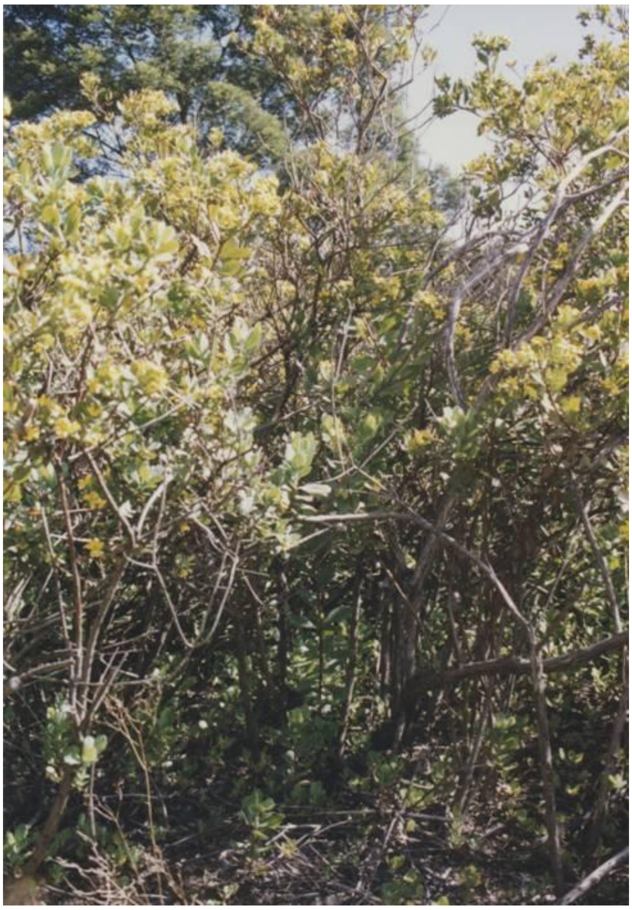


Figure 2.1 Boneseed **a)** flowers and seeds, and **b)** dense population containing seedlings, mature plants and senescent stems.

Table 2.3 Communities and associated plants invaded and/or threatened by C. monilifera (from (Dodkin and Gilmore 1985) and (Weiss 1986))

Community	**Associated species**
Boneseed	
Coastal scrub/woodland	*Eucalyptus pilularis* Sm.
	E. gummifera (Soland. ex Gaertn.) Hochr.
	E. botryoides Sm.
	Acacia mearnsii
Coastal forest	*E. viminalis* Labill.
Roadside woodland/forest	*E. socialis* F. Muell. ex Miq.
	E. incrassata Labill.
	E. dumosa A. Cunn. ex J.Oxley
	E. gracilis F. Muell.
Savannah woodland	*E. odorata* Behr
	E. leucoxylon F. Muell.
	E. camaldulensis
Heath	*E. baxteri*
	E. fasciculosa F. Muell
Bitou bush	
Dune grassland	*Spinifex hirsutus* Labill.
Dune dry heath	*A. longifolia*
	Leucopogon parviflorus
	Leptospermum laevigatum
	Scaevola calendulacea (Andrews) Druce
Headland heath	*Hibbertia vestita* Benth.
	Pimelea linifolia Sm.
	Pultenaea villosa Willd.
	T. triandra
Coastal scrub	*Drypetes australasica* (Mull.Arg.) Pax & K. Hoffm.
	Elaeodendron australe
	syn: *cassine australis* (vent.) Kuntze
Coastal woodland/forest	*Banksia integrifolia* L.f.
	B. serrata L.f.
	Allocasuarina littoralis (Salisb.) L.A.S. Johnson
	E. botryoides
Sclerophyll mallee	*E. planchoniana* F. Muell.
	E. intermedia R. T. Baker
Scherophyll forest	*E. pilularis*
	E. gummifera
	Angophora costata (Gaertn.) Britten
Littoral rainforest	*Acmena hemilampra* (F.Muell. ex F.M.Bailey)
	Cupaniopsis anacardioides (A.Rich.) Radlk.

The negative impact of boneseed invasion in a variety of vegetation types in Australia has been demonstrated over the last century. Boneseed invasion can eliminate entire plant communities from an area and has a detrimental impact on many native animal populations. Therefore, it is vital that effective long-term boneseed control measures are developed for temperate Australian ecosystems.

2.7 Chrysanthemoides biology and ecology

The genus *Chrysanthemoides* comprises two species in South Africa, *C. monilifera* (L.) T. Norl., a small shrub or tree occurring mostly along the southern and eastern coast of the country, and *C. incana* (Burm. F.) T. Norl., a low shrub mainly occurring along the west coast ((Norlindh 1943) in (Kleinjan and Scott 1996)). In addition to boneseed and bitou bush, there are four other (arguably potentially weedy) sub-species of *C. monilifera* which have not yet established in Australia: *C. m. pisifera* (L.) T. Norl., *C. m. subcanescens* (DC.) T. Norl., *C. m. caescens* (DC.) T. Norl., and *C. m. septentrionalis* T. Norl. (Norlindh 1943). The division to sub-species level is warranted within *C. monilifera*, as the species is highly polymorphic over its southern African distribution (Norlindh 1943). The following biological description of boneseed and bitou bush is given by Weiss (1986):

> „Ssp. *monilifera*. An erect shrub, 1-3 m high, the largest plant in the tribe Calendulae. It has toothed obovate leaves, more or less broadly ovate inner involucral bracts, 3-4 mm long, inflorescences with 5-6 bright yellow ray florets, borne in terminal or axillary corymbose cymes, and globose putamina, 6-7 mm in diameter, light brown when dry.
>
> Ssp. *rotundata*. A prostrate shrub, 1-2 m high and 2-6 m wide, with long decumbent stems. It has entire (or slightly toothed) broadly obovate leaves, lanceolate or narrowly ovate and acuminate inner involucral bracts, 4-5 mm long, inflorescences with 11-13 bright yellow ray florets and distinctly obovoid putamina, 5.5-6.5 mm long by 3.5 mm wide, dark brown to black when dry.“

2.8 Distribution in South Africa and Australia

Within the habitat range of *C. monilifera* in South Africa, the distribution of bitou bush is different to that of boneseed. Boneseed is found in the mediterranean-type climate of south-west Cape Province, while bitou bush is found in subtropical to temperate coastal regions. Boneseed is found on a wider range of soil and habitat types in Australia than in South Africa (Norlindh 1943). Boneseed in Australia most closely resembles the *C. m. monilifera* in South Africa that is located mid-slope on mountains in south-west Cape Province, while the bitou bush in Australia most closely resembles *C. m. rotundata* located in the coastal Natal region of South Africa (Scott and Adair 1992).

In Australia, boneseed is found in mediterranean-type and temperate regions (Norlindh 1943), that is, in coastal and inland regions of Victoria, Tasmania, South Australia and Western Australia (Figure 2.2)(Weiss 1986; Adair and Scott 1991; Brougham et al. 2006). Smaller infestations have been found as far inland as Mildura in the north-west corner of Victoria. In contrast, bitou bush mainly grows in coastal and inland sand dunes, in sub-tropical to warm temperate regions (Norlindh 1943) of New South Wales and southern Queensland and covers 80% of the NSW coastline (Holtkamp 2002). Scattered infestations of bitou bush occur amongst the sand dune vegetation as far south as Port Phillip Bay in southern Victoria (Holtkamp 1996). The types of disturbance most favouring the spread and/or establishment of bitou bush are rabbit activity, cattle treading, road construction and maintenance, sandmining, and natural disturbances (Humphries et al. 1991). Both boneseed and bitou bush populations have a potential distribution that is far larger than the area they currently occupy (Dodkin and Gilmore 1985; Brougham et al. 2006).

The control of boneseed in temperate Australia is made all the more urgent by the disastrous impact that this species has on native vegetation and by the assessment that large areas of vegetation within similarly suitable climatic areas are yet to be invaded. Also alarming from a conservation point of view are the common disturbance mechanisms that have been shown to aid the dispersal of bitou bush and have been observed to also aid boneseed dispersal. Prevention of the establishment of new and expanding boneseed populations therefore needs to be part of boneseed management in Australia.

NOTE:
This figure is included on page 28 of the print copy of the thesis held in the University of Adelaide Library.

Figure 2.2 Current (yellow) and potential (dark green) distribution of boneseed in Australia (potential distribution predicted by BIOCLIM model) (from (Brougham et al. 2006)).

2.9 Management of woody weeds in temperate natural ecosystems of the world

2.9.1 Ecological weed control and restoration

The conservation and restoration of rapidly degrading ecosystems is a vital area of work around the globe (Young and Mitchell 1994; Hobbs 2000; Young 2000; Hobbs and Harris 2001; Machlis and McKendry 2005). The theoretical framework for organising, undertaking and managing ecosystem restoration is increasingly being developed (Young 2000). Practitioners, researchers and global organizations (eg. WWF; ICUN; Society for Ecological Restoration International (SERI); Man and Biosphere, UN; SCOPE (Scientific Committee of Problems in the Environment) regularly compile knowledge derived from practical and research communities operating in semi-natural and „wild" ecosystems around the world. For forests, practical methods are available for restoring areas degraded by fire, violent storms, erosion, land abandonment, over logging, open cut mining and invasive species (Mansourian et al. 2005), likewise a great deal of research has been undertaken towards the restoration of fire-prone Mediterranean-type ecosystems (Rokich and Dixon 2007). The restoration of ecosystems degraded by weeds involves long-term management over and above the removal of the degrading weed (Panetta 1981; Vitousek et al. 1997; Walker 2000) at multiple scales across the landscape (Brown et al. 2008; Buckley 2008). Economic decision making tools based on theoretical models can aid decision making regarding the size of areas where weed eradication might be feasible (Cacho et al. 2008) and whether and when a weed can indeed be declared eradicated from an area undergoing restoration from weed invasion(Regan et al. 2006).

Several authors have called for a united approach to setting up restoration projects in different ecosystems of the world (Yates and Hobbs 1997; Keddy 1999; Hobbs and Harris 2001). One suggestion is to use a system where a group of species is distributed over an area, with the particular abiotic factors prevailing in the area impacting upon the final species composition – the „assembly rules" system (Keddy 1999), or „passive restoration" (Rey Benayas 2005). In contrast, „active" planting of secondary successional species can shorten the length of time a system takes to regenerate past the primary coloniser stage. The system therefore becomes more rapidly habitable for a diversity of flora and fauna. Indeed, some degraded ecosystems will never progress past a primary coloniser regeneration „loop", or will suffer high seedling mortality, without active restoration efforts (Rey Benayas 2005). In ecosystems where ecosystem function has been degraded, the restoration of key species that in turn restore ecosystem function and enable the establishment of other desirable native species can be a successful restoration strategy (Prober et al. 2005). In temperate Australian grassy woodlands, carbon supplements and spring burns were used to establish swards of a perennial native tussock grass, which in turn reduced soil nitrate levels to those favoured by native species rather than exotic species (Prober et al. 2005). The recovery of the South African fynbos vegetation after weed control was aided by the distribution of seed of fast growing native species to stabilise the soil, along with seed from each of the major plant guilds, which insured representation of all species groups in the longer term (Holmes and Newton. 2004).

There is a need for specific goals to be identified for areas undergoing restoration and a system for monitoring the success of restoration projects (McIntyre and Hobbs 1999; Hobbs and Harris 2001; Gonzalez del Tanago et al. 2005; Hilera-Lanzos and Diez-Hernandez 2005; Machado 2005; King and Hobbs 2006). The use of „indicator species" has been suggested as a means of determining how successful a project has been (Keddy 1999). Using this method, the measured success of one species represents the increasing health of the entire ecosystem. For this method to be meaningful, an assumption must be made linking the health of the indicator species to the health of its environment. Comparisons of the flora, fauna and ecosystem functioning of restored vegetation systems of differing ages to nearby intact vegetation have shown some restoration efforts to be highly effective. In a temperate New Zealand forest, floristic similarities were found between regenerating vegetation across restoration sites that were 12, 30 or 35 years old and mature forest. Moreover, ecosystem functioning at these sites had also been restored over time, such that 71% of regenerating trees were dispersed initially by birds and the composition of plants, Coleoptera and spiders increased with time relative to both 100 year old naturally regenerating forest and intact mature forest (Reay and Norton 1999). In threatened temperate eucalypt and Banksia woodlands in Australia, there is a need for further research into techniques for reversing degraded biotic diversity, structure and function, and removing degrading pressures. The processes of degradation have been written about extensively and there is now urgency for research into ways of reversing those degrading processes (Yates and Hobbs 1997; Rokich and Dixon 2007).

The concept of „ecological control" describes „the planned use of one or several methods of control when integrated with an understanding of the dynamics of the ecosystem in which the plant occurs" (Groves 1991; Buckley 2008; Firn et al. 2008; Radford et al. 2008). Hobbs and Humphries (1995) advocate controlling invasive species, using an understanding of the dynamics of, and the human impact upon, weedy and native plant propagules. Control measures implemented against one woody weed need to also control other weeds in the area to enhance the restoration of the invaded ecosystem (Gleadow and Narayan 2007; Radford et al. 2008). This type of weed control is more complex than simply reducing the plant numbers of a particular species. It involves consideration of the growth dynamics of other weeds, and woody and herbaceous native species within the invaded ecosystem. It also involves consideration of the degree of impact that the weed has had within that system: the above-ground weed density; the weed soil seed bank density; the remaining above ground native plant density; and the remaining native species stored seed bank. For example, restoration after woody weed clearance of the fynbos vegetation of South Africa in situations where the fynbos occurs on sandy plains, requires the distribution of the seed of long-lived obligate seeders (Holmes 2002). Seed numbers in the soil seed bank of this guild of plants were found to be low. Where a large portion of the seed bank under a woody weed invasion remains near the soil surface, soil disturbance (in order to access more deeply buried seed) ought not to be necessary. However, if a slash and burn technique is used to control the woody weed populations, the shallow native soil seed bank would be destroyed and soil disturbance would be necessary (Holmes 2002).

The restoration of weed-degraded lands can be influenced by physical, abiotic and/or other biotic components of the system, and even by restoration programs targeting co-occurring species or life forms. Therefore, the restoration and management of areas invaded by weeds sometimes involves ameliorating other degrading processes (the causes), rather than continually removing the weed (the symptom), as is shown in the following examples. In degraded wetlands, the restoration of original hydrological structures is sometimes a necessary prerequisite to commencing woody weed control activities (Choi and Bury 2003). Where wetlands in north-western Indiana, USA have been degraded by draining or excess litter accumulation, the result is the encroachment of native and exotic woody species (Choi and Bury 2003). Where ecological restoration involved reintroducing an animal species, *Castor canadensis* (native beaver), to north-western USA riparian habitats, the risk of woody weed invasion increased. Weed invasions increased due to the selective felling of the native cottonwood trees by the beavers, which in turn left open space suitable for colonisation by invasive plants (Lesica and Miles 2004). In tropical Panama, the wild sugarcane *Saccharum spontaneum* L. (Gramineae), creates monoculture grasslands that are not suitable for habitation by native fauna or for agricultural use (Hammond 1999). In addition to successful, but small scale, reforestation projects, it has been suggested that small groups of fruit-bearing trees be planted within the problematic grasslands to attract animal dispersers that would slowly increase the distribution of the trees away from the initial planting. The planting of forest trees could also be useful as an aid to the natural recolonisation of understorey species. Both these methods have proven successful against two other weeds in Panama - *Imperata cylindrica* P.Beauv. and *Dicranopteris linearis* (Burm.f.) Underw. (Hammond 1999). The suitability and efficacy of a control method within a particular ecosystem depends on the sensitivity of that system to each technique, the degrading processes and the final conservation or restoration goals for the area. The following sections describe aspects of physical, grazing, herbicidal, fire, plant competition, biological and other control methods for woody weeds.

2.9.2 Physical and grazing weed control

Physical weed control involves the manual, mechanical or animal-related removal of plants and can be achieved in many ways. Hand/manual weed pulling, slashing, or ringbarking by people, ripping with heavy machinery or grazing by small (rabbits) to large (goats, sheep, kangaroos) animals are some examples. The „Bradley" method of hand-pulling weeds involves pulling out all weeds present (not only the dominant weed species) causing the least disturbance to the surface of the ground as possible. The method involves starting from the least invaded areas and moving in towards the most densely infested areas (Bradley 1971). The physical removal of *C. scoparius* in sensitive conservation areas in Victoria, British Colombia, Canada, resulted in more disturbance to the soil, trampling of other plants and regeneration of seedlings when *C. scoparius* was hand pulled, as opposed to being cut at the base (Ussery and Krannitz 1998). However, increased soil disturbance caused by the physical removal of boneseed in the Belair National Park near Adelaide, South Australia, had no impact on germination of boneseed seed from the soil when compared with undisturbed areas (Thomas et al. 2000). In three vegetation types (tall open and closed forest and closed shrubland) in subtropical northern NSW, Australia, the number of native species increased from 281 to 304 during seven years of weed removal disturbance (Macleay 2004). Native species also increased in abundance over the same period and the number of weed species fell from 48 to 37 species. Weed control disturbance included hand-pulling *L. camara* L., *Paspalum wettsteinii* Hack., and *Ageratina adenophora* (Spreng.) R.M.King & H.Rob. and ring barking *Ligustrum sinense* Lour. and *C. camphora* (Macleay 2004). These results can be used in two ways – either woody weeds are hand-pulled to reduce the detrimental weed impacts on the ecosystem or, where vegetation is not sensitive or is already degraded, hand pulling could be used to stimulate more seed to germinate that is subsequently removed or killed. Some woody weeds in southern Australia (*Cestrum elegans* Brongn., *Ilex aquifolium* L. and *Prunus laurocerasus* L.) need to be removed from contact with the ground (eg. piled on log platforms) after being hand pulled, so that plants do not re-establish from stem fragments (Gillespie 1991). Goat grazing in autumn in mountainous areas of Spain (the Pyrenees) reduced the survival and regrowth rate of weedy *G. scorpius* by 58% and 32%, respectively. However, all grazing at all times of the year reduced the flowering rate the following spring from 38.5% to 2.6% compared to ungrazed areas and the impact increased with higher goat stocking densities (Valderrabano and Torrano 2000). Many volunteers in Australia have a policy of spreading cut boneseed branches evenly over the ground in order to prevent smothering of existing native species. Interestingly, obstructions laid on the ground have been found to aid the establishment of soil flora and fauna, nutrient cycling and hydrologic processes (Whisenant et al. 1995; Tongway and Ludwig 1996). Mulching did not affect the germination of boneseed or native species in the Mt. Lofty Ranges, South Australia (Thomas et al. 2000).

2.9.3 Herbicide control

Globally, herbicides are widely used against woody weeds in forestry (for example against *Acacia* spp.), pastures (for example against *Rubus* spp.) and in rangelands (for example against *A. nilotica*). Several herbicides are registered for use on boneseed in Australia (Appendix 2). Aerial spraying of bromoxynil herbicide onto boneseed seedlings was undertaken after wildfire burnt mature boneseed in Victoria in 1985. However, only one third of all seedlings were killed, as the aeroplane was not able to spray low enough to the ground for adequate coverage by the herbicide (Pescott 1995). In contrast, successful aerial spraying of the related subspecies bitou bush in N.S.W. has been achieved using low rates of glyphosate (Toth et al. 1996). However, glyphosate was aerially sprayed onto bitou bush between 1970 and 1982 without any reduction in the soil seed bank of the population (Cooney et al. 1982). For *Prosopis velutina* Wooton in Queensland, Australia, a high rate of triclopyr + picloram with added parafinic oil and non-ionic surfactants gave better aerial control than glyphosate to all sizes and classes of that woody weed. Control was also better where favourable rains caused a high water table to persist while control was carried out (Sparkes and Midmore 2004). Herbicides can also be applied by handsprayer directly to larger woody weed seedlings, thereby avoiding contact of the herbicide with the vast majority of surrounding natives. Metsulfuron-methyl effectively kills bitou bush plants when applied in this manner (Toth et al. 1996). The herbicides glyphosate, Tordon 50D® (consisting of 2,4-D and picloram), 2,4-D amine, bromoxynil and amitrole have all been registered at 1: 100 dilution for use on bitou bush, but were not registered as overall sprays due to their lack of appropriate selectivity for this weed (Cooney et al. 1982). Application of glyphosate to bitou bush only achieves satisfactory control when plants are not water stressed (Cooney et al. 1982). Glyphosate (360 g L^{-1}) applied to the foliage of boneseed at concentrations of 1: 100, 1: 200, 1: 300 or 1: 400 effectively controls the weed; higher concentrations are needed for larger plants and native species are protected from contact with the herbicide by an increasingly dense boneseed canopy (Earl 1990; Earl 1994).

Both physical and herbicidal weed control methods are expensive and need to be undertaken with great care so as to avoid damage to indigenous plant species (Adair and Scott 1993). Many sclerophyllous Australian native plants are more resistant to herbicides than are their invading woody weeds (Groves 1991; Toth et al. 1996). This difference has been attributed to both the sclerophyllous leaf structure of the Australian species and the slow winter growth rate of Australian natives compared with many exotic species (Groves 1991; Toth et al. 1996). These physical and physiological differences result in there being a potential for killing exotic species with herbicides while the surrounding natives are unharmed or at least not killed. To further increase the difference in herbicide efficacy on exotic over native species, herbicides can be applied when exotic seedlings have emerged but the slower growing native seedlings have not, a situation that often occurs after a disturbance event such as fire (Rokich 2007) . The two herbicides investigated in this study for use on boneseed seedlings growing in native vegetation differ in their known selectivity. Glyphosate inhibits 5-enol-pyruvyshikimate-3-phosphate synthase (EPSPS, E.G. 2.5.1.19) in plants, which limits the synthesis and regulation of aromatic amino acids (Culpepper and York 1998). Glyphosate is known to be a „highly effective and environmentally benign herbicide, that controls a broad spectrum of annual and perennial grass, broadleaf weeds and sedges‟ (Werth et al. 2008). Methsulfuron-methyl is a broadleaf selective herbicide that inhibits acetohydroxyacid synthase in plants (Stidham 1991; Chiconcela et al. 2004; Hutchinson and Langeland 2008).

Although herbicides can be very useful control tools against woody weeds in natural ecosystems, there is a lack of data regarding the dose and timing of application responses of individual native species (Groves 1991). However, Rokich (2007) has shown negative effects of the herbicide Fusilade®, a herbicide commonly used by resoration workers around the world, on the germination and seedling survival of several native species in a Banksia woodland in Western Australia, and issues a caution regarding its use in native vegetation.. One exception is the compilation of herbicide species response data for several grasses native to south-eastern Victoria, Australia (Morgan 1989). The impact of herbicide application on vascular species and the flow-on impacts on dependent fungi, mycorrhizae, soil microbes and vertebrate and invertebrate fauna are unknown. However, untreated woody weed infestations will destroy the habitat of the flora and fauna. In this respect the unknown impacts of herbicides parallel the unknown impacts of changed fire regimes on Australian native vegetation. Management should therefore follow some similar objectives. That is, that the herbicide application known to be most benevolent to the native vegetation be used in a patchy manner with a number of years between applications at any one location. This allows for targeted herbicide use against a weed, whilst accommodating a range of responses by native species.

2.9.4 Fire control

Prescribed burning, also known as controlled burning, can be used alone or in combination with other techniques to rid an area of mature weed biomass and cause heat, smoke and charring disturbance to the soil seed bank (Auld and Bradstock 1996; Campbell and Setter 2002; Paynter and Flanagan 2004). In addition, in fire-prone Mediterranean-type ecosystems (such as Australian kwongan, woodlands and grasslands and South African fynbos and succulent karoo), the use of smoke (and the phytoreactive chemical, butenolide (Flematti *et al*. 2004a, 2004b, 2005 in (Rokich and Dixon 2007)), has been shown to stimulate seed germination and/or an increase in the vigour of seedlings of a large number of plant species (Rokich and Dixon 2007). Burning is a highly effective control measure for *Prosopis pallida* (Willd.) Kunth in Queensland, Australia, killing 93% of plants and requiring only minimal follow up seedling control; however, burning often only kills young plants of other mesquite species (Campbell and Setter 2002). In Victoria, burning in the field caused the mortality of non-soil stored seed and of seedlings of *P.undulatum* at (laboratory tested) temperatures ranging from 90^{o}C to 120^{o}C over time (Gleadow and Narayan 2007). Given only 20% of mature trees re-sprouted within six months of burning, fire also reduced suitable roosting sites for birds, which thereby reduced seed import from nearby areas. Burning also reduced the amount of shaded areas, the preferred location for the establishment of *P.undulatum* seedlings, and is therefore thought to break the population lifecycle for this species (Gleadow and Narayan 2007). In tropical Queensland in northern Australia, fire was used to control *Cryptostegia grandiflora* (Roxb. ex R. Br.) R. Br. after a combination of rust fungus depletion of vine biomass, drought and increasing native grass presence resulted in the presence of enough fine fuel to carry a fire (Tomley and Evans 2004). Where *C. grandiflora* occurs in tropical riparian habitats, low intensity burning, using either two fires in the wet season or a single fire in the early dry season, has been shown to inhibit seedling recruitment of the vine as well as other exotic woody weeds present in the area. It was apparent that this type of burning did not lead to irreversible ecosystem degradation (Radford et al. 2008). Since *Pinus clausa* (Chapman ex Engelm.) Vasey ex Sarg. *Pinus clausa* invaded sandhills at the Eglin Air Force Base, Florida, USA, restoration of the area to an overstorey of *Pinus palustris* P. Mill habitat has been achieved by harvesting *P. clausa*, burning, then planting *P. palustris* (Provencher et al. 2000). *S. terebinthifolius*, a native species of Brazil, Argentina and Paraguay, can also be controlled by fire (Noad 2002). Fire could be used to control invasive *Sapium sebiferum* (L.) Roxb. around Lake Jackson, Florida, U.S.A, as burning decreased the likelihood that seeds would germinate (Burns and Miller 2004). In south eastern Australia, woody weeds such as mature *P. pinaster* trees and *L. laevigatum* are killed by fire, as is mature *Pittosporum undulatum* if the fire is of moderate to high intensity (Adair 1995). Fire kills mature boneseed plants, whilst mature bitou bush plants are able to resprout after being burnt (Scott and Adair 1992). The use of flames from a hand held burner has also been shown to kill 92% of *Jatropha gossypiifolia* L. plants after 10 s, 83% of *Parkinsonia aculeate* L. plants after 10 s and 76% of *C. grandiflora* plants after 60 s, while causing limited off target damage (Vitelli and Madigan 2004). However, in the woody weed invaded fynbos vegetation of South Africa, slashing woody weeds, then burning the slash *in situ* created a fire that was too hot and that killed native seeds in the shallow portion of the seed bank. The slash and burn technique is therefore not recommended for use in the fynbos (Holmes et al. 2000). After a very hot burn, restoration of native species required disturbing the soil to promote the germination of more deeply buried viable seed (Holmes 2002). Summer wildfire also destroyed a large portion of the long-term fynbos soil seed bank (Holmes 2001).

The time of the year, intensity of the burn, soil nutrient status and follow up actions will all have an impact on weed and native populations. Where nutrient enrichment of the soil has occurred prior to burning, burning will not promote the establishment of native species that were not already growing on those nutrient enriched soils (Thomson and Leishman 2005). However, fire frequency *per se* (assuming the fire regime is appropriate), cannot be used as a control method for woody plant species in native vegetation. The high frequency of fire needed to reduce populations of woody invaders and increase native grass density would disadvantage populations of woody native species. Australian native species also respond differently to various intensities of fire and to unburnt situations (Morrison 2002). In Australia, current prescribed fire regimes in an area are often thought to be different from the fire regime that would have naturally occurred. The spatial and temporal fire regimes that are currently applied are often different to historical regimes due to a lack of knowledge of historical fire regimes, land-clearance for agricultural use, urbanisation of the area, or confusing fire policies, laws and local burning regulations. Management strategies regarding frequency of burning vary widely across temperate Australia. Currently, altered fire regimes and other disturbances threaten an estimated 11 species of vascular plants with extinction within the next 20 years (Burgman et al. unpublished data in (Lindenmayer and Burgman 2005)). In general, less burning occurs now than would have occurred under Aboriginal land management (Nicholson 1981). Gill (1981) suggests that after levels of environmental awareness increased in the Victorian community during the 1960s and 70s it became acceptable for the „fire regime" designed for an area to consider ecological benefit, as well as benefits to timber, fodder and water production. For example, the optimal burning frequency for maintaining a *T. triandra* grassland is 1 to 5 years, as burning at longer intervals will maintain open woodland vegetation instead (Morgan and Lunt 1999; Morgan 2001). And populations of the rare obligate seedling shrub *Grevillia barklyana* F Muell. ex Benth. (Proteaceae) may be limited by fire frequencies of less than ten years or greater than 25 years (Vaughton 1998).

2.9.5 Plant competition control

There appears to be potential for promoting the growth of native species over that of resprouting/re-emerging weed individuals (Weiss and Noble 1984; Groves 1991; Rokich and Dixon 2007); however, limited work has been done to investigate the efficacy of this technique. In Australia, Weiss and Noble (1984) demonstrated competition between a woody native and woody invasive species, by finding that the native *A. longifolia* was morphologically similar to *C. monilifera* (in this case bitou bush) and could outcompete the weed at low moisture levels. Also in Australia, a non-weed invaded dense stand of the grass *Poa labillardieri* Steud. has been observed growing adjacent to a dense population of *U. europaeus*. Preliminary trials showed that increasing *P. labillardieri* density had some potential for *U. europaeus* seedling suppression (Carland 2003). Woody plants are thought to utilise resources from subsoil layers, while grasses utilize resources from the topsoil (Jurena and Archer 2003). Thus, the successful establishment of woody seedlings is thought to rely on the intermittent germination of woody seedlings where topsoil resources are available in gaps between grasses (Jurena and Archer 2003). With a high density of grass seed present, the competition for light, nutrients, soil moisture and space on the surface layer of the soil should provide optimal conditions for both dense grass establishment and the death of woody seedlings competing with that grass. Several weeks after burning, when a dense mat of grasses has established, the emerging woody seedlings are likely to be outshaded. Similarly, increasing the proportion of grass root biomass, relative to that of woody seedlings, will reduce the soil moisture available to woody seedlings (Polley et al. 2003). In tropical north-west Queensland, Australia, Radford (2001) found that the native perennial grass *Astrebla lappacea* (Lindl.) Domin had low levels of mortality after a controlled grass fire that was used to kill seedlings of the woody weed *A. nilotica*.

Plant allelopathic properties can also be used to control invasive species. In lowland forests and waste areas of Taiwan the climbing vine *Mikania micrantha* Kunth can be controlled using the allelochemicals of a native species, *Delonix regia* (Bojer ex Hook.) Raf.. Application (to the surface of test pots) of 1-2 g of mulched *D. regia* leaves or flowers, killed 75-90% of *M. micrantha* seedlings after 3 weeks (Kuo et al. 2002).

2.9.6 Biological control

Biological control involves the use of a predatory, pathogenic, competitive or herbivorous agent to control a pest species (Sheppard et al. 2005; Morin et al. 2006; Sheppard et al. 2006). Classical biological control involves transferring an agent from one location to another, while inundative biological control involves increasing the densities of an agent that is already present in an area (Briese 1999). In South Africa the gall-forming rust fungus *Uromycladium tepperianum* (Sacc.) McAlp. reduced populations of *A. saligna* (Labill.) Wendl. (Fabaceae) by up to 95% during the first eight years after establishment (Morris 1999).

The positive aspects of biological control involve its usefulness in difficult to access terrain, and the self-sustaining, inexpensive and weed species-specific control that occurs when agents are established. Biological control can be a cost effective weed control technique (van Wilgen et al. 2004; Page and Lacey 2006). For example, in the South African fynbos the benefits of increasing the supply of water (woody invasives consume more water than does uninvaded natural fynbos), utility of land, and restoration of biodiversity values outweigh the costs of biological control research (van Wilgen et al. 2004). Similarly, the future benefits (including preventing potential distribution over uninvaded suitable sites) of using specific biocontrol agents to control *A. longifolia* and the mediterranean shrub *L. camara* are estimated at 4333:1 and 34:1 respectively (van Wilgen et al. 2004).

Negative aspects of biological control include the high initial research costs and the difficulty of establishing agent populations amongst novel predators in the new environment. Also, agent populations may not suppress weed populations due to poor dispersal or reproduction. There are a number of reasons why biological control is not always successful including: predation, climatic variation across the range of the target weed and ineffectiveness of climate matching between the agents origin and new area of distribution (Ireson et al. 2002; Klinken et al. 2003). For example, the woody weed *U. europaeus* invades grazing and adjacent native vegetation in cool temperate regions of Australia and has been one of 21 weeds in Australia subject to a biological control program (Appendix 3). The gorse spider mite *Tetranychus lintearius* Dufour was released for control of gorse in 1998. The mite has been heavily predated upon at 116 sites in Victoria and 90 sites in Tasmania after initially establishing successful populations. An introduced mite, the Chilean predatory mite *Phytoseiulus persimilis* Athias-Henriot and a native coccinellid *Stethorus histrio* Chazeau reduce *T.*

lintearius population numbers. These two predators will potentially reduce the efficacy of this biocontrol agent (Ireson et al. 2003). *L. camara* is a weed of natural ecosystems, forestry plantation and grazing lands in sub-tropical and tropical Australia (Day and McAndrew 2003). Of the thirty biocontrol agents released for the control of this weed, 16 have established in the field. However, none of these agents singly or in combination have brought *L. camara* populations under control. The lack of survival of agents in the climatic conditions experienced in differing parts of the range of this weed in Australia are thought to be the cause of agent population levels remaining too low for impact on weed populations (Day et al. 2003). An example of this is the survival at different temperatures of *Aconophora compressa* Walker, a hemipteran biocontrol agent from Mexico for *L. camara*. Individual agents survive for less than a day at temperatures of 39^{o}C, a summer temperature common in many parts of Australia where *L. camara* is growing. The survival of nymphs and adults of *A. compressa* declines up to 39^{o}C, although survival is slightly longer when temperatures fluctuate rather than remaining constant (Dhilpeehan et al. 2005). In south-east Queensland the seed damaging fly *Ophiomyia lantanae* Froggatt does not limit population densities of various *L. camara* biotypes (Vivien-Smith et al. 2006). However, the fly does reduce seed dispersal as frugivores choose not to consume damaged fruits. *O. lantanae* seed damage both increased and decreased germination rates depending on the *L. camara* biotype. However, the large remaining *L. camara* soil seed bank meant that recruitment the following season would probably not be seed limited (Vivien-Smith et al. 2006).

2.9.7 Impact of biological control on boneseed

Biological control has been, and remains, particularly suited to the control of *C. monilifera* in Australia, as populations often grow on rocky slopes that are difficult to access to apply other forms of weed control (Holtkamp 1986). Boneseed and bitou bush appear not to have any natural enemies in Australia that cause damage significant enough to limit population growth (Adair and Scott 1991). Investigations in South Africa for potential biological control agents yielded „113 phytophagous arthropods, 3 fungi and a mycoplasm" residing on *C. monilifera* and *C. incana* (Scott and Adair 1992). Of these, 21 species were deemed to have the highest priority for host-specificity investigations on plant species relevant and/or important in Australia. The 21 species had initially been observed to have high levels of host specificity (in their country of origin), caused a high level of damage to target plants, had climatic distributions similar to those of the weed populations in Australia, had low levels of predation and were thought to be able to be reared under laboratory conditions (Scott and Adair 1992).

Successful establishment of biological control agents in novel Australian environments is often hampered by biotic resistance, that is, predation of the agents by native species (Meggs 1995). The biological control program for *C. monilifera* has therefore tested and released many agents in the hope that some would overcome such resistance and cause a population decline of the weed species. The biological control program for *C. monilifera* commenced in 1987. By 1989 four agents had been approved for release in Australia, *Comostolopsis germana* Prout (Lepidoptera: Geometridae), *Chrysolina picturata* Vogel and two undescribed *Chrysolina* sp. (Coleoptera: Chrysomelidae) (Adair and Scott 1989; Kleinjan and Scott 1996). A further four species of tortoise beetle, (Chrysomelidae: Cassidinae), *Cassida spatiosa* Spaeth, and the undescribed *Cassida* sp.1, 2, and 3 were under investigation (Kleinjan and Scott 1996).

By the late 1990‟s *C. germana* had established in areas of coastal NSW. Predation had a detrimental impact on the establishment of all other species; however, by the mid 2000‟s *Cassida* spp. had begun to have an impact on bitou bush (Cherry 2006). Currently, *Mesoclanis* spp. seed flies have successfully established on bitou bush in sub-tropical regions of NSW. The *Tortrix* sp. leaf roller moth has established over a small area of boneseed in temperate Victoria, and at six bitou bush sites in NSW, where it is most successful on headland sites where plants contain higher levels of nitrogen (Cherry 2006). However, no agent or suite of agents has as yet caused a large reduction in the population growth of either boneseed or bitou bush. Future possible biocontrol agents currently undergoing genetic identification or host specificity testing are the boneseed rust *Endophyllum osteospermi* Wood, the boneseed leaf buckle mite, *Aceria* sp., the bitou leaf buckle mite *Aceria* sp., the tip wilt cerambycid *Obereopsis pseudocapensis* Breuning for bitou bush, and a tip wilt pyralid for boneseed (Cherry 2006).

2.9.8 Other control methods

There are a number of possible ways to control weed populations in addition to those described. The weed problem could be approached from an economic viewpoint. In South Africa, a study into the potential for commercial utilisation of wood from the invasive

Australian trees *A. cyclops*, *A. saligna* and *A. mearnsii* for pulp, paper and board estimated there to be enough wood to service the annual mill requirements for that country for many years (Theron et al. 2004). The authors caution that careful monitoring of large scale harvesting is required, given the potential risks of environmental damage and mill dependency on a limited supply of weed species (Theron et al. 2004). The control of a sole or dominant pollinator species could also limit weed reproduction where seed production is a vital life cycle step. Control of the exotic honey bee, *Apis mellifera* L., in Australia would reduce the seed set of the woody weed *L. camara*. *A. mellifera* is the primary pollinator of *L. camara* across much of the weeds range and the only pollinator found in parts of southern Queensland. Seed production by *L. camara* increased with increasing *A. mellifera* abundance (Goulson and Derwent 2004). Also, molecular techniques have been suggested for neutralizing the invasiveness of certain weed populations (Li et al. 2004).

There are a number of potential weed control techniques available for the control of boneseed in native vegetation in temperate regions of Australia. Some techniques have been used in isolation; namely manual removal, herbicide application and biological control, with a low level of long-term success over large areas of land. Limited testing of combinations of control techniques has occurred in Australia and the integrated control of boneseed using several weed control techniques is not currently common practice in southern areas of Australia. There is a need for such integrated control to be developed using techniques that will cause as little harm as possible to the invaded native vegetation.

2.10 Conclusion

Natural processes and human economic activities degrade and threaten susceptible ecosystems and species around the world. While these problems are known to many sections of the world‟s community and often documented, the more difficult task of finding feasible management strategies for ameliorating such processes is a priority in many ecosystems. Invasive species are one of those degrading processes, and this study aims to address the development an integrated control strategy for a particular weed and commonalities between the management of similar weeds. However, ultimately changes to global and country specific economic and social policies will also be required to slow the spread of this problem - not least in the area of climate change, where the potential distribution of invasive species is being altered. In temperate areas of southern Australia, many ecosystem types are degraded and under threat from invasive species. Woody weeds in particular threaten grasslands and woodlands in southern Australia and there is an urgent need for control that eliminates the weeds while having a beneficial impact on the native species. In the past, much weed control has focused solely on killing a particular plant and only the part of that plant‟s population that appears above ground. Instead it is vital that control measures focus on killing multiple weeds at the same time, on killing propagules stored in the soil or elsewhere and on types and timing of weed control methods that enhance, or at the very least cause the least damage to populations of native species. Boneseed is an aggressive woody weed that has a long history of invasion in temperate Australian native ecosystems and is a priority for control in this country. Weed control measures used against woody weeds include physical control methods, application of herbicides, burning weed populations, introducing destructive biological control agents and using other plant species to outcompete the weed. All of these control methods need to be used sparingly in native vegetation due to off target effects and differing time spans required for the various native plant life forms to regain reproductive maturity. One of the great problems with judgements regarding weed control timeframes, as with any ecological management, is that many data such as biological and community dynamics after natural or unnatural disturbances, remain unknown. Conservative practice would therefore require that control methods be used sparingly, with the underlying knowledge that lack of control would inevitably result in destruction of the ecological community. Control of boneseed on a landscape scale in Australia has not yet been achieved, partly due to various control strategies having been used in an non-integrated manner. Whether the integration of several weed control strategies could significantly reduce or eliminate a boneseed population and simultaneously restore the native vegetation of the invaded area in southern Australia was the focus of this thesis.

Chapter 3: Materials and methods

3.1 Materials and methods used throughout thesis

3.1.1 Experimental sites

Two experimental sites were established within the warm, temperate coastal fringe of Port Phillip Bay in Victoria in southeastern Australia: one in the Arthurs Seat State Park to the south-east of Melbourne and the other in the You Yangs Regional Park to the west of Melbourne. Both parks contain dense boneseed infestations.

3.1.1.1 Species rich closed woodland site

Arthurs Seat State Park (-38°22‟S 144°55‟E) is a 572 ha nature reserve 75 kms south-east of Melbourne with high flora and fauna values (Parknotes). The Seat is a 305 m high peak that sits 1.5 km from the bay shoreline. The geology of the area consists of rocks from the Ordovician period (510 to 435 million years ago) and the Silurian period (435 to 405 mya), granitic outcrops from the Devonian period (370 mya) and basaltic rocks from the Tertiary period (40 to 20 mya). Sediments at Arthurs Seat consist of Tertiary period quartz stones, ferruginous gravel, sand and clays and the younger Quaternary to present day alluvium from inland and coastal water courses (Parknotes). The geology of the steep slopes of Arthurs Seat, where the study site was located, is classified as Devonian granite; the dominant soils are stony Tenosols with some Yellow and Brown Dermosols (VictorianResourcesOnline 2007) and have a generally moderately acid pH of 5.5 - 6.0. The vegetation within the reserve includes open and semi-closed woodland dominated by *E. viminalis*, rocky outcrops and heathland and includes several areas of pristine native vegetation.

The experimental site encompassed 2.3 ha on an NNW facing (approximately 20°) slope. The soil was composed of shallow A horizon of grey clay over a heavy clay B horizon at approximately 5 cm deep. The site was located within a Mediterranean climatic area with mean monthly maximum temperatures ranging from 14°C in July to 27°C in February and minimum temperatures ranging from 6°C in July to 18°C in February. The total annual rainfall at Mornington (-38.27°S, 145.07°E) was 858, 522, 714 and 675 mm in the experimental years of 1996, 97, 98 and 99 respectively, compared to the long term average (from 1889 to 1999) of 734 mm yr^{-1}. The northern half of the site comprised shorter boneseed plants amongst bracken with an open tree canopy. The southern half was dominated by tall, dense boneseed and had more tree cover. Where near-monocultures of boneseed occur at Arthurs Seat (Figure 3.1a), their habit was similar to that of monocultures in the You Yangs site (Figure 3.1b and c, also see description below). However, due to light deprivation by the semi-closed canopy of the eucalyptus over-storey, boneseed stands often grew taller and less densely than at the You Yangs. This allowed a greater abundance and species diversity of native vegetation to survive and a build up of plant litter amongst boneseed plants. The field site location was not burnt in the January 1997 wildfire, but was burnt in the 1983 Ash Wednesday bush fires.

3.1.1.2 Degraded open woodland site

The You Yangs Regional Park (-37°56‟S 144°26‟E) near Geelong, 55 kms south-west of Melbourne, has had a multi-use history including: sand mining, grazing, blocks of plantation trees, a small school and its current primary use of recreation (Parknotes; Pescott 1995). The You Yangs are a granitic outcrop (maximum elevation 364 m) surrounded by colluvial slopes and basaltic lava plains (Parknotes; DPIVictoria 2003). The park retains many native flora and fauna species but is highly degraded in many areas, due to dense boneseed infestation of 1300 ha of the 2000 ha park (Bray 2006), particularly on the slopes. The principal conservation function of the park is the preservation of populations of the rare orchid *P. truncata* (Pescott 1995), a species that is threatened by boneseed (Bray 2006). *P. truncata* has been found in only one other location outside the You Yangs and is therefore considered to be of high conservation value. Currently, 40 hectares of the You Yangs have a high priority for boneseed control for this reason (Bray 2006). The park vegetation consists of open woodland including areas dominated by *A. mearnsii*, *Acacia paradoxa* DC. and *Acacia pycnantha* Benth.. Boneseed was planted at the You Yangs in the 1950‟s and 1960‟s to control erosion (Bray 2006). In the 1950s there was a dramatic increase in boneseed density at the You Yangs, following the control of rabbit populations and removal of domestic livestock (Pescott 1995). Dense boneseed infestations have resulted in little to no vegetation existing beneath boneseed plants (Figure 3.1b and c) and many original mid-storey species are now locally extinct (Bray 2006).

The experimental site was located in an area with almost complete boneseed cover and encompassed approximately 10 ha of the upper, mid and lower parts of a north facing hill slope. The soil profile consists of an A horizon of coarse sandy soil generally slightly acid pH

6.0 - 7.0, above a coarse, pebbly granitic B horizon at variable depths overlying granite rock formations. Large granite surface boulders occurred every 5 to 10 m. The You Yangs Regional Park has a Mediterranean climate with mean monthly maximum temperatures ranging from 15°C in July to 28°C in February and minimum temperatures ranging from 4°C in July to 17°C in February. Rainfall data for this site was available from two nearby locations, Avalon Airport (10 km from the You Yangs experimental site) and Laverton (30 km from the site). Total annual rainfall in the experimental years of 1996, 1997, 1998 and 1999 was 441, 291, 398 and 455 mm respectively, as measured at Avalon Airport, and 502, 332, 461 and 485 mm respectively, as measured at Laverton. Rainfall throughout the experimental duration was lower than the long-term average (from 1940 to 1999) of 554 mm yr^{-1}, as measured at Laverton. In particular, winter rainfall (June, July and August) in 1997 (56 mm) was less than half the long-term winter average and the low rainfall between 1997 and 1998 occurred during the post-fire seedling establishment period. The field site location was burnt by wildfire in 1985. The 1985 wildfire caused a rapid expansion of the boneseed population density and distribution at the You Yangs due to mass stimulation of seed germination, an abundance of space for new plant growth and no boneseed control occurring in the park during the three years after the fire (Bray 2006).

a) species rich site

b) degraded site

c) degraded site

Figure 3.1 Appearance of boneseed infestations prior to experimental weed control treatments at **a)** the species rich and **b)** and **c)** the boneseed degraded experimental sites. Manual boneseed removal has occurred at front edge of infestation in a) resulting in a ground cover of native species.

3.1.2 Experimental design

3.1.2.1 Species rich site experimental layout

An approximately 2.33 ha species rich (SR) site was set up at Arthurs Seat in the Mornington Peninsula State Park, with six 30 m transects running parallel with the contours of the hillside, that is, horizontally across the slope. The site was divided into two „areas" based on a visual and measured assessment of boneseed vegetation structure differences (see Tables 3.3 and 3.4). Species rich site areas 1 and 2 each contained three transects and each transect included six replication plots for experiments. Six 1.5 m^2 plots were randomly placed along each transect, three above and three below the transect line. Each plot was divided into four sub-plots, each with side lengths of 62.5 cm. There was a 30 cm wide cross-shaped buffer zone in each plot, between the four subplots.

3.1.2.2 Degraded site experimental layout

Experimental plots of 12 m^2 were set up prior to the controlled burn at the degraded (D) You Yangs site. Plots were grouped into 5 blocked „areas" according to five visually determined and measured boneseed population structure differences (see Tables 3.3 and 3.4). There were six treatment plots per block/area giving a total of 30 treatment plots across the experimental site.

The term „area" is therefore used throughout this thesis to refer to the grouped sets of plots at each site that are used for experimental replication. Plots were replicated five times at the degraded site and six times at the species rich site.

3.1.3 Experimental timetables and treatments applied at each site.

Pre-fire vegetation descriptions, including pre- and post-fire soil seed sampling, implementation of controlled burning, application of herbicide treatments, and manual plant removal treatments were undertaken at each of the two experimental sites according to the below timetables (Figures 3.1 and 3.2). The distribution of native grass seed was also undertaken at the species rich site after burning (Figure 3.1). Treatment effects on boneseed seedlings, bare ground, some native plant species and groups and secondary weed species were also counted and assessed according to the below timetables.The timing of controlled burns was highly dependant on all three factors of, suitable weather conditions, the priority of the burn compared to other controlled burns being undertaken by Parks Victoria staff, and the consequent availability of staff, fire trucks and equipment. The Arthurs Seat site in particular is located in a semi-urban bushland area and, after several false starts, all requirements for burning were finally met and the burn took place 14 months after the commencement of this study. The timing of herbicide treatments was dependant upon rainfall at each site and the subsequent growth rates of post-fire emergent boneseed seedlings. Herbicide treatments and the later handpulling of flowering boneseed plant treatments, were timed to occur prior to post fire seed set in order to prevent the entry of fresh propagules into the soil seed bank (Tables 3.1 and 3.2).

Table 3.1 Treatment application and data collection timetable for experimental plots at the species rich closed woodland site.

1997		1998		1999	
Jan		Jan		Jan	
Feb	Pre-fire vegetation sampling Pre-fire mature boneseed pulled to dry on ground	Feb		Feb	
Mar	Pre-fire soil seed data collection	Mar		Mar	
Apr		Apr	Controlled burning Distribution of seed of *P. sieberiana*	Apr	Late herbicide application
May		May		May	Hand-pulling of flowering boneseed seedlings treatment Vegetation data collection
June		June		June	Soil seed data collection
July		July		July	
Aug		Aug	Vegetation data collection Early herbicide application Soil seed data collection	Aug	
Sept		Sept		Sept	Vegetation data collection Soil seed data collection
Oct		Oct	Vegetation data collection	Oct	
Nov		Nov		Nov	
Dec		Dec		Dec	

Table 3.2 Treatment application and data collection timetable for experimental plots at the degraded open woodland site.

1997		1998		1999	
Jan		Jan		Jan	
Feb	Pre-fire vegetation sampling Pre-fire soil seed data collection	Feb		Feb	
Mar	First controlled burn attempt	Mar		Mar	
Apr	Boneseed in unburnt areas slashed Second controlled burn attempt	Apr	Vegetation data collection	Apr	
May		May		May	
June	Vegetation data collection	June		June	
July	Soil seed data collection	July		July	
Aug	Early glyphosate or metsulfuron-methyl herbicide application	Aug	Late glyphosate or metsulfuron-methyl herbicide application	Aug	
Sept		Sept	Hand-pulling flowering boneseed seedlings treatment	Sept	Vegetation data collection Soil seed data collection
Oct	Vegetation data collection	Oct		Oct	
Nov		Nov		Nov	
Dec		Dec	Vegetation data collection	Dec	

3.1.4 Description of boneseed infestations and native vegetation within each site: density, fuel loads, soil seed banks and native ecosystem degradation

Boneseed infestations were allocated to treatment blocks/areas at the degraded site and three transects each within areas at the species rich site, based on the population structure of the boneseed and of the native vegetation (see this section and also Part 2 of this chapter). Within each block/area, the vegetation biomass, size structure, live or dead composition and the litter layer and soil seed bank were sampled. Sampled parameters are then compared across blocked boneseed infestation types.

3.1.4.1 Boneseed population canopy structure and cover, presence of native species, presence and type of litter

Measurement of existing pre-fire vegetation at the degraded open woodland site was undertaken using non-destructive point quadrat sampling. Two 10 m transects were set up 1.5 m inwards from two opposite edges of each of the 30 treatment plots. A 3 mm diameter, 2 m high stainless steel rod was placed vertically every metre along each ten metre transect. The plant species that touched the pole at any point, and the number of times that that species (rather than individual plants) touched the pole were recorded as measurements of plant diversity and density (Bowman et al. 2001). Boneseed height, litter depth and the principal components of the litter were also recorded at each measurement point. Point quadrat sampling was also undertaken at one metre intervals along each transect at the species rich site, however unfortunately data for that site became unavailable.

3.1.4.2 Boneseed biomass, litter and boneseed plant size frequency distribution

Vegetation and litter biomass were collected from eight 1.5 m^2 paired plots at the species rich closed woodland site and from fifteen 1.5 m^2 paired plots at the degraded open woodland site. The material collected was divided (on site) into live and dead plant material. All litter within the 1.5 m^2 frame was also separately collected. The lowest 3 to 4 cm of live or dead boneseed stems protruding from the ground were cut off and collected separately. The diameter of these stems was later measured using digital callipers. The remaining live and dead vegetation collected was air-dried for several months, before being divided into fine (width <6 mm), medium (width 6-25 mm) and coarse (width>25 mm) fuel load classes (Bradstock and Auld 1995), oven dried and weighed.

3.1.4.3 Soil cores for seeds of boneseed and native species

Soil cores were taken prior to burning (see Table 3.3 and Chapter 4, Table 4.2), in order to ascertain the initial boneseed soil seed bank. Fresh seed was also separated from soil cores at the end of each experiment, to compare soil seed bank replenishment after burning (at both the species rich and degraded sites) and treatments (at the degraded site only). had been applied. At the species rich site, soil cores were taken using an 11 cm diameter by 15 cm deep soil auger. Fifteen soil cores were taken from (pre-determined) random positions along each of the six transects. At the degraded site, soil cores were taken from two, ten metre long, parallel transects on opposite sides of each treatment plot. This design left the central area of each plot available for placing vegetation-sampling quadrats. The soil cores were taken using the same auger as above, placed at ten random positions along each transect.

Soil cores were placed in plastic bags, labelled and stored in a cool dry room prior to being sieved. Two sieve sizes were used when extracting boneseed seeds from soil cores. The first sieve, for separating out large biomass, had a mesh aperture of 6.35 mm. The second sieve extracted whole and fragmented boneseed seeds, and had a mesh aperture of 3.35 mm. Whole seeds were cut open with secateurs to determine their viability as assessed by having „filled" (Bender et al. 2003), „turgid and normal" (Norcini and Aldrich 2008) pale green embryos. Although far more time consuming, this procedure was deemed more reliable than the use of Tetrazolium (TZ) germination tests of seed viability, due to reported inconsistencies with TZ tests (Norcini and Aldrich 2008). Seed fragments were recorded as either 1/3 or 2/3"s of a seed. The number of seeds in each core was used to calculate the number of seeds m^{-2}.

3.1.5 Pre-burn vegetation preparation, burn conditions and implementation methods at the species rich and degraded sites

The degraded open woodland site was burnt in autumn 1997, in horizontal strips from the top of the slope working towards the bottom. The first burn attempt (F1) was on 26th March 1997. Due to difficulty experienced with burning the boneseed plants only part of the site was burnt. Slashing (brushcutting) was then undertaken in blocks 1 and 3 (infestation sub-types 1 and 3). A second burn (F2) was undertaken three weeks after the first (on 17th April) in areas of unburnt boneseed. This second burn was undertaken in the brushcut block 1 and 3 areas and in the uncut block 4 area (infestation sub-type 5).

At the species rich closed woodland site, mature standing boneseed plants were hand-pulled 14 months prior to burning (in April 1998). This was done in an attempt to create an even, self-perpetuating burn.

3.1.6 Controlled burn measurements

The temperature of each controlled burn was measured using both thermocouples connected to electronic dataloggers and thermo-sensitive mineral crayons.

3.1.6.1 Dataloggers

The temporal charactaristics of each controlled burn were logged using electronic dataloggers attached to thermocouples. This provided a measure of the duration of the temperatures experienced on the litter surface and at 2, 4, 6 and 8cm depth in the soil profile. Three dataloggers (Data Electronics brand, „Datataker 50®") were used at each experimental site. The dataloggers were connected to 10 m thermocouple wires through holes that were drilled and silicon sealed in the side of the dust proof cases in which each logger was placed when buried in the burn area.

Ten thermocouples were used with each of the three dataloggers. Each datalogger had five analogue channels that were split so that both positive and negative were in a circuit with the ground, effectively meaning that ten channels could be used for measuring temperatures. A separate digital channel was also programmed as an „on/off" switch. The ten wires connected to each logger were divided into two groups of five. The five wires were placed on the litter surface, then 2, 4, 6 and 8 cm below the soil surface. This was done by hammering a trowel vertically into the ground, thereby creating a sheer face of soil, then digging out a small trench in front of the trowel. A flat metal peg replaced the trowel with five pre-drilled holes placed at 2 cm intervals along it and through which the wires were threaded and pushed into the soil (Moore pers. comm..). Each of the ten analogue channels was programmed to record temperature every five seconds for over ten hours, giving a temperature profile before, during and after the fire front passed over the wires (Moore 1997).

3.1.6.2 Aluminium thermo-sensitive mineral crayon envelopes

Shavings of temperature sensitive mineral crayons, otherwise known as thermo-crayons (BOC gases, „Templstik®"), were placed into grooves on an aluminium flashing envelope, then taped into place. The aluminium flashing was then folded over to enclose the strips, folded at the edges, and pinched shut using pointy nosed pliers. Four thermo-crayon envelopes were placed in pairs in the biomass plots and in all treatment plots. Twelve different temperature sensitive crayons were used with melting points of: 60^o, 85^o, 100^o, 120^o, 150^o, 180^o, 200^o, 250^o, 320^o, 450^o, 500^o and 700^o Celsius.

The dry weights of the destructively sampled plots at each site (see Chapter 3) were expected to be similar to that of their respective unsampled pair plots. The thermo-crayon temperature sensors were placed in the unsampled plots, on the litter surface and at approximately 3 cm below the soil surface. This was done to investigate whether a correlation could be drawn between the amount and type of standing vegetation or litter present, and the temperature at which that biomass burnt during the subsequent controlled burn.

3.1.6.3 Assessment of degree of burning of boneseed seeds at the degraded open woodland site

Scoring 20 seeds taken from the soil surface of each quadrat compared burning in quadrats. The seeds were collected after burning in June 1997 from twenty randomly chosen intersections of the quadrat strings. Seeds were categorised as unburnt, semi- burnt or completely charcoal. This method was used to investigate the possible correlation between the degree of burning experienced by a quadrat and the number of seedlings that subsequently germinated in that quadrat.

3.1.6.4 Species rich closed woodland site

The timing of the application of two herbicides, glyphosate and metsulfuron-methyl, was investigated at the species rich closed woodland site. Separate plots were treated with one of the two herbicides at 5 months after burning (August 1998 – at the end of the first growth season for boneseed) or at 12 months after burning (April 1999 – at the beginning of the second growth season for boneseed).

Flowering seedlings were hand-pulled in May 1999, 14 months after the controlled burn. Seedlings were pulled from 12 plots that had previously been sprayed with herbicide (6 with each of the two herbicides) and 6 plots that had not been sprayed. At the species rich site, a sub-sample of one in ten flowering seedlings were oven dried at 60-80^{o}C for at least 48 hours. The basal stem diameter (using digital callipers), above-and below-ground (stem and root) dry weight and the number of buds, flowers, developing ovules and seeds per seedling were measured.

Grass seed was spread on the post-fire ash bed in subplots within each treatment, two weeks after burning for *P. sieberiana* (approximately 100 seeds of this C3 grass species) and five months after burning (and prior to the optimal summer growth period) for *T. triandra* (approximately 400 seeds of this C4 grass species) (Table 5.1). The seed of the two native grasses species was distributed after controlled burning to investigate whether increased densities of grass could reduce the number of boneseed seedlings. The seed was spread by hand in parallel lines and then in perpendicular parallel lines across each designated sub-plot. Grass cover at Arthurs Seat was recorded at the data collection times 1 and 2 (Table 5.1) as a percentage cover for each grass species, as well as total percentage cover of all grass species. Grass height and density were recorded at data collection times 3 and 4 (Table 5.1). Subplot treatment data at this site were then divided into subplot treatments with or without *P. sieberiana* added, as *T. triandra* plants failed to establish.

Soil cores were taken along transects prior to burning, and again after burning in August 1998, May 1999 and September 1999. Vegetation data was collected from all sub-plots after controlled burning, in August 1998, October 1998, May 1999 and September 1999.

3.1.6.5 Degraded open woodland site

The most effective timing for herbicide application at the degraded site was investigated by treating 12 separate plots at 5 months (August 1997 - herbicide application 1) and 12 plots at 17 months (August 1998 - herbicide application 2) after the fire. Applying herbicides 5 months after burning was expected to have an impact on the greatest number of the seedlings, including those that had germinated both after burning and after the first spring growth season. Treatments at 17 months were intended to control seedlings just before flowering and seed set. Flowering usually occurs at between 12 and 18 months of growth depending on climatic conditions. The seedlings experienced water deficiency stress during the summer following burning and flowering was delayed until around 17 months after burning (Table 5.2).

Flowering seedlings were hand-pulled 17-18 months (September 1998) after fire from plots that had either received herbicide 5 months after fire, or had not had any herbicide applied to plots. Hand-pulled seedlings were collected, dried and measured as for the species rich site (see above).

Soil cores were taken before burning in February 1997, then after burning in July 1997 and September 1999. Vegetation data (species counts and cover assessments) were collected after burning from all plots at June 1997, October 1997, April 1998, December 1998 and September 1999.

3.1.7 Herbicide application treatment

3.1.7.1 Herbicide application methods

At five months after fire, the emerged boneseed seedlings were at the cotyledon stage of growth, and it was feasible to use a 2 m long gas pressurized handheld boom sprayer. By 17 months after burning at the degraded site and 12 months after burning at the species rich site, boneseed seedlings were taller and so a gas powered handgun sprayer was used. Boneseed seedlings were sprayed to wetting point. As stated in Chapter 2, literature review, the two herbicides investigated in this study for use on boneseed seedlings growing in native vegetation differ in their known selectivity. Glyphosate is a broad spectrum herbicide and metsulfuron-mehtyl is a broadleaf sensitive herbicide. Herbicide rates for applications for the second growth season were higher than the application rates for the first growth season due to the larger size of the boneseed seedlings.

3.1.7.2 Species rich site herbicide application rates

Early herbicide application (August 1998): Metsulfuron-methyl was applied at 20 g product (12 g a. i.) ha^{-1} in a volume of 400 L ha^{-1} with 2 % Pulse® penetrant. Glyphosate was applied at 720 g a.i. ha^{-1} in 400 L with 2 % Pulse® penetrant.

Late herbicide application (April 1999): Metsulfuron-methyl was applied at 6 g per 100 L solution. Spray volume varied between 0.7 and 0.3 litres per 1.5 m^2 plot. Glyphosate was applied at 720 g a.i. per 100 L solution. Spray volume varied between 0.1 and 0.2 litres per 1.5 m^2 plot.

3.1.7.3 Degraded site herbicide application rates

Early herbicide application (August 1997): Metsulfuron-methyl was applied at 6 g a.i. ha^{-1} with Pulse® penetrant added at 0.2 % v / v and made up with water to a spray volume of 400 L ha^{-1}. Glyphosate was applied at 360 g a.i. ha^{-1} and a spray volume of 400 L ha^{-1}.

Late herbicide application (August 1998): Metsulfuron-methyl was applied at 6 g active per 100 L solution with 0.2 % Pulse® penetrant. Spray volume varied from 3.7 to 4.2 litres per 12 m^2 plot. Glyphosate was applied at 720 g a.i. per 100 L solution with 0.2 % Pulse® penetrant. Spray volume varied from 2.8 to 3.9 litres per 12 m^2 plot.

3.1.8 Plant recording techniques

Throughout the experiments the number and/or cover of boneseed, native species, other weeds, and bare ground were recorded in quadrats within treatment plots.

3.1.8.1 Quadrat counting frames

At the degraded site, a 1 m^2 quadrat frame was divided into 64 squares of 12.5 cm^2 using string. At the species rich site the quadrat frame was 62.5 cm^2, as this was the size of sub-plots at this site and had 25 squares of 12.5cm^2.

3.1.8.2 Quadrat placement within treatment plots

At the degraded open woodland site quadrats were randomly placed in plots using 1 m coordinates on a 9 m^2 grid in the centre of each 12 m^2 plot. Six quadrats were placed on the burnt areas of each plot, and six additional quadrats were placed in any plots that contained unburnt areas. Burnt patches within a plot that were large enough to fit one or more quadrats were assigned numbers for each possible quadrat placement. These numbers were combined with any random grid coordinates that also fell on burnt areas and six quadrat locations were chosen from all possible placements.

At the species rich closed woodland site, six 1.5 m^2 plots were randomly assigned a 1.5 m interval position along the permanent transects. Trees or logs were avoided by flipping the frame into the closest available position. Three plots were located 0.5 m above and three were 0.5 m below each transect on the hill slope.

3.1.8.3 Boneseed plant parameters recorded at both sites

Across both sites, the numbers of boneseed seedlings were counted as the number of growing tips present per quadrat. The height of boneseed seedlings was recorded at the last two measurement times for each site. Heights were recorded using a rigid ruler for the tallest, shortest and tallest majority height of seedlings over four quadrat squares combined. Boneseed cover was estimated over each quadrat.

At the end of the experiment at the degraded site the number of first year flowering boneseed plants m^{-2} and the amount of new seed m^{-2} on the soil surface were compared. This was done to assess how much new seed was entering the soil seed bank and how many mature plants were contributing new seed. At the species rich site, soil core transects were outside treatment plots, so new seed recovered in the soil cores taken at the end of the experiment was representative of weed control plots, as the transects received burning but no post-burn weed control treatments.

3.1.8.4 Native vegetation and secondary weed parameters recorded and methods of recording for both sites

Experimentation sought to determine whether applying a low dose of glyphosate to the post-fire emergent boneseed seedlings, prior to the emergence of native species, would enable the native plant species to survive. Although metsulfuron-methyl only targets dicotyledonous species, and therefore should be tolerated by native grass species, it is soil active, and so the influence of an early low dose application was investigated. Both herbicides were also spot sprayed onto older boneseed seedlings after the second growth season in order to identify whether this timing and reduced direct herbicide contact would improve native seedling survival.

The number of seedlings of the invasive climber *B. heterophylla* (Figure 3.3) and woody native species (*Acacia* spp., *Eucalyptus* spp. and *Prostanthera nivea* A.Cunn. ex Benth.) were counted as the number of growing tips present per quadrat. At the degraded site, grasses, herbaceous species including annuals and other weeds, bryophytes (mosses) and the native rock fern *Cheilanthes austrotenuifolia* H.M. Quirk & T.C. Chambers were all recorded as present or absent in a square rather than as cover, due to their small size. Additional notes were made of large *A. calendula* diameters and/or if a particular plant covered other squares in addition to the one in which it was recorded as being present. At the species rich site, there were a greater number and cover of species other than boneseed than at the degraded site. As well as this greater natural abundance of other species, native grass seed had been distributed on three of the four subplots per plot. Consequently, grasses, herbaceous species, annuals and the bracken fern *Pteridium esculentum* (G.Forst.) Cockayne were recorded as a percentage cover. Grasses were recorded as a percentage cover at the earlier recording dates. However, due to vigorous plant growth at this site, by the later recording dates, the cover of individual grass species, total grass cover, and other species cover, was recorded as a percentage cover for the whole quadrat. Grass height and density were also recorded later in the experiment.

Figure 3.3 Flowering *B. heterophylla*, the main secondary weed at the species rich site, and juvenile boneseed seedlings (lower right hand corner).

3.1.9 Statistical analysis used throughout this thesis

3.1.9.1 Statistics used in Chapter 4

A general analysis of variance with randomised blocking (ANOVA, (Genstat 2002)) was performed to ascertain whether significant differences existed in the numbers of viable boneseed seeds found in the soil within sites, before and after the occurrence of fire (Quinn and Keough 2002). Data were square root transformed in order to fit the assumptions of a Gaussian distribution (Genstat 2002)) (Sokal and Rohlf 1981). Transformation of data was required for this test as the residuals from an initial application of ANOVA did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data. Data were back transformed for display.

3.1.9.2 Statistics used in Chapter 5

For both experimental sites, an analysis of variance with covariates (ANCOVA) (Quinn and Keough 2002) was used to test for significant differences (P<0.05) between treatments at and between each measurement time. Data for both sites were balanced and satisfied the requirements of performing the ANCOVA test (Lorimer 2001) (Kenward 1987) . The number of measurement times required to be used as covariates was ascertained by performing an anti-dependence test (anti-dep.) (Genstat 2002). „Contrast" analyses were performed between treatments at a given time to find the level of statistical significance between those groups (Kenward 1987; Hancock 2000; Lorimer 2001) . The experimental approach at both sites was to adapt weed control treatments to the biotic and abiotic conditions of the site as they changed over time. The timing of implementation of initial controlled burning was also highly dependent on weather conditions and the practicalities of the priorities and availability of staff and heavy fire fighting equipment, as is the case for any ecological burning. Due to this adaptive approach, the timing of treatments and vegetation counts/sampling did not occur at regular intervals and the subsequent statistical analyses were complex. We are grateful for the assistance of Michelle Lorimer and others at Biometrics SA for their help in analysing the effects of treatments on boneseed seedlings over time at both experimental sites. (See Tables 5.2 to 5.7 and Tables 5.11 to 5.14). The numbers of boneseed seedlings present over time after burning are presented with lower case letters denoting significant differences between treatment effects *at* each sampling time, in Table 5.2 (species rich site) and Table 5.5 (degraded site) and the percentage changes in boneseed plant numbers *between* each sampling time, in Table 5.3 (species rich site) and Table 5.6 (degraded site). The consequences of the timing of application of different weed control treatments to areas with more or less boneseed seedlings and more or less favourable rainfall are then discussed in the discussion section of chapter five.

Percentage boneseed ground cover in treatment plots and subplots at the species rich site was analysed using a split-plot ANOVA (Genstat 2002). Data were arcsine transformed to fit assumptions of a Gaussian distribution, as determined by normal and residual plots (Genstat

2002; Quinn and Keough 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data.. Control and hand-pulled flowering boneseed seedling treatments only were compared. The early glyphosate herbicide treatment was excluded from the analysis, as subplots with *P. sieberiana* added were not sprayed due to the assumption of total grass mortality after glyphosate application (Culpepper and York 1998) at the rate used for these experiments.

Mean boneseed seedling heights in treatment plots and subplots at the species rich site were analysed using a split-plot ANOVA (Genstat 2002; Quinn and Keough 2002). Data were log (x + 1) transformed to fit assumptions of a Gaussian distribution, as determined by normal and residual plots (Genstat 2002; Quinn and Keough 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data..

The mean number of first year flowering boneseed plants m^{-2} in treatment plots and subplots at the species rich site was analysed using a split-plot ANOVA (Genstat 2002; Quinn and Keough 2002). Data were square-root (x + 1) transformed to fit assumptions of a Gaussian distribution, as determined by normal and residual plots (Genstat 2002; Quinn and Keough 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data.

For the degraded site, boneseed ground cover was compared for all treatments using a one-way ANOVA with randomized blocking (Genstat 2002). Data were arcsine transformed to fit assumptions of a Gaussian distribution, as determined by normal and residual plots (Genstat 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data.

Mean boneseed seedling heights in treatment plots at the degraded site were analysed using a general ANOVA with randomized blocking (Genstat 2002; Quinn and Keough 2002). Data were untransformed as they fitted the assumptions of a Gaussian distribution, as determined by normal and residual plots (Genstat 2002; Quinn and Keough 2002).

The mean number of flowering boneseed seedlings m^{-2} in treatment plots at the degraded site were analysed using a one-way ANOVA with randomized blocking (Genstat 2002) (Quinn and Keough 2002). Data were $\log(x + 1)$ transformed to fit assumptions of a Gaussian distribution, as determined by normal and residual plots (Genstat 2002; Quinn and Keough 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data.Data from the species rich site were not analysable due to the prevalence of zeros in the data.

At the degraded site the relationships (slopes) between boneseed seedling biomass (dry weight) and the fecundity of each respective flowering seedling was analysed using a regression analysis with groups (Quinn and Keough 2002), on untransformed data for plots in which no prior herbicide had been applied and plots where seedlings had previously been sprayed with either metsulfuron-methyl or glyphosate herbicides.

3.1.9.3 Statistics used in Chapter 6

The number of *B. heterophylla* plants in treatment plots and subplots at the species rich site were analysed using a split-plot ANOVA (Genstat 2002; Quinn and Keough 2002). Data were square-root transformed in order to fit the assumptions of normality as ascertained by normal and residual plots (Quinn and Keough 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data.

The percentage ground cover of *A. calendula* at the degraded site was analysed for control and all treatment plots using a one-way ANOVA with randomised blocking (Genstat 2002; Quinn and Keough 2002). Data were untransformed as they fitted the assumptions of normality as ascertained by normal and residual plots, and therefore the results of an ANOVA using these data could e considered valid (Sokal and Rohlf 1981)

3.2 Measured vegetation charactarisation at experimental sites

The boneseed infestations and invaded native vegetation at each site appeared to contain areas showing different structural charactaristics. The native species rich site contained a mixture of boneseed plants and native species, while the degraded site consisted of native vegetation that had been severely degraded to a near monoculture of boneseed. Structural differences of the vegetation across each boneseed infestation site were also observed (Table 3.3). Two areas of vegetation within the species rich site appeared to have different charactaristics (species rich site areas 1 and 2), as did five areas within the degraded site (degraded site areas 1 to 5). The apparently least degraded ecosystem (species rich site area 1), was comprised of sparsely spaced live boneseed plants that appeared to provide low amounts of ground cover, whereas the most degraded ecosystem (degraded site area 5) was a monoculture of mature boneseed plants that gave continuous ground cover (Table 3.3).

The composition of litter was observed to change within different areas of each site (Table 3.3). At the species rich site, the litter was primarily composed of fine (<6 mm in diameter) native grass, herb and fern material. Also present were fine *E. viminalis* leaves from the tree canopy and sticks and litter from mid-storey native shrubs such as *Cassinia aculeata* A. Cunn. Ex DC.. The litter at the degraded site was mostly composed of coarse and medium sized boneseed material, predominantly boneseed seeds, which were categorised as medium sized biomass (between 6 and 25 mm in diameter – see 3.2.3.2). There were fewer components of native plant species in the litter and appreciably large numbers of boneseed seed on the soil surface at the degraded site (Table 3.5). Litter at the degraded site area 5 was characterised by bare ground with large, old, live boneseed stems (Table 3.3).

At the degraded site, boneseed invasion appeared to have reduced the density and diversity of native species, resulting in a litter layer that was composed predominantly of boneseed debris (Table 3.3). The decrease in cover of native vegetation appeared inversely related to increasing cover of boneseed infestation (Table 3.3).

Table 3.3 Descriptions of boneseed population structures within different areas within each experimental site.

Boneseed infestation site & area within each infestation	Species rich 1	Species rich 2	Degraded 1	Degraded 2	Degraded 3	Degraded 4	Degraded 5
Description of boneseed population structure	Sparse live plants	Boneseed canopy continuous, but not dense	Patchy with many gaps, most plants separate from one another	Mostly continuous boneseed, many dead plants forming layers of sticks 45^{o} to ground	Not continuous canopy, even distribution with no large gaps	Similar to degraded type 3, but boneseed plants and canopy continuous and more dense, no gaps	Tall plants, continuous canopy, no foliage between ground layer and 0.5 to 1m where canopy begins
Litter composition[A]	Bracken fern and native grass litter, also *E. viminalis* leaves and bark	Native grass and herbaceous species, also *E. viminalis* leaves and bark	Patches of native grass litter, patches of boneseed seeds, sticks and leaves	Boneseed seeds, also *A. mearnsii* leaves and sticks	Few boneseed seeds, sticks and leaves, also some *A. mearnsii* leaves and sticks	Few sticks, leaves and bare ground, thick layer of boneseed seeds	100% boneseed seeds, logs and few leaves, also much bare ground
Native & other weed vegetation composition	Bracken fern and native grasses, other monocots and herbaceous species	Native grasses, other monocots and herbaceous species	Patches of grass to 30cm tall	Individual grass tussocks to 30cm	Individual grass tussocks to 30cm	Individual grass tussocks to 30cm	Virtually nil
Groundcover to 1 m by native vegetation & weeds other than boneseed[B]	100%	100%	Nil to 40%	10%	10%	10%	Virtually nil

A Litter components listed in order of decreasing quantity for each boneseed population infestation type and sub-type.
B Vegetation less than 1 m tall. Boneseed mostly formed a thin canopy higher than 1 m.

3.2.1 Measures of structural differences between 'areas' within boneseed populations at each site

The biomass of boneseed plants and the number of boneseed seeds in the soil seed bank were measured to ascertain any differences within boneseed infestations at the species rich and the degraded sites. The composition of the litter layer (fallen and dead biomass up to 50 cm from ground level) and any presence of native species beneath boneseed populations were also measured. These measured parameters were used to support the „area" groupings (blocking at the degraded site and grouping of two groups of three transects at the species rich site, as decribed in the experimental design section 3.2.2), given to boneseed infestations by visual assessment.

3.2.1.1 Standing plant and litter biomass

Standing plant biomass at the species rich site predominantly consisted of fine and medium sized biomass with comparatively low levels of coarse sized matter (Figure 3.4). Within the fine and medium size catagories there appeared to be around double the amount of live standing biomass compared to dead biomass, while within the coarse size category no dead biomass was recorded. Within this site, area 1 appeared to consist of almost double the fine sized biomass and nine times the amount of medium sized biomass of area 2. No coarse sized biomass was recorded in area 2 at this site (Figure 3.4).

Standing plant biomass across the degraded site appeared to consist of around double the fine sized biomass as coarse biomass and just under three times the medium sized biomass as coarse biomass (Figure 3.4). Across the site there appeared to be more dead biomass than medium in both the fine and medium size catagories and an equal proportion of live and dead coarse sized standing biomass (Figure 3.4). Within this site, areas 4 and 5 appeared to consist of similar amounts of standing biomass, which was almost double the amount of standing biomass found in area 1 (Figure 3.4).

Litter biomass at the species rich site appeared to consist primarily of fine sized plant material, with 3.5 times the amount of fine compared to medium sized material recorded (Figure 3.4).

Litter biomass at the degraded site appeared to consist primarily of medium and coarse sized plant material, with more than three times the amount of medium compared to fine sized material found (Figure 3.4). At the degraded site, an increase in mean litter biomass from degraded site areas 1 to 5 was appeared to be associated with an increase in mean boneseed height and density, except at the degraded site infestation area 5 (Table 3.5). An increase in mean litter mass appeared to occur in conjunction with a two-fold increase in litter density (mean litter biomass/litter layer depth) from 0.8 at the degraded site area 1 to 1.9 at the degraded site area 5 (Table 3.4). Boneseed seeds formed a heavy, compact layer on the ground surface and the few scattered boneseed leaves did not confer an aerated litter layer.

Total biomass at the species rich site (6.61 kg m^{-2}) consisted of more litter biomass than standing biomass. As most of the litter was fine sized, and when combined with the greater proportion of fine sized standing biomass than other category at this site, there appeared to be more fine sized plant material present overall than any other size category (total fine sized material, 4.16 kg m^{-2}) (Figure 3.4). Fine sized plant material (available as fuel for burning) appeared to represent 63% of the total plant biomass found at this site, with the majority of that fine fuel being located in the litter layer rather than in the standing boneseed canopy (Figure 3.4).

The total biomass at the degraded site (14.05 kg m^{-2}) appeared to consist of more standing biomass than litter biomass (Figure 3.4). There was more medium sized standing and litter biomass and more coarse sized litter biomass than fine sized biomass at this site. The total amount of fine sized material available as fuel for a fire (3.7 kg m^{-2}) was just under a quarter of the total biomass required to be burnt, and the majority of that available fine fuel was situated in the boneseed canopy rather than in the litter layer (Figure 3.4).

3.2.1.2 Boneseed height

At the species rich site, boneseed plants appeared to be shorter in area 1 where bracken fern was present under the closed eucalypt woodland canopy, than where bracken was absent, in species rich area 2 (Table 3.5). At the degraded site, the heights of boneseed plants appeared to be similar across the site although some areas tended towards taller plants than others (Figure 3.5).

3.2.1.3 Soil seed bank

Prior to burning, at the species rich site (where there was an average of 403 viable boneseed seeds m^{-2}), there appeared to be a greater number of boneseed seeds in the soil in the species rich area 2 (617 $\pm$ 120 viable boneseed seeds m^{-2}) than in the species rich area 1 (189 $\pm$ 49 viable boneseed seeds m^{-2}) (Table 3.5).

At the degraded site there was an average of 2737 viable boneseed seeds m^{-2} prior to the application of burning and weed control treatments, with the average size of the soil seed bank ranging from around 1930 to 2740 seeds m^{-2} across the site (Figure 3.5). The variability in the size of the boneseed soil seed bank appeared to increase with increasing seed bank size (Table 3.5). The maximum number of boneseed seeds in the soil seed bank was found at the degraded site area 3 (19,780 viable seeds m^{-2}); however, high numbers of boneseed seeds in the soil were also found in areas 4 and 5 (Table 3.5).. There was a trend towards more viable boneseed seeds being recorded at the degraded site areas 3, 4 and 5 than were found at degraded site areas 1 and 2 (Table 3.5).

3.2.1.4 Boneseed population canopy structure, cover and plant size frequency distribution

At the species rich site, where boneseed plants grew amongst bracken fern in area 1, the boneseed population was composed only of plants with stem diameters of up to 6 mm, with an average of 5.3 boneseed plants m^{-2} (Table 3.5, Figure 3.4a). Where boneseed was observed to be taller at the species rich site area 2 (where boneseed plants grew up to 3.5 m in height), there were around eight boneseed plants m^{-2}, and there was a trend towards a more evenly distributed range of stem sizes up to 40 mm in diameter (Figure 3.4b).

At the degraded site, in areas 1 and 4, the large soil seed bank (Table 3.5) and good availability of light through the boneseed canopy appeared to enable the growth of many boneseed plants (an average of 60 and 65 plants m^{-2} respectively, Table 3.5), with small stem diameters (up to around 10 mm) amongst a few boneseed plants with much larger stem diameters (up to 60 to 220 mm)(Figure 3.4c and d). The degraded site infestation area 5 had stands containing around 17 boneseed plants m^{-2} (Table 3.5) and there appeared to be fewer boneseed plants with small stem diameters (up to 15 to 20 mm), fewer dead plants, and more large boneseed plants (up to 220 mm in stem diameter) than were found at the other degraded site infestation areas measured (Figure 3.4c, d and e). The number of touches to a single point quadrat through the boneseed canopy appeared to increase across degraded site areas from 1 to 5, implying an increase in the density of the boneseed canopy across these areas (Table 3.5).

Table 3.4 Fine, medium and coarse sized biomass (kg m^{-2} dry weight) in standing boneseed and boneseed litter at the native species rich and degraded experimental sites.

Dry weight (kg m^{-2})	Species rich area 1	Species rich area 2	Total species rich site	Degraded area 1	Degraded area 4	Degraded area 5	Total degraded site
Litter							
Fine [A] litter [B]	*	*	2.72	*	*	*	0.96
Medium [A] litter [B]	*	*	0.78	*	*	*	3.19
Coarse [A] litter [B]	*	*	0.39	*	*	*	2.23
All size classes litter	*	*	**3.88 ± 0.5**	*	*	*	**6.37 ± 0.7**
Standing biomass							
Live fine	0.51 ± 0.05	0.4 ± 0.19	0.91	0.32 ± 0.11	0.18 ± 0.09	0.53 ± 0.17	1.03
Dead fine	0.43 ± 0.08	0.1 ± 0.1	0.53	0.37 ± 0.22	0.83 ± 0.22	0.51 ± 0.19	1.71
Total fine	**0.94 ± 0.11**	**0.49 ± 0.1**	**1.44**	**0.69 ± 0.18**	**1.01 ± 0.21**	**1.04 ± 0.23**	**2.74**
Live medium	0.74 ± 0.09	0.1 ± 0.1	0.84	0.35 ± 0.15	0.43 ± 0.23	0.76 ± 0.28	1.54
Dead medium	0.39 ± 0.16	0.02 ± 0.02	0.41	0.35 ± 0.3	1.22 ± 0.91	0.53 ± 0.18	2.1
Total medium	**1.13 ± 0.24**	**0.12 ± 0.07**	**1.25**	**0.71 ± 0.25**	**1.65 ± 0.16**	**1.29 ± 0.24**	**3.64**
Live coarse	0.04 ± 0.03	0	0.04	0.08 ± 0.06	0	0.58 ± 0.29	0.66
Dead coarse	0	0	0	0.14 ± .014	0.4 ± 0.4	0.12 ± 0.08	0.66
Total coarse	**0.04 ± 0.03**	**0**	**0.04**	**0.22 ± 0.13**	**0.4 ± 0.39**	**0.69 ± .025**	**1.32**
All size classes standing biomass	**2.11 ± 0.32**	**0.61 ± 0.17**	**2.73**	**1.61 ± 0.55**	**3.05 ± 0.33**	**3.02 ± 0.66**	**7.68**
All size classes litter + standing biomass			**6.61**				**14.05**

[A] Biomass size classes: fine kg m^{-2} (<6 mm diameter), medium kg m^{-2} (6-25 mm diameter), course kg m^{-2}(>25 mm diameter).
* Litter not divided to this level
[B] Weights of visually assessed percentages of litter size classes.
Destructive litter and vegetation sampling was undertaken for degraded site areas 1, 4 and 5 only.

Table 3.5 Numbers of boneseed seeds in the pre-fire soil seed bank, native vegetation description and litter composition within boneseed infestation areas within each of the species rich (SR) and degraded (D) experimental sites.

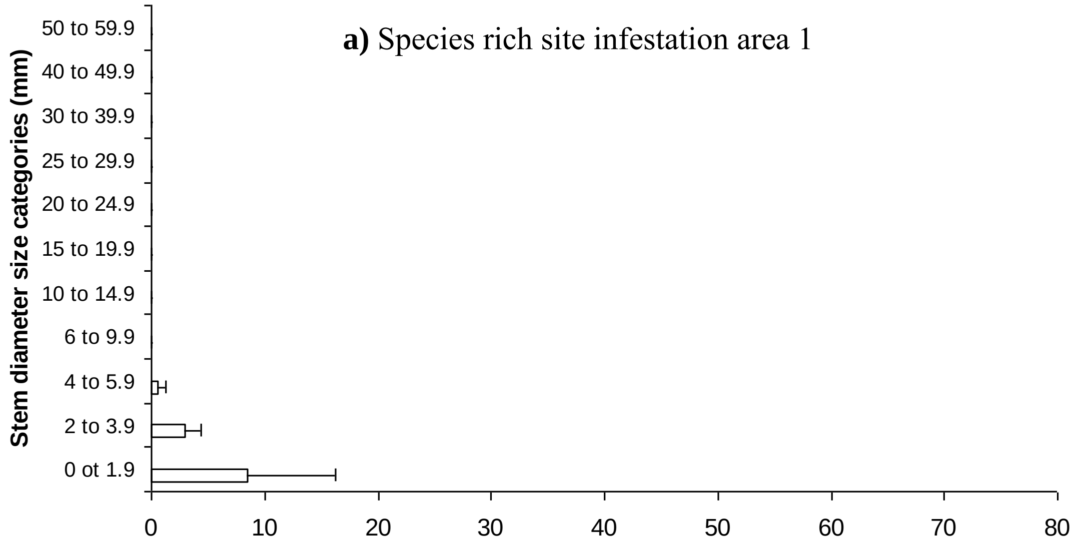
Boneseed population infestation areas and measured structural charactaristics	**Species rich 1**	**Species rich 2**	**Total species rich site**	**Degraded 1**	**Degraded 2**	**Degraded 3**	**Degraded 4**	**Degraded 5**	**Total degraded site**
-mean height (m) [A]	0.7	2.5		1.27	1.17	1.43	1.56	1.82	
-maximum height (m)	1.5	3.5		2.3	1.8	2.25	2.30	2.95	
-boneseed plant density m^{-2} (mean ± s.e.m.)									
- live	5.3 ± 3.1	7.4 ± 1.9		37.2 ± 28.8			29.9 ± 13.9	12.1 ± 4.5	
- dead	0	0.6 ± 0.4		22.3 ± 13.1			34.8 ± 9.5	4.7 ± 4.1	
- total	5.3 ± 3.1	8 ± 2.0		60 ± 29.6			65 ±10.4	16.8 ± 4.0	
- no. vegetation touches [B]				1.89	2.05	2.43	3.68	4.63	
- boneseed canopy density (mean height/touches)				67	57	59	42	39	
- boneseed population ground cover (%)	20	40		40	90	70	70	100	
-boneseed cover: density ratio				0.6	1.6	1.2	1.7	2.6	
Litter depth (cm ± s.e.m.)	3.91 ± 0.31	3.61 ± 0.49	3.75 ± 0.29	4.42 ± 0.57			3.14 ± 0.33	4.85 ± 2.01	4.137 ± 0.68
Viable native seeds in soil [C]	Few Acacia seeds	Few Acacia seeds		None found	None found	None found	None found	None found	
Viable boneseed seeds m^{-2} to 15 cm deep									
-mean ± s.e.m.	189 ± 49	617 ± 120	403 ± 70	1970 ± 246	1926 ± 167	3439 ± 365	2453 ± 451	3604 ± 316	2737 ± 143
-maximum	526	2,315		7,575	8,627	19,780	17,255	16,834	
-minimum	0	0		0	0	0	0	0	

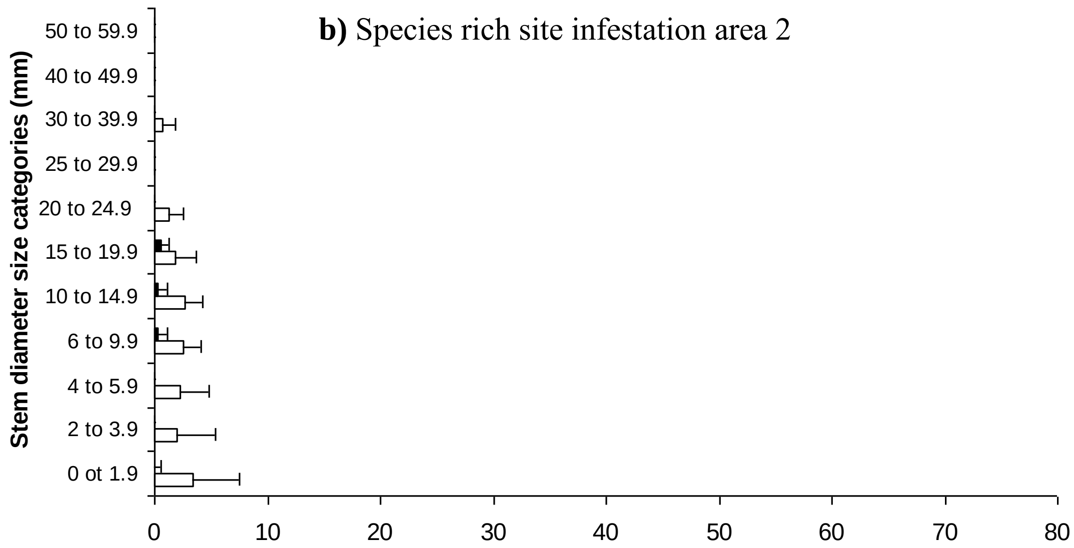
„Areas" are blocked at the degraded site or contain transects at the species rich site, according to the vegetation descriptions found here and in Tables 3.3 and 3.4. „Areas" contain replication plots for experiments.

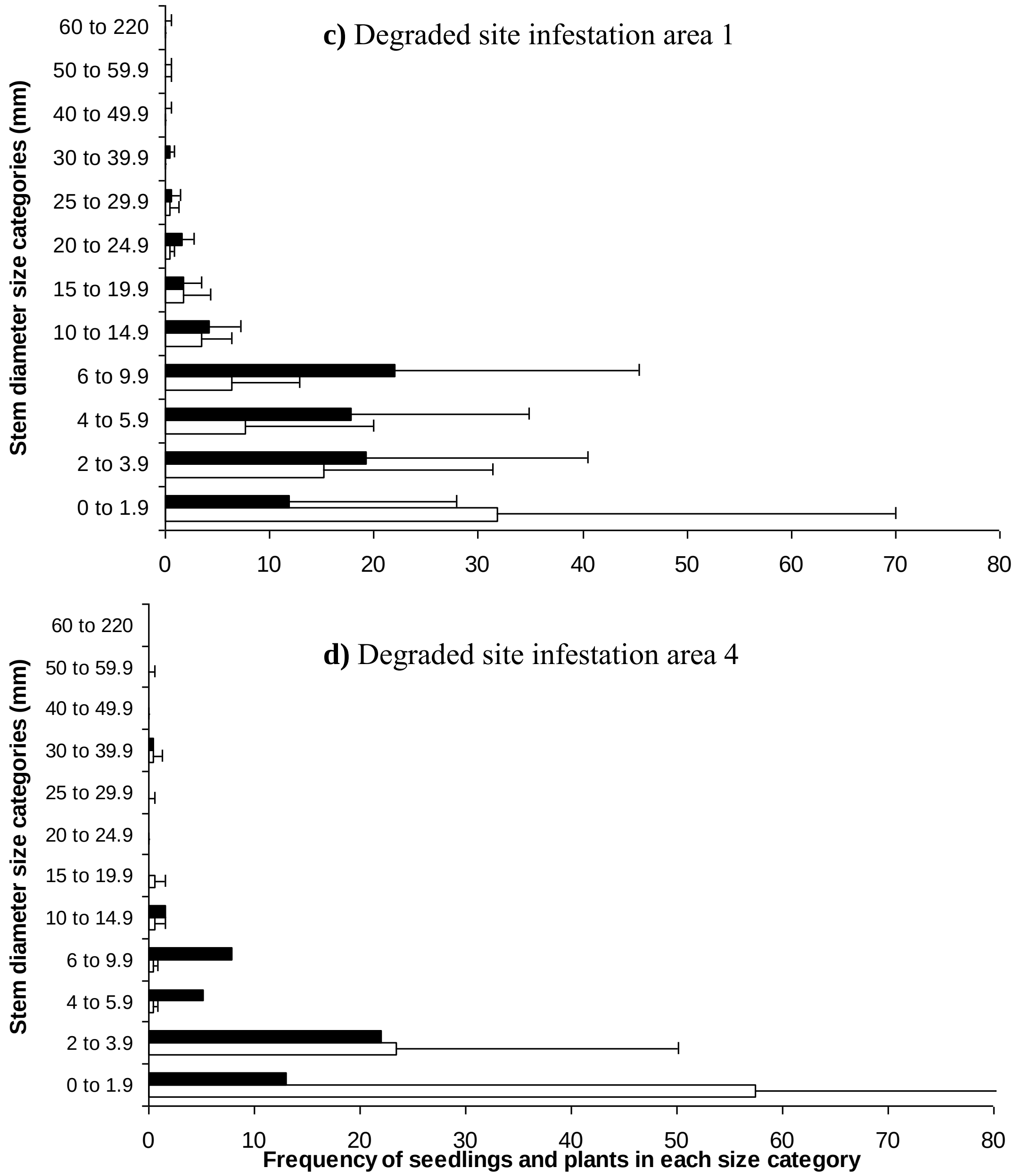
[A] Standand error of means not available for logistical reasons.

[B] Number of vegetation touches to a vertical pole.

[C] At the species rich site the dominant tree species, *E. viminalis,* has canopy stored seed.


a) Species rich site infestation area 1
Stem diameter size categories (mm)
50 to 59.9
40 to 49.9
30 to 39.9
25 to 29.9
20 to 24.9
15 to 19.9
10 to 14.9
6 to 9.9
4 to 5.9
2 to 3.9
0 ot 1.9
0
10
20
30
40
50
60
70
80


b) Species rich site infestation area 2
Stem diameter size categories (mm)
50 to 59.9
40 to 49.9
30 to 39.9
25 to 29.9
20 to 24.9
15 to 19.9
10 to 14.9
6 to 9.9
4 to 5.9
2 to 3.9
0 ot 1.9
0
10
20
30
40
50
60
70
80


c) Degraded site infestation area 1
d) Degraded site infestation area 4
Stem diameter size categories (mm)
60 to 220
50 to 59.9
40 to 49.9
30 to 39.9
25 to 29.9
20 to 24.9
15 to 19.9
10 to 14.9
6 to 9.9
4 to 5.9
2 to 3.9
0 to 1.9
0
10
20
30
40
50
60
70
80
Frequency of seedlings and plants in each size category

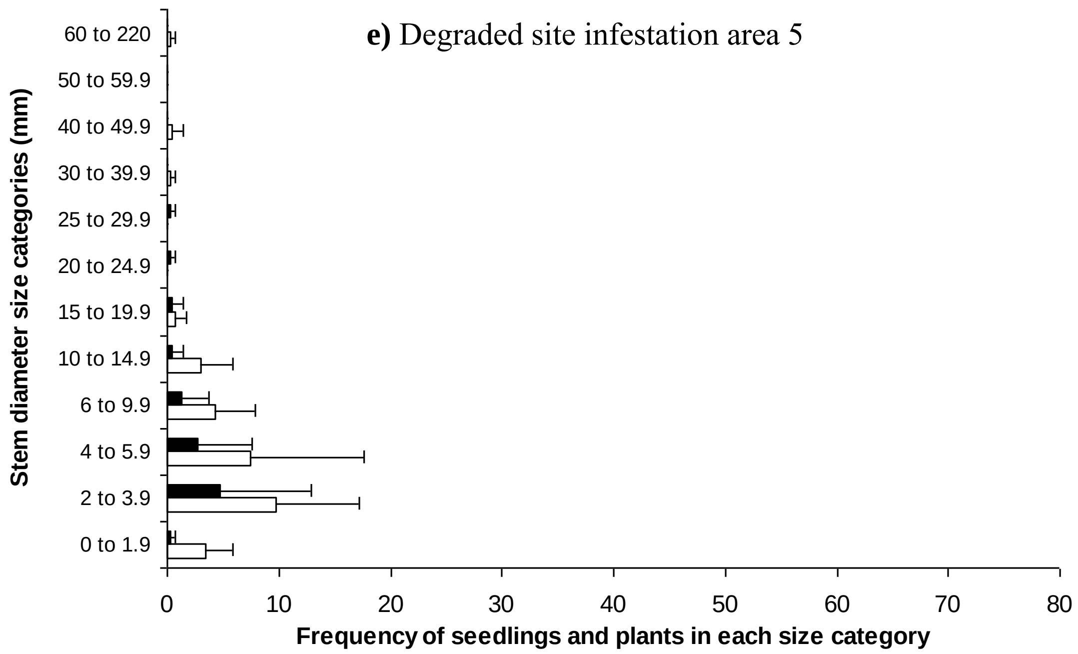


Figure 3.4 Average stem diameter (mm) distribution of live (open bars) and dead (solid bars) boneseed plants at species rich boneseed infestation areas 1**(a)** and 2**(b)**, and degraded infestation areas 1 **(c)**, 4 **(d)** and 5 **(e)**. Error bars show standard deviation from the mean.

3.3 Vegetation descriptions

Boneseed infestations appeared to display a variety of population structures and a range of numbers of viable seeds in the soil seed bank across the experimental sites. Pre-treatment vegetation was described by comparing means for numbers of seeds in the soil, the amounts of boneseed vegetation in live and dead biomass size categories, average boneseed heights, the mean total number of live and dead plants, and the dry weight of the litter layer.

Notable variations in the structural charactaristics of the boneseed populations included the species rich Arthurs Seat State Park site having a trend towards a lower mean total boneseed biomass, a generally lower overall mean litter weight (Table 3.2), a corresponding higher proportion of fine sized litter (Table 3.2) and the lower number of viable seeds in the soil. These charactaristics supported the initial visual assessment that the area had suffered a limited amount of degradation due to weed invasion and remained native „species rich". The corresponding opposite reasoning supported the designation of the label „degraded site" to the infestation found at the You Yangs Regional Park. The species rich site was recognisable by the mixture of boneseed and a range of native species present, both in the standing vegetation and in the litter layer.

The degraded site was represented by almost monoculture boneseed with bare ground covered only with a few scattered boneseed leaves and sticks. Native species existed in small patches; however, for the most part the boneseed population at the degraded site was characterized by reduced light availability at ground level, which was observed to be a result of a dense ground cover by the boneseed plant stems and canopy. The degraded woodland site had a trend towards a larger mean total biomass m^{-2} of litter than the species rich site, with that litter consisting mostly of boneseed seed and stems, and a greater biomass of standing plants (other than trees and most of which were boneseed plants) than did the species rich site (Table 3.4). At both sites, litter tended to represented the largest mean component of the total biomass when fine (<6 mm diameter), medium (6 to 25 mm in diameter) and coarse (>25 mm diameter) standing biomass are examined seperately (Table 3.4). Fine and medium sized litter appeared to represent the larger components of the litter layer at the species rich site, while medium sized litter appeared to represent the largest component of the litter layer at the degraded site.

The reduction or elimination of the viable boneseed soil seed bank must be a key objective of long-term boneseed population control and sampling the seed bank therefore needs to be a priority when planning for the management of boneseed populations..The number of boneseed seeds at a degraded site type infestation was an order of magnitude higher than beneath a species rich site type infestation. Therefore, 10 to 100 random soil cores (15cm depth) will further help to distinguish between boneseed population types.

Measurements or visual estimates of boneseed plant height, density and canopy density can distinguish between the structures of boneseed infestations described here and, along with measurement of viable seed in the soil, could provide a basis for management planning. The visual difference between a dense ground cover of native species compared with no native species present at ground level resulting from boneseed invasion is easy to ascertain. The management implications of reducing these different soil seed bank types are discussed in the following chapters. In addition, the following chapters will discuss management targets and options for controlling post fire boneseed populations represented by the different structural charactaristics at each site.

Boneseed infestations will vary in all the various ecosystem types that they invade; however, if management is to be practical and effective across a variety of landscapes, a means of assessing the extent of the problem is needed (Bennett et al. 2006; Brown et al. 2008; Buckley 2008; Crossman and Bass 2008). Different control measures may be suitable for different ecosystems depending upon the sensitivity of the natural ecosystems involved and the size of the weed population and the difficulty of weed control in that population (Adair 1995; Cacho et al. 2008). Knowledge of the extent of the boneseed weed problem along with judicious choice of control measures will limit the amount of disturbance and off target damage to soils, native seed banks and existing native plants. The adaptive management of temperate open woodlands that have been degraded by boneseed could follow an adaptive management protocol as described for threatened temperate grasslands in Australia (Lunt 2003). Using boneseed and native species cover, ground cover, litter depth, composition and the extent of fine litter/fire fuel present, and soil seed numbers as indicators of the level of degradation of ecosystem integrity, various integrated management strategies could be trialled in small areas of a site and continually improved upon based on the most effective results at that site. One exception would be a very new boneseed infestation, where common sense would suggest immediate and intensive management aimed at eradication of the new infestation. Using this adaptive approach, successful weed control methods against various boneseed plant and soil seed bank densities (as investigated in this study), could then be combined with the site specific requirements of the invaded area, be they specific fire regime requirements, conservation of particular threatened plant or animal species, or regard for the potential for reinvasion of the site by existing secondary weeds.

3.3.1 Management considerations for boneseed populations of a species rich infestation type and a degraded infestation type

3.3.1.1 Species rich closed woodland

The species rich site had the lowest number of boneseed plants present above ground and the lowest number of viable boneseed seeds in the soil. Management in this situation would need to preserve the existing native flora diversity and density. At the species rich site the native shrub understorey species were absent in areas where boneseed was present. The species richness at this site was maintained by the eucalypt canopy along with native grass and herbaceous plants at ground level. Native shrubs and grasses were present in patches where boneseed was absent. Management of this type of boneseed infestation at this site would therefore involve removing the boneseed population, including the soil seed bank, with minimal harm to the existing native plant species and aiding the recovery of the scattered mid-storey shrubs.

3.3.1.2 Degraded open woodland

At the degraded site, the state of the native vegetation inferred the long-term negative impact of boneseed invasion. The viable boneseed seed bank was an order of magnitude larger than that at the species rich site, providing evidence of a more established boneseed population. The dense boneseed cover (70 to 100%) had caused changes to all strata layers of the standing native vegetation as well as to the composition of the litter layer. The density and degree of compaction of the litter layer has implications for the degree of aeration of the litter layer and its ability to combust, should fire be the desired management tool. Weed control in these areas would be focused on reducing the above ground vegetation and the large boneseed soil seed reserves. Existing native vegetation should be preserved and its survival aided; however, restoration of such area would likely require either active revegetation or active protection from invasion of the area by secondary weed species for an extended period of time while the area restored itself by natural seed dispersal and growth processes.

Distinguishing between boneseed infestation types is important, as this information can aid decisions regarding the methods, labour intensity and cost of boneseed population control measures. A variety of boneseed plant densities and structures appear to occur within a boneseed infestation, with a resultant variety in the size and position of plant biomass available for controlled burning. The differing amounts of boneseed seed located in the soil seed bank and the amount of ground cover of remaining native species also appeared to vary within the infesttions. The importance of these aspects of the boneseed population structure with regards to weed control are investigated and discussed in the following chapters.

Chapter 4: Burning boneseed: fuel loads and destruction of the soil seed bank

4.1 Introduction

The greatest hindrance to controlling boneseed in Australia appears to be the large reserve of viable seed that has accumulated in the soil beneath boneseed populations (Noble and P.W. 1989). In Australia, boneseed plants produce up to 50,000 seeds per individual (Weiss 1986; Weiss et al. 2008) and an average of 800 to 2500 seeds m^{-2} have previously been found to be viable and accumulate in the soil each year (Lane 1976). This study has found an average of 1926 to 3604 seed m^{-2} at the degraded You Yangs site and 189 to 617 seeds m^{-2} at the comparatively species rich Arthurs Seat site (Table 3.3, Chapter 3). In South Africa the boneseed soil seed bank averages between 100 to 300 viable seeds m^{-2} (Milton 1980). Likewise, comparisons of viable bitou bush seed in soil beneath South African and Australian populations have found South African soil to variously contain 1 to 4% of the numbers of bitou bush seeds found in Australian soils, or 3 to 85 seeds m^{-2} (Weiss and Milton 1984; Scott and Adair 1992). An average of 13% of buried boneseed seeds remain viable after three years, with more viable seed found at a depth of 10 cm than towards the soil surface (Weiss 1986). Furthermore, observations in Australia, at sites where flowering boneseed has been manually removed for many years, suggest that some seeds can remain viable for in excess of ten years (Adair pers. comm.)(Parsons and Cuthbertson 1992). A priority for successful management of boneseed is therefore to significantly reduce the soil seed bank. Noble (1989) suggested that 95% of the boneseed seed in soil would need to be eliminated if populations of both boneseed and the related species bitou bush were to be controlled in Australia.

Several weed control techniques have been employed to kill boneseed plants, either in smaller areas, such as physical and chemical methods, or across landscapes, as is the aim of biological control (see Chapter 2) (Parsons and Cuthbertson 1992; Scott and Adair 1992; Brougham et al. 2006). The only technique used on its own which has resulted in the elimination of boneseed is persistent physical removal, and then only in small areas. No long-term landscape scale control of boneseed has been achieved. Many natural ecosystems in Australia are well adapted to the disturbance of various fire regimes (Gill 1981) and there would appear to be potential for integrating burning for boneseed control with burning for ecological purposes in weed-infested areas. In pot trials, fire temperatures over 150°C for more than one minute have been shown to kill boneseed seeds (Lane 1981). In the laboratory, exposure of cracked boneseed seeds to 100°C heat for 30 seconds caused an almost 100% germination response (Lane and Shaw 1978) and in the field a cool, slow burn was found to stimulate boneseed seeds to germinate (Lane and Shaw 1978). Furthermore, mature boneseed does not resprout after burning (Scott and Adair 1992; Adair 1995). This study presents a detailed investigation of the effects of different fuel loads and fire temperatures on viable boneseed soil seed banks of differing densities, including seed densities far higher (up to 19,000 m^{-2}, Table 3.3, Chapter 3) than reported previously. The population of boneseed at the You Yangs began to expand in the 1950"s and 60"s (Wheeler 1974) and underwent a rapid increase in density and distribution after a large wildfire burnt most of the park in 1985 (Bray 2006). This chapter examines an attempt to eliminate the standing boneseed population and boneseed soil seed bank at the highly degraded You Yangs site using controlled burning. This chapter also examines efforts to eliminate the boneseed population and the smaller boneseed soil seed bank at the Arthurs Seat species rich site using controlled burning.

The use of fire as a method of boneseed control is dependent upon the composition of surrounding natural vegetation, since boneseed plants themselves are not overly flammable (Melland pers. obs.). Indeed, landholders surrounding the You Yangs State Park perceive the existing boneseed population to be a useful fire retardant. One technique to improve the fire-carrying capacity of woody weeds is that of „fell and burn". This technique has been applied to Australian woody weeds in South African fynbos (native vegetation); however, the resultant fire was found to be too hot, resulting in damage to the natural soil structure and native seed bank reserves (Holmes et al. 2000; Holmes 2002). The impact of the techniques of „burn only" (boneseed plants left standing) or „fell and burn" (boneseed plants are cut prior to burning) on boneseed seeds in the soil is investigated in this chapter. This chapter tested the hypothesis that controlled burning could be implemented to remove standing boneseed plants and to eliminate the amount of viable boneseed seeds in the soil across boneseed infestations with differing fuel levels.

4.2 Methods

4.2.1 Pre-burn vegetation preparation, burn conditions and implementation methods at the species rich and degraded sites

The degraded open woodland site was burnt in autumn 1997, in horizontal strips from the top of the slope working towards the bottom. The first burn attempt (F1) was on 26th March 1997. Due to difficulty experienced with burning the boneseed plants only part of the site was burnt. Slashing (brushcutting) was then undertaken in areas 1 and 3. A second burn (F2) was undertaken three weeks after the first (on 17th April) in areas of unburnt boneseed. This second burn was undertaken in the brushcut areas 1 and 3 and in the uncut area 5.

At the species rich closed woodland site, mature standing boneseed plants were hand-pulled 14 months prior to burning (in April 1998). This was done in an attempt to create an even, self-perpetuating burn.

4.2.2 Controlled burn measurements

The temperature and durations of each controlled burn were measured using both thermocouples connected to electronic dataloggers (Data Electronics brand, „Datataker 50®") and thermo-sensitive mineral crayons (BOC gases, „Templstik®"), as detailed in Materials and Methods Chapter 3, Section 3.2.6.

4.2.3 Statistical analysis

A general analysis of variance with randomised blocking (ANOVA, (Genstat 2002)) was performed to ascertain whether significant differences existed in the numbers of viable boneseed seeds found in the soil within sites, before and after the occurrence of fire (Quinn and Keough 2002). Data were square root transformed in order to fit the assumptions of a Gaussian distribution (Sokal and Rohlf 1981; Genstat 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA (Genstat 2002) did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981)(Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data. Data were back transformed for display.

4.3 Results

4.3.1 Controlled burn: temperature variability

4.3.1.1 Species rich site

Burn temperatures were largely homogeneous at the species rich closed woodland site, whereas at the degraded open woodland site the spatial distribution of temperatures was variable (Figure 4.1). Mature boneseed plants at the species rich site were manually pulled and allowed to dry on the ground for 14 months prior to burning. Following this fire preparation, the fire consumed all boneseed biomass as the felled fine sized live and dead boneseed canopy material increased the fine fuel available for burning by 24% (Table 3.2). The burn at the species rich site was homogeneous (Figure 4.2c) with all temperature sensors on the soil surface reaching a temperature of at least 200^{o}C (Figure 4.3). Moreover, the thermocrayon sensors revealed that greater than 80% of all temperature measurements taken across the site reached a temperature of 300^{o}C. Heat from the fire penetrated to 3 cm deep in the soil with 25% of all thermocrayon temperature sensors located at that depth attaining 80^{o}C and approximately 5% recording 100^{o}C.

4.3.1.2 Degraded site

In degraded native vegetation, the only boneseed structure sub-type to burn homogeneously was the degraded site infestation area 2 (see chapter 3 for boneseed infestation descriptions) where all temperature measurements were 200^{o}C or higher with 80% achieving a temperature of 300^{o}C (Figures 4.1 and 4.4). In all other areas at this site controlled burning of the predominantly monoculture boneseed was heterogeneous (Figure 4.4, Figure 4.2d). Thermocrayon temperature measurements revealed that, with the exception of degraded site area 2, all areas of infestation at the degraded site were subject to a wide range of fire temperatures (Figure 4.4). For example, soil surface fire temperatures of between 50 and 300^{o}C were recorded for the degraded site area 1. In an effort to improve fire persistence and spread in these degraded areas, unburnt mature boneseed plants were cut and left to dry on the ground for two weeks prior to a second burn in as yet unburnt areas of the site. However, the brushcutting (slashing) of mature boneseed plants at the degraded site areas 1 and 3 had no effect on improving the homogeneity of the subsequent burn.

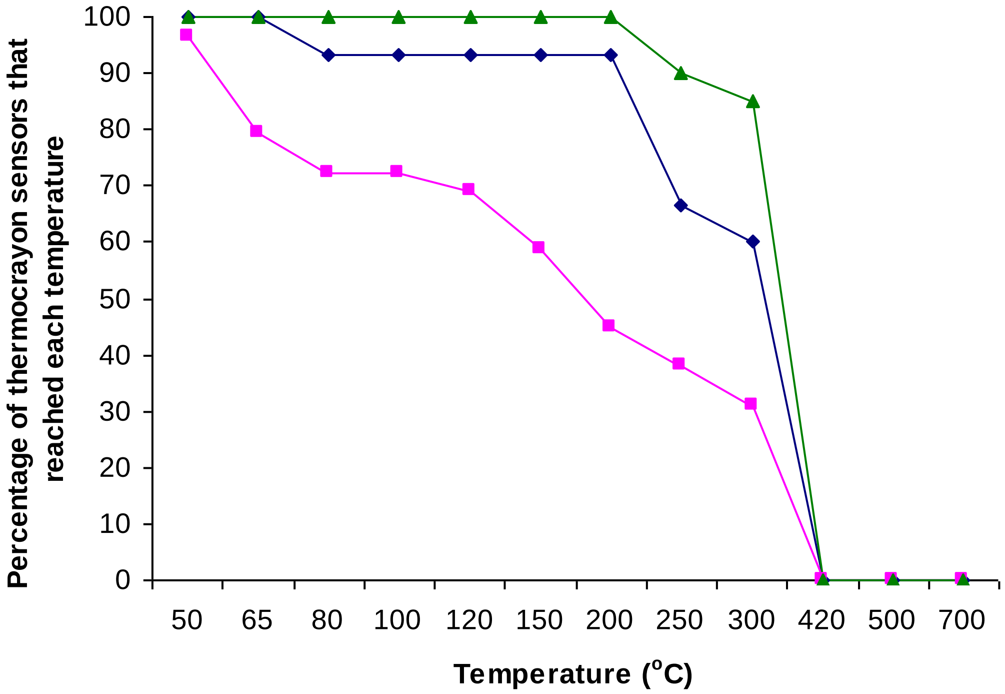


Figure 4.1 The percentage of soil surface temperature sensors (n) that recorded a given temperature for the species rich site (triangles), and the degraded site (not including the degraded site infestation area 2; squares) and degraded site infestation area 2 (diamonds).

a)

b)

c)

d)

e)

Figure 4.2 Homogeneous controlled burning preparation and results at the species rich site **a)**, **b)** and **c)**, and heterogeneous controlled burning at the degraded site **d)** and **e)**. Photos show **a)** slashing or manually removing mature boneseed plants that increased fine fuel loads at ground level and increased boneseed biomass consumed by the fire, **b)** controlled burning of ground and low shrub layers, **c)** post-fire ash bed clear for native species regeneration and access for boneseed seedling control, **d)** a mosaic of clear ground and mature plants remaining after a cooler burn, and **e)** boneseed plants that remained standing in areas that burnt at low temperatures increased the difficulty of access for controlling post-fire emergent seedlings.

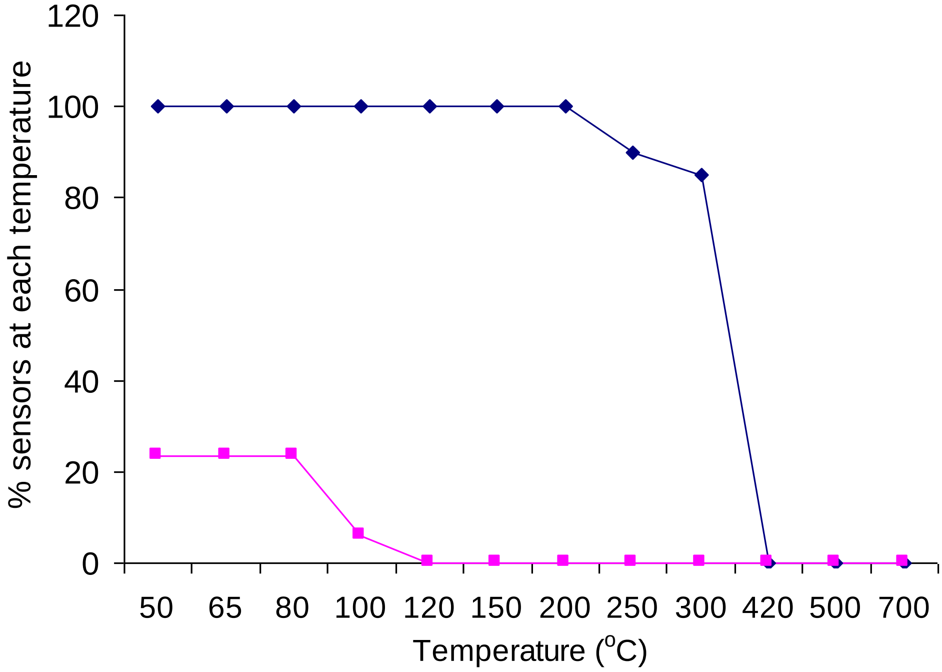


Figure 4.3 Controlled burn temperatures at the species rich site: the percentage of soil surface temperature sensors that reached a given temperature are shown for the soil surface (diamonds), and 3 cm below the soil surface (squares).

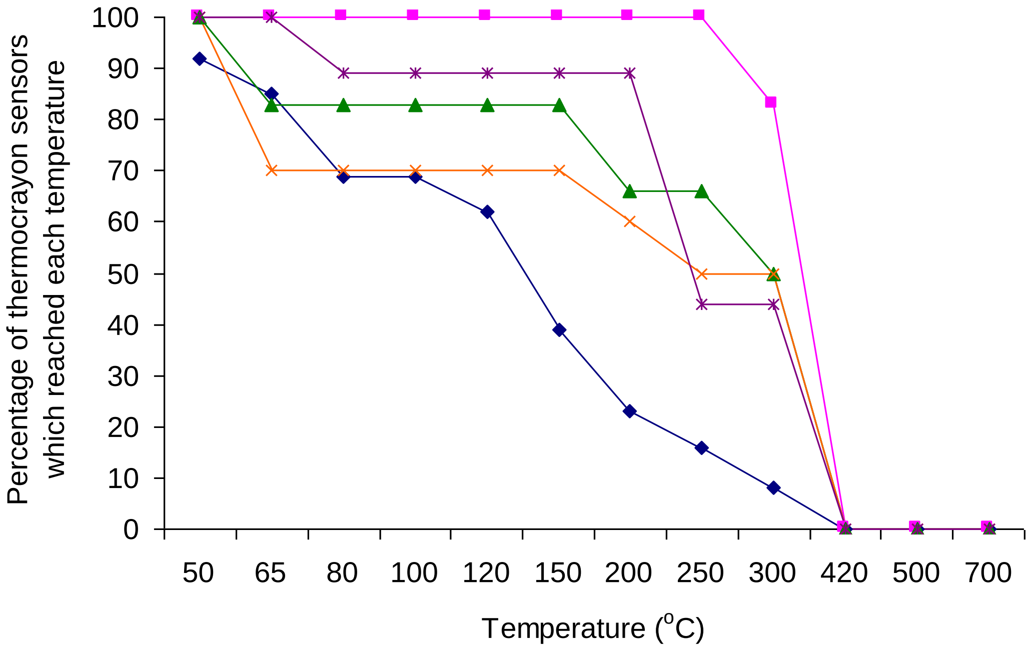


Figure 4.4 Controlled burn temperatures for the degraded site infestation sub-types: the percentage of thermocrayon sensors that reached a given temperature for area 2 (squares), area 4 (asterisks), area 3 (triangles), area 5 (crosses) and area 1 (diamonds).

4.3.2 Controlled burn: temperature duration

4.3.2.1 Species rich site

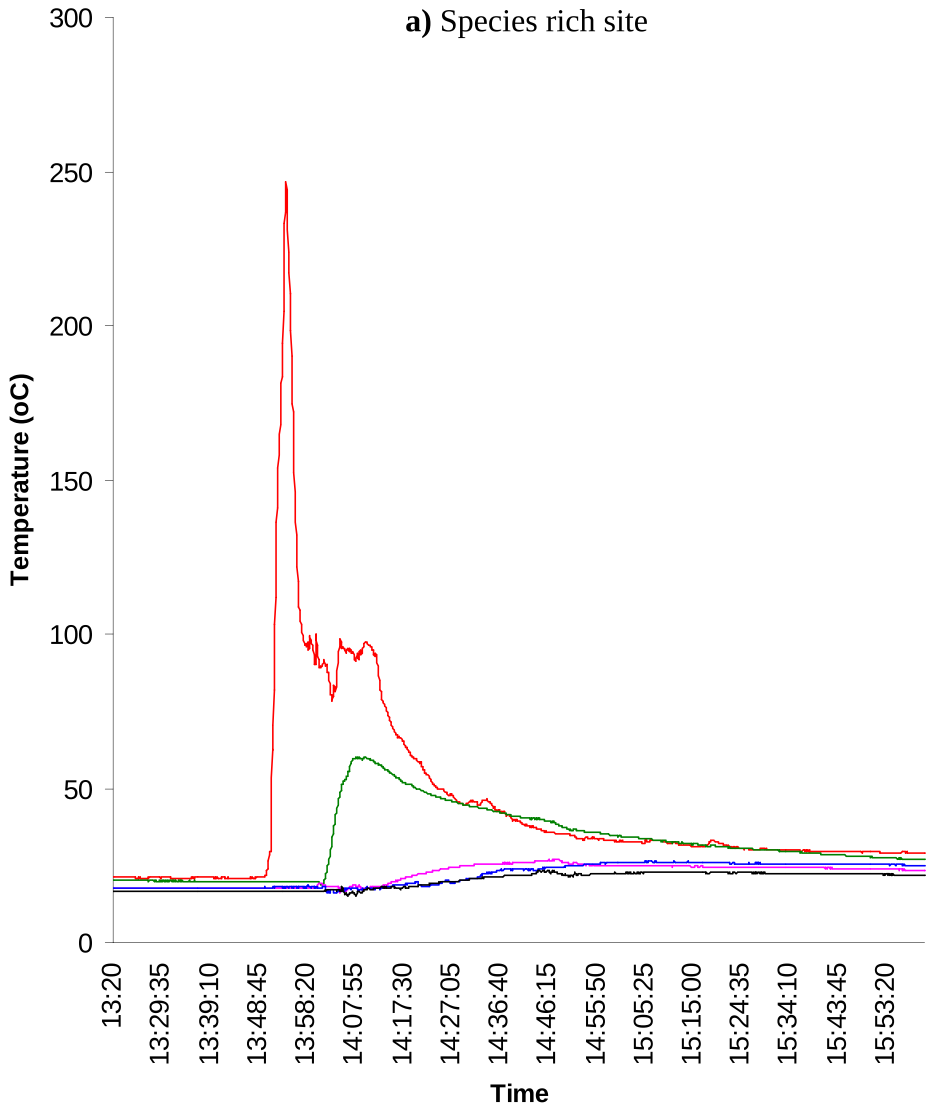
Thermographs represent the temperature profile of burning that occurred at the native species rich site (Figure 4.5a), and at the degraded site (Figure 4.5b). At the species rich site, temperatures over 100^{o}C were recorded for 5 minutes and 25 seconds, which is more than double the length of time that this temperature was recorded at the degraded site (Figure 4.5). As well as heating the soil to over 100^{o}C for longer, the burn at the species rich site maintained heat over 50^{o}C for greater than 30 minutes, indicating that the fire travelled across the site much more slowly than did the fire at the degraded site.

At the species rich site, the soil 2 cm below the surface experienced temperatures over 50^{o}C (Figure 4.5a) for almost 15 minutes. This indicates that the fire on the surface was hot enough to cause the convection of heat further down into the soil profile. The time lag between the surface and each soil depth reaching their maximum temperature was: 14 min 30 s to 2 cm; 53 min 40 s to 4 cm; 1 hr 12 min 5 s to 6 cm; and 50 min 50 s to 8 cm. The maximum temperature recorded by the data logger was 246.6^{o}C (Figure 4.5a), yet the thermocrayon sensors at the species rich site recorded temperatures at or over 300^{o}C (Figure 4.3). Therefore, the time above 100^{o}C and 50^{o}C recorded by the datalogger is a conservative representation of the fire temperatures that were actually achieved at the species rich site.

4.3.2.2 Degraded site

At the degraded site the duration that temperatures were above 50^{o}C and 100^{o}C was variable and less than that at the species rich site (Figure 4.5b). The fire passed over the datalogger sensors relatively quickly at the degraded site. The time lag between the surface and each soil depth reaching their maximum temperature was: 3 min to 2 cm; 46 min 55 s to 4 cm; 1 hr 15 min 40 s to 6 cm; and 14 min 35 s to 8 cm.

At the location of datalogger 1 in area 1 of the degraded site, the temperature remained over 100^{o}C for two minutes and ten seconds. However, the burn at the degraded site resulted in temperatures less than 100^{o}C in most other locations across the site. These lower temperatures occurred for much shorter durations as the monoculture boneseed in degraded native vegetation was difficult to keep alight during controlled burning. The surface temperature reached a maximum of 228°C. The below ground thermocouple wires registered only small increases in temperature (Figure 4.5).



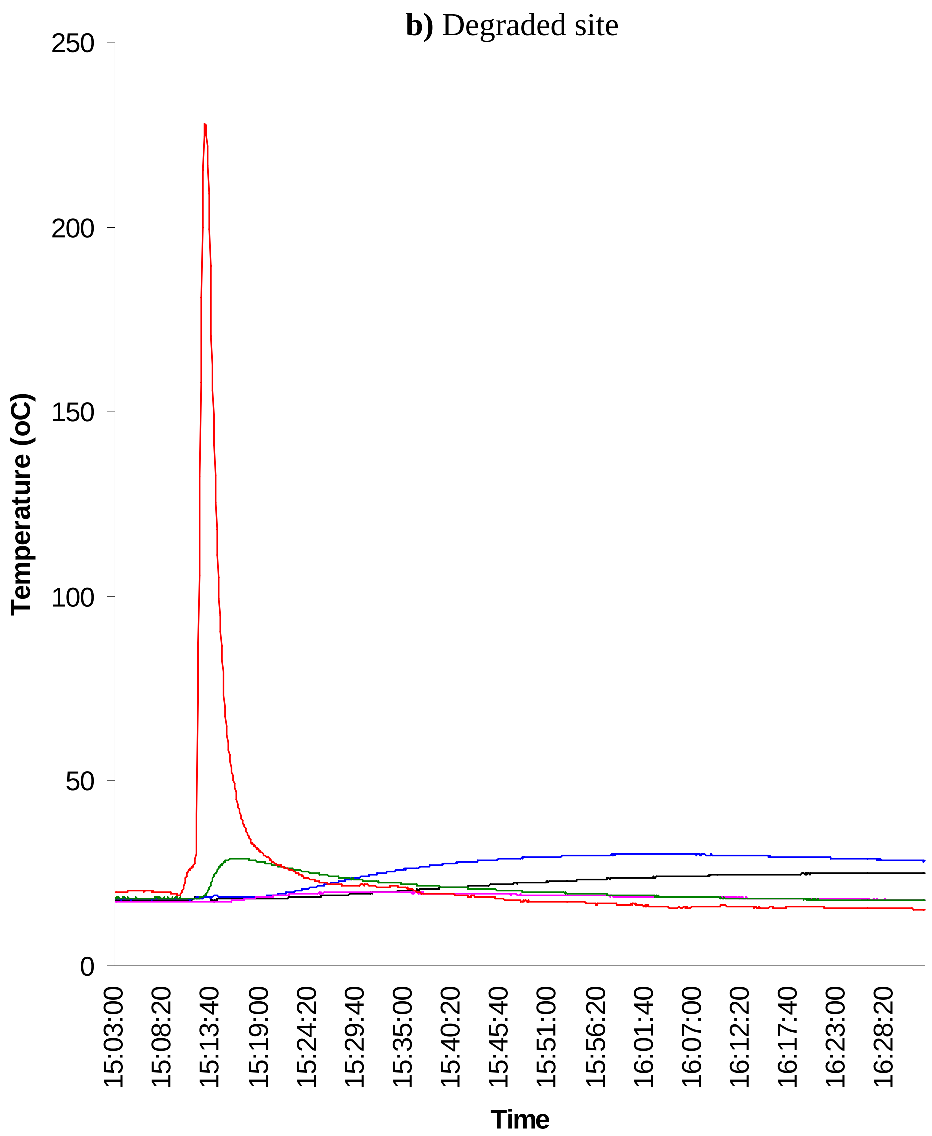


Figure 4.5 Comparison of burn temperature durations between **a)** the homogeneous burn achieved at the species rich site and **b)** the heterogeneous burn achieved at the degraded site. **a)** The duration of soil heating over 100°C and 50°C (respectively) are shown for the soil surface (red; 5 min 25 s; 32 min 45 s), and within the soil profile at depths of 2 cm (green; 0 min; 14 min 55 s), 4 cm (pink; 0 min; 0 s), 6 cm (blue; 0 min; 0 s), and 8 cm (black; 0 min; 0 s). **b)** The duration of soil heating over 100°C and 50°C (respectively) are shown for the soil surface (red; 2 min 10 s; 4 min 4 s), and within the soil profile at depths of 2 cm (green; 0 min; 0 s), 4 cm (pink; 0 min; 0 s), 6 cm (blue; 0 min; 0 s), and 8 cm (black; 0 min; 0 s).

4.3.3 Impact of fuel loads on burn temperatures

The fine sized fraction of understorey shrub biomass at ground level and litter provide the fuel required for fire spread (Cheney 1981). At the species rich site, all boneseed biomass was dry, due to plant senescence, at ground level since mature plants were hand-pulled 14 months prior to the burn (Figure 4.2a). This resulted in an average of 3.66 kg m^{-2} of dry fine fuel on the ground at the time of controlled burning (Figure 3.2). At the species rich site, 63% of total biomass was in the fine fuel fraction (mostly litter), while at the degraded site, 21% of total biomass was in the fine fuel fraction (almost equally standing and litter material) (Table 3.2). The dry fine fuel on the ground also included eucalypt litter and herbaceous material, most of which had dried over the previous summer.

After mature boneseed plants in degraded site areas 1, 3 and 5 were slashed to the ground two weeks prior to burning, the fine dead plant material from the canopy (average 0.57 kg m^{-2} for areas 1, 3 and 5 only) was added to the fine material in the litter (overall site average of 0.96 kg m^{-2}) (Figure 3.2). This resulted in an average of 1.52 kg m^{-2} of dry fine fuel available for burning in the degraded site areas 1, 3 and 5. The other structural levels within the degraded site were not slashed, so their standing vegetation fine fuels (overall site average of 0.91 kg m^{-2}) remained in the boneseed canopy. Fine fuel in the canopy was of limited value in sustaining a burn as it was located too high above the ground.

There was a greater mass of litter at the degraded site (see previous chapter, Figure 3.1) than at the species rich site; however, most of the degraded site litter weight was medium and coarse sized (Table 3.2), rather than the fine fuels on the ground required to sustain a controlled burn. Although the overall litter and fine fuel biomass were least at the species rich site, the litter was predominantly composed of fine fuel such as native grasses and herbs (Table 3.2). The boneseed at the species rich site was hand-pulled and dried on the ground prior to burning, resulting in similar amounts of fine fuels at the species rich site and the degraded site. The hotter fires achieved at the species rich site compared with the degraded site, except the degraded site area 2, were therefore attributed to the larger amounts of fine fuel in the species rich site litter (Figures 4.6, and 4.2b and c). At the degraded site area 2, the standing boneseed plants were mostly dead due to drought stress and formed a dense layer of sticks leaning at an angle to the ground. In this situation the boneseed population burnt as hotly as where native fine fuels were present in the litter layer at the species rich site (Figure 4.6). Partially browned-off boneseed that was not slashed, as occurred in the degraded site area 4, burnt less effectively. Areas with green boneseed plants required slashing in order to sustain a fire at all (Figure 4.2d). When slashed, burning green boneseed plant material achieved cooler burn temperatures than either slashed or unslashed dead/dry boneseed plant material (Figure 4.6).

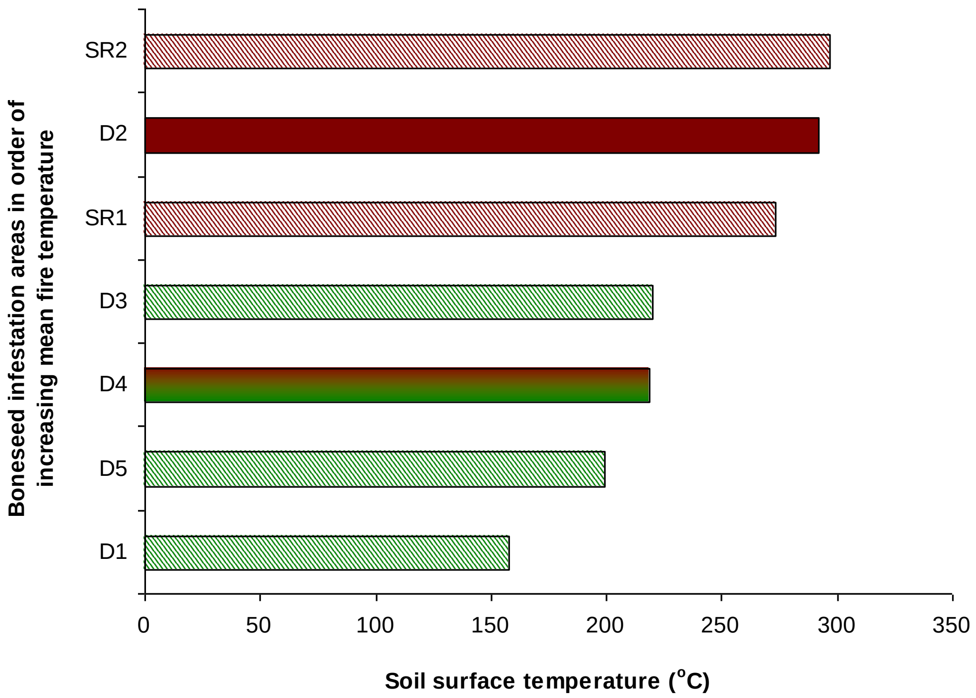


Figure 4.6 Pre-burn vegetation conditions and slash status with resultant burn temperatures at boneseed infestation areas at the species rich (SR) and degraded (D) sites. Average maximum fire temperature in boneseed infestation sub-types is shown in order of increasing soil surface temperature. Vegetation was either slashed prior to burning (diagonally striped bars) and or left standing (solid colour bars). The condition of the vegetation was: majority live vegetation (green bars), majority dead or drought stressed vegetation (brown bars), half live and half dead vegetation (half green and half brown bar).

4.3.4 Depletion of the boneseed soil seed bank

Controlled burning killed almost all viable boneseed seeds (sampled and tested as per methods described in section 3.2.4.3) in the soil in both boneseed populations examined (Table 4.4). Fire reduced the soil seed bank at both sites ($P<0.05$) (Tables 4.2, 4.3 and 4.4). There were no differences in the level of reduction of viable seeds across blocked areas and transects within each site ($P>0.05$). At the species rich site, the homogeneous burn ultimately (12 months after fire) eliminated all the viable seeds in the soil seed bank and destroyed all boneseed plant stems (Table 4.4, Figure 4.2c). At the degraded site, burning had an effective, but variable impact on reducing viable boneseed seed in the soil (Table 4.4, Figure 4.2d and e).

The steep decline in soil seed numbers between the pre-burn and post-burn sampling dates of both sites sharply contrasts with the slight decline that occurs from the post-burn samples until the end of the experiments (Table 4.4). Fire reduced the number of viable seeds by 83-91% across both sites. Thereafter, other combinations of seedling control treatments, seedling emergence and natural mortality (see Chapter 5) reduced the soil seed bank by a further 4-17% (Table 4.4).

The majority of boneseed seed was located in the top 3 cm of the sandy soil at the degraded site and in the first centimetre of the fine clay soil at the species rich site. The degraded site had an approximately 3 cm deep layer of seeds on the soil surface, after which seeds became mixed with soil. Most seeds were found in the top to 6 cm from the top of the litter layer to 3 cm into the soil proper. In some places at the degraded site seeds were observed to be buried more deeply than if they had simply fallen to the ground, possibly as a consequence of dirt scratching by rabbits or burial by ants.

4.3.4.1 Species rich closed woodland site

At the species rich site, the number of viable seeds in the soil was an order of magnitude less than at the degraded site. Burning at the species rich site eliminated the entire boneseed soil seed bank, by both directly killing the seeds and by stimulating seedling emergence (see Chapter 5). Fire reduced the number of viable seeds by 83% on average four months after the burn. However, by 13 months after the fire, after the first post-fire spring/summer period, there were no viable seeds remaining (Figure 4.4). A 100% soil seed bank decline caused by the fire was confirmed 17 months after the burn, after the second winter growth season, when no viable boneseed seeds were found in the soil. Wildfire also appears to eliminate the boneseed soil seed bank, as no boneseed seeds were found four days after a wildfire that burnt in the Arthurs Seat State Park in January 1997, in locations where mature boneseed plants had been present before the fire (Melland pers. obs., Figure 4.7).

4.3.4.2 Degraded open woodland site

The number of viable seeds in the soil seed bank at the degraded site decreased on average by 91.2% by four months after burning. Two and a half years after burning, a further decline in soil seed numbers occurred across most of this site, so that on average only 4.8% of the pre-fire boneseed soil seed bank remained. Importantly, only 216 seeds m^{-2} survived the fire, with a site mean of 177 seeds m^{-2} remaining viable from 12 months after burning. Weed control treatments after burning were aimed at the emergent seedlings rather than directly at the soil seed bank and there were no significant differences between the numbers of viable seeds that had survived the fire found in different plots after post-fire treatments had been applied.

4.3.4.3 Degraded site infestation area 1

The slashed degraded site infestation area 1 vegetation recorded the coolest (Figure 4.6) and most patchy burning temperatures, with 60% of the area lightly burnt, and 33% of the area unburnt (Table 4.5). As a consequence, degraded site infestation area 1 also recorded the highest percentage (16%) of pre-fire seeds surviving in the soil seed bank (Table 4.4).

4.3.4.4 Degraded site infestation area 2

In the unslashed degraded site area 2 vegetation, the boneseed population structure enabled the fine fuel from the canopy to be consumed by the fire. The even burn in this area resulted in the least number of viable seeds remaining in the soil. The degraded site area 2 had the highest level of black charring to the soil surface (Table 4.5) and all mature plant biomass was destroyed. Across the majority of degraded site area 2, only 1% of the original soil seed bank remained after the controlled burn, equating to an average of 19 ± 7 viable seeds m^{-2} (Table 4.4).

4.3.4.5 Degraded site infestation areas 3, 4 and 5

In the remaining areas of the degraded site, degraded site areas 3, 4 and 5, controlled burning was heterogeneous in its effect on the soil seed bank (Table 4.4). The percentage of the pre-fire soil seed bank which remained viable by four months after burning ranged from 4 to 14% (Table 4.4), depending upon whether more or fewer patches of hotter or cooler burning occurred at the locations of the soil transects.

Table 4.2 General ANOVA with randomized blocking of boneseed soil seed counts pre and post fire at the species rich (SR) site (Tables 3.3 and 4.2).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Area stratum					
Fire	1	1326.85	1326.85		
Area.Transect stratum					
Fire	1	214.91	214.91	0.89	0.445
Residual	2	483.81	241.91	2.66	
Area.Transect.Units stratum					
Fire	1	2621.73	2621.73	28.83	<.001
Residual	124	11276.71	90.94		
Total	129	15924.01			

ns, not significant, P>0.05.

Table 4.3 General ANOVA with randomized blocking of boneseed soil seed counts pre and post fire at the degraded (D) site (Table 3.3 and 4.2).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum					
Fire	4	7434029	1858507	1.98	
block.Units stratum					
Fire	1	86051434	86051434	91.51	<.001
Residual	50(4)	47018269	940365		
Total	55(4)	132808124			

ns, not significant, P>0.05.

Table 4.4 Boneseed soil seed bank decline after burning at the species rich and degraded sites.

Boneseed population infestation areas at the species rich (SR) and degraded (D) sites	Average maximum fire temperature (^oC)[E]	Average number of viable seeds $m^{-2} \pm$ s.e.m. in soil four months after burning[G]	Percentage soil seed bank decline due to fire	Average number of viable seeds $m^{-2} \pm$ s.e.m. in soil, more than 12 months after burning[C]	Percentage soil seed bank decline more than 12 months after burning[C]
SR1		$64^a \pm 18$	65	0	100
SR2		$72^a \pm 16$	88	0	100
Species rich site mean	285	67 ± 12	83	0	100
D1		$341^a \pm 192$	83	118	94.01
D2 whole block		$353^a \pm 334$	80	49	97.46
D2 hot burn		19 ± 7[A]	99.99 [A]		
D3		$130^a \pm 50$	96	109	96.83
D4		$427^a \pm 175$	83	266	89.16
D5		$165^a \pm 64$	95	342	90.51
Degraded site mean	218	323 ± 95	88	176.8	93.40
		221 ± 59 [B]	91		

[A] Five of the six plots of the degraded site area 2 burnt more hotly and evenly than all other areas of the degraded site.
[B] Site average using only the five plots of degraded site area 2 used to calculate [A].
[C] Long-term soil seed bank decline measurements were taken at the species rich site at 13 and 17 months after burning (no viable soil seed was found at either time). At the degraded site, long term seed bank decline was measured two and a half years after burning.
[D] See Table 3.4 for mass of fine fuel available at ground level for boneseed vegetation areas.[E] See Figure 4.6 for fire temperatures of boneseed vegetation areas.[F] See Table 3.5 for numbers of viable boneseed seeds in the soil in boneseed vegetation areas before burning.[G] Lower case letters denote that there was no significant difference across different areas within each site, in the decline of the soil seed bank due to controlled burning. Letters do not denote a comparison between experimental sites.

Table 4.5 Percentage of quadrats unburnt, partly burnt or completely charcoal at the degraded site.

	Degree of burning [A]		
Boneseed infestation areas at the degraded site (D)	Unburnt	Partly burnt	Completely charcoal
D1	33	60	7
D2	0	11	89
D3	20	33	45
D4	10	23	67
D5	0	33	67

[A] Soil surface charring categories were as follows: unburnt = no blackening to seeds; partly burnt = blackening to part of the seed; completely charcoal = whole seed was charcoal. Measured by assessing the burn category of a seed from each of 20 fixed grid locations per quadrat.

Figure 4.7 No boneseed seedlings emerged and no viable boneseed was found in the soil after the January 1997 wildfire in the Arthurs Seat State Park in locations where mature boneseed had been present prior to the fire.

4.4 Discussion

The control of a boneseed population partially involves both the removal of the above ground plants as well as the large viable soil seed reserves. Controlled burning was effective at removing mature boneseed plants and most boneseed seeds from the soil at both the species rich and degraded sites. Burning was hotter and more uniform at the species rich site than at the degraded site. This appeared to be largely due to the larger amount of fine fuel available at the species rich site compared to the degraded site. The most important component of available fuel appeared to be fine sized (<6 mm in diameter) native grass and herbaceous species litter at ground level.

4.4.1 Persistence of the boneseed soil seed bank

The fire at the species rich site caused an 83% decline in the soil seed bank by four months after burning, due to a combination of seed death and seedling emergence. However, after 13 months no viable seeds remained. The fire at the degraded site caused 80 to 96% mortality with an average of 87% seed bank decline across the site. This was a particularly successful outcome given the uneven burning that occurred at the degraded site. The efficacy of the burn at the degraded site was probably due to a large proportion of the soil seed bank occurring at the soil surface. Due to this deep layer of seeds on the surface, the soil seed bank was saturated and seeds could not enter and be buried by normal mechanisms. In contrast, the far fewer pre-fire seeds at the species rich site (approx 400 seeds m^{-2}) were more evenly distributed within and on top of the soil. Therefore, a greater proportion of seed was unprotected by soil at the degraded site and able to be burnt by the fire. Despite this, due to the very large pre-fire soil seed numbers, burning was less successful at eliminating the soil seed bank at the degraded site.

By four months after burning the average seed bank at the degraded site (165 to 427 m^{-2}) was similar to the original pre-fire seed bank size at the species rich site (396 seeds m^{-2}). The number of seeds that survived the fire remained constant over 2.5 years following burning at the degraded site, rather than declining to 0, as occurred at the species rich site. Therefore, the impact of the fire in the species rich site was greater. This was likely due to the lower initial seed bank and the high and evenly distributed burn temperatures at the species rich site penetrating further into the soil across more of the site than the lower and spatially variable temperatures at the degraded site burn. A dense layer of boneseed seed at the degraded site was also likely to have insulated the soil against the fire, leading to lower soil temperatures.

Boneseed seed death rates after burning occurred at temperatures somewhat higher than have been reported for many woody species. At the degraded site, low soil seed mortality (14.3%) was recorded in areas with a maximum temperature of 100°C, 64 - 72% mortality occurred where most sensors recorded 150 - 200°C, while 82 - 97% mortality occurred where 250 - 300°C was the most common temperature recorded. Across the species rich site, temperatures of 250 - 300°C resulted in 65 – 88% initial post-fire mortality (Table 3.5, Table 4.4). Seed of Fabaceae in Mediterranean-type habitats in Australia, California and South Africa are killed when subjected to temperatures of 120 to 150°C for a few minutes ((Enright 2001) and references therein). Similarly, low temperatures of a grass fire caused high mortality in the seed bank of the invasive *A. nilotica* in *Astrebla* grasslands in northern Australia (Radford et al. 2001). Increasing levels of seed death occurred in *Acacia suaveolens* (Sm.) Willd. with increasing exposure to temperatures above 80°C Auld (1986), whilst 90 to 100% of viable seed of *G. monspessulana* was killed when fire temperatures 1 cm below the surface of the soil were over 70°C. When fire temperatures in the top centimetre of soil were lower than 70°C then the reduction in the viable soil seed bank of this species was variable (Lloyd 2000). Slow fire spread and surface temperatures above 100°C for around five minutes resulted in more downward movement of heat into the soil and a greater overall impact on the boneseed soil seed bank. Therefore, it appears that hotter controlled burn temperatures for longer durations are required to kill a larger percentage of the boneseed soil seed bank than for some other woody species.

During burning, survival (or stimulation to germinate) of seed in the soil is thought to increase with increasing depth in the soil (Gill 1981; Ferrandis et al. 1999), as soil is an effective insulator with perhaps only 5% of the heat from a fire penetrating into the soil (Packham 1971). The number of boneseed seeds in the soil seed bank decreased with depth (Melland data not shown), as has been found for other species (Ne'eman and Izhaki 1999). Therefore, burning needs only to be hot enough to heat and/or chemically stimulate the top few centimetres of soil to impact upon the majority of the boneseed soil seed bank. The overall seed kill and germination achieved at the species rich site reflects this. The heat reached to 3 cm depth while most seeds were located to around 1 cm depth, resulting in most seeds being destroyed. At the degraded site the fire heated only the surface layer of soil in most places;

which only killed most of the surface layer seeds. Likewise, seeds of *A. nilotica* on the soil surface and 1 cm below the surface were killed or germinated after fire (Radford et al. 2001). Auld (1986) concurs, finding for *A. suaveolens* that innate seed dormancy was broken for seeds in the top 1 cm of soil in cool burns and in the top 4 cm for hot burns. The hot burns (which resembled a moderate/high intensity wildfire) caused seed death in the top 1 cm of soil. In Spain, the lethal effect of fire on hard Cistaceae seeds in the soil was confined to the top 0 to 2 cm, with seeds in the 2 to 5 cm soil layer remaining undamaged (Ferrandis et al. 1999). Raison (1986) found that for a burn which reached temperatures of 600 ^{o}C in the litter and 450, 54 and 42^{o}C in soil depths of 0, 2 and 5 cm respectively, the effects of soil heating continued after the fire had passed. The blackened soil was now exposed to direct solar radiation as the shade and insulation of the understorey and litter had been removed (Raison et al. 1986).

Persistent soil seed banks enable obligate seeding species to recruit seedlings after parent plants have died (Holmes and Newton. 2004). Recruitment can occur where parent plants have been killed by fire or have senesced due to a long interval between fires and their seeds are stimulated to emerge directly or indirectly by fire (Holmes and Newton. 2004). In South African fynbos, a native habitat of boneseed, the average fire return interval is 15 years, with two fires likely to occur in 25 years (Holmes 2002). In Australia there is no single „normal" fire frequency in boneseed-invaded ecosystems, instead the vegetation burns in accidental wildfires and/or in occasional controlled burns. There had been 14 years since the last fires at the degraded and species rich sites. At the degraded site the number of growth rings on boneseed stems suggested that some live and many dead plants had grown since the year of the last fire. Since boneseed evolved under the South African fire regime, it is likely that some boneseed seeds persist in the soil for at least 15 years. Anecdotal evidence from consistently hand-weeded areas has suggested that seedlings are able to emerge after 15 years (Adair pers. comm.).

In Australia, the boneseed soil seed bank persists both on the soil surface and buried at various depths in the soil. Ants have been observed to bury boneseed seeds, while rabbits and larger mammals bury them in disturbed soil (pers. obs.). Seeds of *A. suaveolens* situated 5 - 10 cm below the soil surface have been found located in ant (*Pheidole* spp.) nests and germinated from 8 cm depth in the soil (Auld 1986). Boneseed cotyledons were observed to have belowground shoots up to 5 cm long (Melland pers. obs.). Australian native bush rats break open boneseed seeds (Adair pers. comm.) and burial would protect a portion of the boneseed seeds from this predation. Seed burial also occurs for many fynbos species in boneseed‟s country of origin (Holmes and Newton. 2004). Larger seeded species are less likely to have persistent soil seed banks due to heavy predation levels and in (small seeded) Asteraceae species tested for germinability, burial imposed a secondary dormancy (Holmes and Newton. 2004). This was a prerequisite for soil persistence, as it prevented seeds that had lain on the surface germinating as soon as they were buried. In this study, areas of boneseed infestation where both measured high numbers of seeds in the soil and high numbers of predated seeds were observed, burning still did not appear to cause seed numbers to become a limiting factor for seedling recruitment.

4.4.2 Boneseed fuel types and amounts required for effective burns

Fine fuels are „considered to contribute to the zone of continuous flaming combustion, and are {therefore} important in determining the rate of {fire} spread" (Cheney 1981). In the temperate vegetation area around Melbourne there is a natural available fuel load of between 0.3 to 2 kg m^{-2}, with a usual fuel load of around 0.75 kg m^{-2}. This fuel is composed of around 70% leaf litter, 10% shrubs, 10% twigs, 5% grass and 5% bark (Gill 1981). The boneseed infested areas at the species rich site had amounts of fine fuels within the range for temperate native vegetation; 0.96 kg m^{-2} for unslashed boneseed, and 1.52 kg m^{-2} for slashed boneseed (where canopy fuel was relocated to ground level). At the degraded site, with dried boneseed on the ground, there was a higher than normal fuel load of 3.56 kg m^{-2} (Table 3.4). The fuel dynamics of the region to the west of Melbourne, where the degraded site was located, are described as consisting of „grassy fuel – some tree or shrub litter‟. The area to the southeast of Melbourne (where the species rich site is situated) is described as „shrubland fuel – aerial and ground litter‟. The main difference being that grassy fuel is located at ground level, while in shrublands, canopy foliage is available as fire fuel (Gill 1981). At the degraded site, boneseed had changed the grassy fuel ecosystem such that there was minimal grass remaining. The native grass fuel type had been replaced by medium to coarse sized biomass that was not as successful at carrying a fire. At the species rich site, the shrubland fuel ecosystem persisted to a greater extent and was able to carry a fire in a similar way as would occur in a native shrubland ecosystem.

In the current study, dataloggers were set up to measure the spike of heat as the flame front passed over the thermocouples. However, at the degraded site the fires were largely „stationary", due to high litter moisture and lack of available fine fuel, and to the low flammability of boneseed. At the species rich site, the fire „moved" of its own accord in places. However, as the strip burning method was used, there was only a short distance for the fire to cover before it came to the previously burnt strip, where there was no more available fine fuel. Therefore, the rate of fire spread (as opposed to the burn duration in one location) was not ascertained for these burns and fire intensity could not be directly calculated. Soil temperatures and fire behaviour are instead used for comparisons between these burns and burns in other studies.

The high level of spatial variation in fuel loads and burn temperatures amongst boneseed vegetation types is a significant finding in itself due to the flow-on management implications. Variation in vegetation structure has also been found to have a variable impact on fire behaviour in woodlands in south-west Western Australia (Hobbs and Atkins 1988; Grant et al. 1997). The heterogeneity of fuel loads, due to heterogenous spatial patterns of standing and litter fuels, in wood and shrubland vegetation types contrasts with the more homogeneous distribution of fuel present in forest fires (Hobbs and Atkins 1988). Even in a near monoculture stand of boneseed within natural open woodland, the amount of fuel available for burning was variable. In turn, the fire had a greater or lesser impact on boneseed soil seed mortality, germination or survival across the site depending upon levels of available fuel. The degraded site had experienced drought conditions during the summer prior to burning and as a consequence some boneseed plants were drought stressed while others had died. However, many plants still had green foliage. Although the quantities of live and dead plant material within stands of shrubs and perennial grasses in Australian native vegetation are known to be spatially variable, the effect of this variation on the behaviour of the fire is largely unknown (Cheney 1981). In this study, areas of dead boneseed clearly burnt better than areas of live boneseed. Boneseed is an obligate seeding species, with mature plants being killed by fire. A hot even controlled burn was shown to be an effective means of removing or killing all above ground boneseed biomass.

4.4.2.1 Patchy burning in unslashed boneseed in degraded native vegetation

Vegetation structures that were not slashed and where the foliage of a dense boneseed canopy began from 50 cm to 1 m from the ground were difficult to burn. Only bare stems filled this gap and the litter layer of boneseed leaves was usually a maximum of 5 cm deep. Undertaking a self-perpetuating controlled burn was made even more difficult if plants were not contiguous. A portion of the biomass of shrubs can be added to litter mass to give a total amount of available fine fuel, but only where this shrub layer is thought to be a component of the fuel bed (Cheney 1981). This would be variable in a boneseed infestation. Certainly dry, low, dense, leaning boneseed stems could be considered available fuel. But any fine fuels on standing plants could not, as the fuel is too far removed from the ground.

At the degraded site, burning was successful for weed control where the boneseed ground cover was continuous and low, with an average height of just over 1 m, and a large proportion of the stand dead and fallen. This type of infestation carried a fire through the foliage at around 300^{o}C, resulting in an even burn that consumed the mature above ground plant biomass and charred seeds on the surface of the ground. The heat from this type of burn penetrated to around 3 cm deep in the soil, warming seeds there to around 50^{o}C, and killing 99.99% of the soil seed bank.

The heating of soil by fire in heterogeneous vegetation mainly occurs under existing plants and is negligible in bare areas (Hobbs and Atkins 1988). This was reflected in the difficulty experienced with undertaking burning, the low temperatures recorded, and lower mortality of the soil seed bank in areas with a sparse boneseed population. Boneseed seeds will be variably affected by a fire burning in vegetation with spatially variable fine fuel loads, as are found in a boneseed infestation. The fine fuel sized natives at ground level are essential in order to sustain a burn that will kill boneseed. The structure of live unslashed boneseed plants is inadequate for sustaining a fire. When boneseed plants die and accuumulate as sticks closer to the ground, then burning can be effective without the presence of other fine fuel sized species.

4.4.2.2 Burning slashed boneseed

Improved burn efficacy was achieved at the species rich site and at the degraded site by slashing or hand-pulling the boneseed plants, and waiting for them to dry prior to burning, thereby bringing more dry fine fuel close to the ground. Boneseed was drier and was therefore more effective fuel at the species rich site, than in the slashed locations at the degraded site, as it had been allowed to dry for 14 months as opposed to 2 weeks for the latter. The species rich site also had more grass and litter available at the ground level, due to a less dense boneseed population. Boneseed at the species rich site was taller as the dominant native tree

E. viminalis provided a more closed canopy than the sparse *A. mearnsii* at the degraded site. At the species rich site, the fire was able to persist in the vegetation due to the fine fuel and, as a result, the medium and coarse fuel were also burnt adding to the heat of the burn. Although the degraded site had more medium sized dry fuel available for burning than was present at the species rich site (Table 3.4), this did not compensate for the lack of fine fuel at that site. Morgan (1999) found annual grassland fires to reach temperatures of over 100^{o}C for < 1min, while grassland burnt at 4-7 year interval held temperatures above 100^{o}C for 2-3 mins. The difference in fire behaviour was correlated with fuel load (Morgan 1999). A predominance of fine, rather than medium sized fuel is required to initially carry a fire through a boneseed infestation. Felling boneseed 14 months prior to burning resulted in all the mature boneseed being consumed and the area being accessible for follow up control measures.

4.5 Conclusion

This chapter found that controlled burning can be implemented to remove standing boneseed plants and to significantly reduce or eliminate the amount of viable boneseed seeds in the soil across boneseed infestations with differing fuel levels. The results of controlled burning amongst a boneseed population were found to be variable and the most likely scenario for a successful even burn was where there was sufficient fine fuel available at ground level to carry a fire through the boneseed stems to the boneseed canopy. This occurred in less severe boneseed infestation areas where native grasses and herbaceous plants still existed at ground level. Where diverse native vegetation still existed, there was abundant fine fuel for fire and there were less than 500 viable boneseed seeds m^{-2} in the soil, brushcutting of boneseed prior to controlled burning in autumn was found to be beneficial but not essential. Under these circumstances controlled burning resulted in peak surface temperatures of 250 to 300^{o}C, which killed and removed all standing boneseed plants and killed all boneseed seeds in the soil. Where there was a dense boneseed infestation in severely degraded native vegetation there were few native native plants present and the area was predominantly a boneseed monoculture. Under these circumstances there was little fine fuel available at ground level to carry a fire, with the ground mostly covered in a thick layer of boneseed seeds. Seed density measured between 2000 to 19,000 viable boneseed seeds m^{-2} in this type of infestation. Brushcutting the boneseed in late spring prior to controlled burning in autumn was found to be required, unless the boneseed plants were predominantly dead and the canopy was in contact with the ground. The variable temperatures of the burns in this type of infestation did not eliminate all standing boneseed plants, nor the entire soil seed bank. Boneseed soil seed levels were significantly reduced, to around 230 viable seeds m^{-2}. Fire was found to cause seed germination and seedling emergence under lower as well as higher temperatures. Post-fire emergent seedlings must be controlled prior to the input of new propagules into the soil seed bank. The following chapters will address post-fire boneseed seedling control.

Chapter 5: Effects of herbicides, manual removal and sown native grass on post fire boneseed populations

5.1 Introduction

Controlled burning caused an 84 to 100% decline in the viable boneseed soil seed bank, by killing seeds or causing them to germinate (Chapter 4). However, in order to successfully control or eliminate boneseed using fire, the seedlings that emerge in the years following burning must be controlled. Post fire control must occur to prevent new boneseed seed from replenishing the boneseed soil seed bank and to enable native plant species to grow, both of which will contribute to long term ecosystem restoration.

Weed control techniques used on unburnt boneseed populations could potentially control the post fire emergent seedlings. Several weed control techniques have been used previously against boneseed populations, including herbicide application, pushing over mature plants/hand weeding, slashing, and biological control (Adair and Edwards 1996; Adair and Scott 1997; Brougham et al. 2006). However, none of these techniques directly targets the soil seed bank. Biological control has always had the greatest potential for control at a landscape scale; however, to date no agents have successfully established on boneseed in the field (Weiss et al. 2008). Removing boneseed plants by handpulling alone can result in seed emergence from the soil seed bank for over 10 years (Adair pers. comm.). However, the local soil disturbance created by handpulling mature plants has been found to have no effect on seedling emergence and therefore no direct impact on decreasing the soil seed bank over time (Thomas et al. 2000). Similarly, the gaps in the canopy created by slashing boneseed also have no direct impact on boneseed seedling emergence (Thomas et al. 2000). Herbicide application has not resulted in permanent removal of boneseed populations in most cases. Herbicide application in winter (or mid-autumn for the second application time at the species rich site) was investigated, as Toth (1996) found that winter herbicide application caused more damage to actively growing bitou bush and less damage to the dormant or slower growing native species. However, those studies were conducted on mature bitou bush plants in New South Wales, rather than the juvenile boneseed and native seedlings treated in this experiment. Also, it was investigated whether herbicide applied at the end of the first growth season after burning would kill boneseed seedlings before many of the native species had emerged. The effectiveness of this strategy depended to some extent on whether the controlled burn would induce the germination of native seeds. Therefore, the aim was to avoid herbicide damage to native species in as many of the following ways as possible: a) use as low a rate of herbicide as possible, b) spray immediately after the first winter growth season as this was potentially when the most boneseed and the least numbers of native seedlings had emerged, c) spray when the native species were growing more slowly than the boneseed, and d) spray when boneseed seedlings were older and potentially fewer in number so native species could be avoided by using a spot-spraying technique, rather than the hand-held boom sprayer of the earlier timing. Reducing the vigour of woody weed seedlings using herbicides could give surrounding native grass seedlings a competitive advantage and further reduce the potential for survival of the weed (Groves 1991). As well, the potential for high densities of native grass to outshade woody weed seedlings has not been tested in the field. Therefore, the effect of adding seed of the two locally indigenous grass species, *P. sieberiana* and *T. triandra*, on the survival of post fire emergent boneseed seedlings was investigated. None of these methods has previously been tested in an integrated manner for boneseed control after fire.

This chapter tested the hypotheses that the weed control measures of herbicide application, hand-pulling of flowering boneseed plants and the addition of competitive native grass species could be utilised either alone or in combination to control post-fire emergent boneseed seedlings. Treatments were timed to reduce the number of seedlings present, prior to new boneseed seed entering the soil seed bank. Therefore this study also tested the hypothesis that applying weed control treatments after the first or the second growth season after burning would have a differential effect on post-fire seedling control.

5.2 Materials and methods

5.2.1 Experimental design and treatment

The experimental design and experimental timetables for all experiments contained in this thesis are described in full in Chapter 3, Materials, methods and vegetation description of boneseed infestations – see sections 3.2.1, 3.2.2 and 3.2.3. For the experimental timetable for the species rich site see Chapter 3, Table 3.1, and for the experimental timetable for the degraded site see Chapter 3, Table 3.2.

The experimental approach at both sites was to adapt weed control treatments to the biotic and abiotic conditions of the site as they changed over time. The timing of implementation of initial controlled burning was also highly dependent on weather conditions and the practicalities of the priorities and availability of staff and heavy fire fighting equipment. Therefore and due to this adaptive approach, the timing of treatments and vegetation counts/sampling did not occur at regular intervals at each of the experiment sites. Treatments that were designed to cause mortality to the maximum number of boneseed plants prior to any of those plants setting seed, such as herbicide applications, were also timed to enable maximum emergence of seedlings. Therefore, the timing of weed control treatments depended on rainfall and climatic conditions at each site that were favourable or otherwise for boneseed plant germination, emergence and growth. These conditions were naturally different at each site.

5.2.1.1 Species rich closed woodland site

The timing of the application of two herbicides, glyphosate and metsulfuron-methyl, was investigated at the species rich closed woodland site. Separate plots were treated with one of the two herbicides at 5 months after burning (August 1998 – at the end of the first growth season for boneseed) or at 12 months after burning (April 1999 – at the beginning of the second growth season for boneseed).

First year flowering boneseed plants were hand-pulled in May 1999, 14 months after the controlled burn. Seedlings were pulled from 12 plots that had previously been sprayed with herbicide (6 with each of the two herbicides) and 6 plots that had not been sprayed. At the species rich site, a sub-sample of one in ten flowering seedlings were oven dried at 60-80^{o}C for at least 48 hours. The basal stem diameter (using digital callipers), above-and below-ground (stem and root) dry weight and the number of buds, flowers, developing ovules and seeds per seedling were measured.

Grass seed was spread on the post-fire ash bed in subplots within each treatment, two weeks after burning for *P. sieberiana* (approximately 100 seeds of this C3 grass species) and five months after burning (and prior to the optimal summer growth period) for *T. triandra* (approximately 400 seeds of this C4 grass species) (Table 3.1). The seed of the two native grasses species was distributed after controlled burning to investigate whether increased densities of grass could reduce the number of boneseed seedlings. The seed was spread by hand in parallel lines and then in perpendicular parallel lines across each designated sub-plot. Grass cover at Arthurs Seat was recorded at the data collection times 1 and 2 (Table 3.1) as a percentage cover for each grass species, as well as total percentage cover of all grass species. Grass height and density were recorded at data collection times 3 and 4 (Table 3.1). Subplot treatment data at this site were then divided into subplot treatments with or without *P. sieberiana* added, as *T. triandra* plants failed to establish.

Soil cores were taken along transects prior to burning, and again after burning in August 1998, May 1999 and September 1999. Vegetation data was collected from all sub-plots after controlled burning, in August 1998, October 1998, May 1999 and September 1999.

5.2.1.2 Degraded open woodland site

The most effective timing for herbicide application at the degraded site was investigated by treating 12 separate plots at 5 months (August 1997 - herbicide application 1) and 12 plots at 17 months (August 1998 - herbicide application 2) after the fire. Herbicide application methods and rates are detailed in Chapter 3, Section 3.2.7. Applying herbicides 5 months after burning was expected to have an impact on the greatest number of the seedlings, including those that had germinated both after burning and after the first spring growth season. Treatments at 17 months were intended to control seedlings just before flowering and seed set. Flowering usually occurs at between 12 and 18 months of growth depending on climatic conditions. The seedlings experienced water deficiency stress during the summer following burning and flowering was delayed until around 17 months after burning (Table 5.8).

First year flowering plants were hand-pulled 17-18 months (September 1998) after fire from plots that had either received herbicide 5 months after fire, or had not had any herbicide applied to plots. Hand-pulled seedlings were collected, dried and measured as for the species rich site (see above).

Soil cores were taken before burning in February 1997, then after burning in July 1997 and September 1999, as detailed in Chapter 3, Section 3.2.4.3. Vegetation data (species counts and cover assessments) were collected after burning from all plots at June 1997, October 1997, April 1998, December 1998 and September 1999, as described in Chapter 3, Section 3.2.8.

5.2.5 Statistics used in this chapter

Statistics used in this chapter are fully detailed in Chapter 3, Section 3.2.9.2. For both experimental sites, an analysis of variance with covariates (ANCOVA) (Quinn and Keough 2002) was used to test for significant differences (P<0.05) in the number of post fire emergent boneseed seedlings between treatments at and between each measurement time (Tables 5.2, 5.3, 5.4, 5.5, 5.6, and 5.7 for the species rich site, and Tables 5.11, 5.12, 5.13, and 5.14 for the degraded site)(Kenward 1987; Hancock 2000; Lorimer 2001). The numbers of boneseed seedlings present over time after burning are presented with lower case letters denoting significant differences between treatment effects *at* each sampling time, in Table 5.8 (species rich site) and Table 5.15 (degraded site) and the percentage changes in boneseed plant numbers *between* each sampling time, in Table 5.9 (species rich site) and Table 5.16 (degraded site). Percentage boneseed ground cover in treatment plots and subplots at the species rich site was analysed using a split-plot ANOVA (Table 5.10a)(Genstat 2002; Quinn and Keough 2002). Mean boneseed seedling heights in treatment plots and subplots at the species rich site were analysed using a split-plot ANOVA (Table 5.10b)(Genstat 2002). The mean number of flowering boneseed seedlings m^{-2} in treatment plots and subplots at the species rich site was analysed using a split-plot ANOVA (Table 5.10c)(Genstat 2002). For the degraded site, boneseed ground cover was compared for all treatments using a one-way ANOVA with randomized blocking (Table 5.18a)(Genstat 2002; Quinn and Keough 2002). Mean boneseed seedling heights in treatment plots at the degraded site were analysed using a general ANOVA with randomized blocking (Table 5.18b)(Genstat 2002; Quinn and Keough 2002). The mean number of first year flowering boneseed plants m^{-2} in treatment plots at the degraded site were analysed using a one-way ANOVA with randomized blocking (Table 5.18c)(Genstat 2002; Quinn and Keough 2002). At the degraded site the relationships (slopes) between boneseed seedling biomass (dry weight) and the fecundity of each respective flowering seedling was analysed using a regression analysis with groups, on untransformed data for plots in which no prior herbicide had been applied and plots where seedlings had previously been sprayed with either metsulfuron-methyl or glyphosate herbicides (Table 5.19) (Lorimer 2001; Genstat 2002).

5.3 Results

5.3.1 Post-fire boneseed seedling emergence

At both sites the decline of the viable boneseed soil seed bank after burning was due to a combination of seed death (Chapter 4) and seedling emergence. The variable fire temperatures stimulated between 4 and 74% of boneseed seeds to germinate across both sites in the four months following fire (Table 5.1).

5.3.1.1 The native species rich site

At the species rich site the hotter burn temperatures, 250 to 300°C on the soil surface and 50°C at 2 cm below the surface, killed seeds in the litter layer and top layer of soil and caused the germination of seeds deeper down in the soil profile. After four months at this site, boneseed seedling emergence ranged from 4 to 17% (Table 5.1), the soil surface was charred (Table 4.3) and many emerging seedlings germinated from seed that had been buried more than 2 cm deep in the soil. Burn temperatures close to 300°C caused less seedling emergence (4 to 17%, Table 5.1) as well as decreasing the soil seed bank by up to 97% (Table 4.2), indicating that the hotter fire killed more seeds.

5.3.1.2 The degraded site

By contrast, at the degraded site area 1 (average of 158°C) where temperatures of less than 100°C occurred in many places a significantly larger proportion (74%) of the boneseed soil seed bank emerging as seedlings (Table 5.1). Many boneseed population structures at the degraded site (infestation areas 3, 4 and 5) experienced fire temperatures around 200°C and had boneseed seedling emergence rates of approximately 25% of the pre-fire soil seed bank (Figure 5.1). After four months, boneseed seedling emergence was 11% for the hottest burnt areas of the degraded site (Table 5.1). In these hotly burnt areas an average of 216 ± 74 boneseed seedlings m^{-2} emerged after fire (Table 5.1), fewer than for any other area of this site. Lower burn temperatures caused greater seedling emergence, indicating that fires of lower temperatures killed fewer seeds (Figure 5.1c). The lower temperature burns did not heat the soil as deeply as the hotter burns (see Chapter 4) and seeds that were buried deeper were neither killed nor stimulated to germinate.

Table 5.1 Boneseed seedling emergence four months after burning at the species rich site, and three months after burning at the degraded site, as a proportion of the pre-fire boneseed soil seed bank.

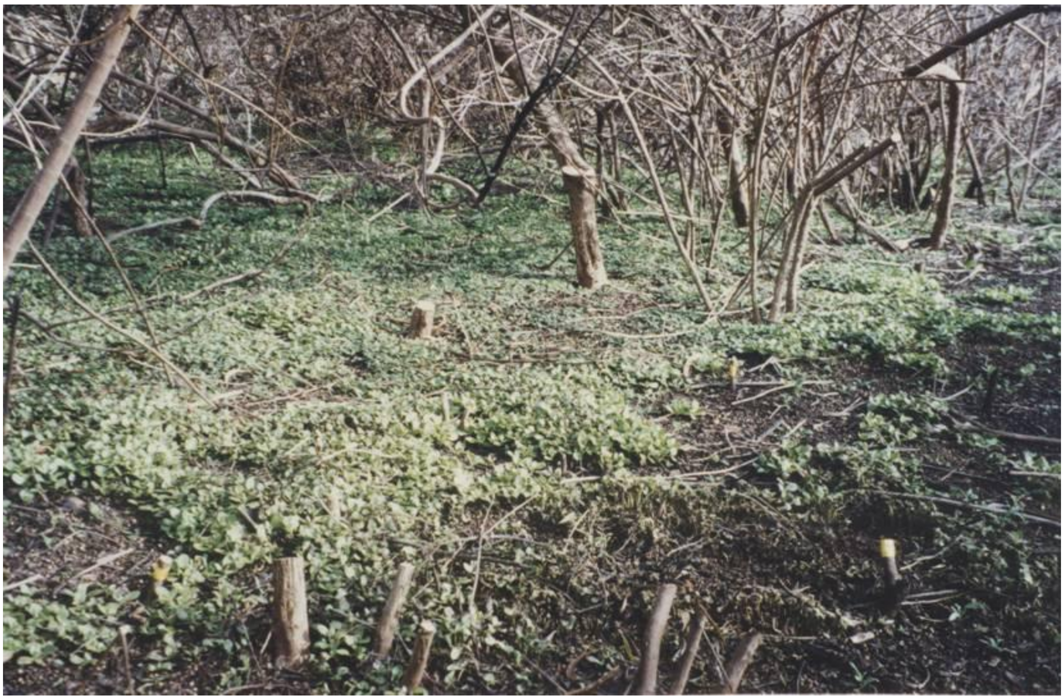
Boneseed infestation sub-type	**Average maximum fire temperature ^{o}C**	**Average number pre fire viable seeds m^{-2} $\pm$ s.e.m., (median)**	**Average number of seedlings m^{-2} emerged after burning $\pm$ s.e.m.**	**Seedling emergence as a % of pre-fire soil seed bank**
1	273	189 $\pm$ 49, (105)	31 $\pm$ 6.73	17
2	297	617 $\pm$ 120, (421)	27 $\pm$ 4.76	4
Whole species rich site mean	285	403 $\pm$ 70, (210)	29 $\pm$ 4.06	7
1	158	1970 $\pm$ 246, (1315)	1461 $\pm$ 300	74
2	292	1926 $\pm$ 167, (1526)	216 $\pm$ 74[A]	11
3	220	3439 $\pm$ 365, (2104)	1077 $\pm$ 234	32
4	219	2453 $\pm$ 451, (1473)	647 $\pm$ 198	26
5	199	3604 $\pm$ 316, (2736)	851 $\pm$ 233	24
Whole degraded site mean	218	2737 $\pm$ 143 (1894)	856 $\pm$ 115	32

[A] Using all six plots of the degraded boneseed infestation sub-type 2 resulted in an overall degraded site average of 242 $\pm$ 74 seedlings m^{-2} that emerged after fire or 14% of the pre-fire soil seed bank.

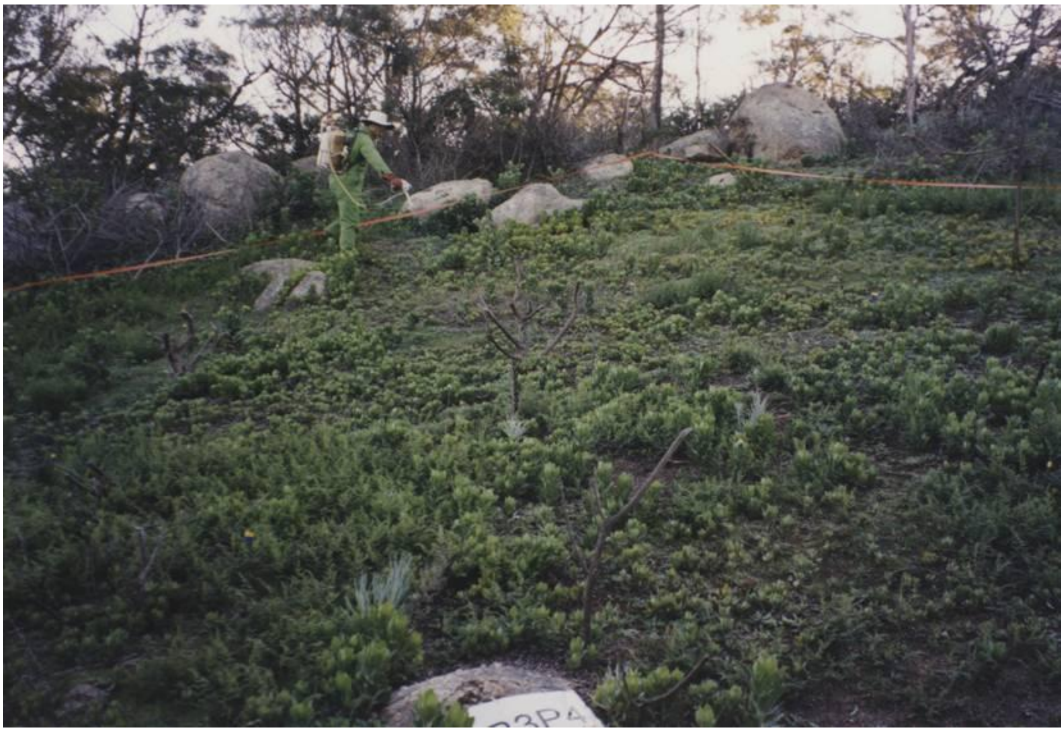
a)

b)

c)



d)



e)

Figure 5.1 Boneseed control treatments and treatment timing at the species rich **a)** and **b)** and degraded **c)**, **d)** and **e)** sites. Photos show **a)** *P. sieberiana* (in square patches), boneseed seedlings and other species growing on ash bed four months after burning, **b)** elimination of boneseed using fire, metsulfuron-methyl applied four months after burning and (in top right and bottom left corners of frame) competition from native grass, **c)** dense boneseed seedlings five months after burning showing fungal infection of seedlings (lower right hand corner of photo), **d)** spraying of boneseed seedlings in degraded native vegetation 17 months after fire, and **e)** successful boneseed population control using metsulfuron-methyl applied 17 months after burning.

5.3.2 Effects of post-fire boneseed control treatments on reducing the number and impact of boneseed seedlings

5.3.2.1 Effect of herbicide, hand-pulling treatments and distributed native grass seed on reducing numbers of post-fire boneseed seedlings and boneseed seedling growth at the species rich site

At the species rich site boneseed seedlings were counted four times after the April 1998 controlled burn: in August 1998, October 1998, May 1999 and September 1999 (Figure 5.1). The ante-dependence test showed that up to two previous measurements were required as covariates to analyse these data ($p<0.001$ at order 2) (Tables 5.2 and 5.3)(Kenward 1987; Hancock 2000; Lorimer 2001). Subplots with the native grass *P. sieberiana* added after controlled burning were not sprayed with the early glyphosate herbicide application as it was assumed that the grass would have been killed by glphosate application (Werth et al. 2008).The treatment „Gly98-Pull99" was therefore removed from the ante-dependence and contrast analyses. At the species rich site there was a significant difference between one or more treatments at each time after August 1998 (ante-dep $p<0.001$) after accounting for the boneseed numbers at up to two previous times for each treatment (Tables 5.4, 5.5, 5.6 and 5.7).

At the end of the first growth season after burning at the species rich site, boneseed seedling densities averaged 30 seedlings m^{-2} (Table 5.8). The numbers of boneseed seedlings in control plots remained almost the same throughout the experiment, with only a 9% reduction (Table 5.8 and 5.9). No significant difference in boneseed numbers was found between treatments at the end of the first growth season (Table 5.8), prior to the early herbicide treatments being applied later that same month. Eight weeks after the early herbicide treatments (October 1998), seedling numbers in plots treated with either metsulfuron-methyl or glyphosate herbicide had been reduced by 99 and 100% respectively (Table 5.8). The number of seedlings in the early herbicide treatment plots was significantly less than in untreated plots nine months after the treatments were applied (May 1999, metsulfuron-methyl treated plots Table 5.8, Figure 5.1b).

Metsulfuron-methyl was shown to be effective in killing all boneseed seedlings when applied in May 1999 (Tables 5.8 and 5.9). This herbicide and timing is one successful control strategy for completely controlling the boneseed infestation in a species rich temperate ecosystem. Glyphosate herbicide applied at this time resulted in a 99.5% reduction of boneseed seedlings (Table 5.9). Although there was no statistical difference between the effects of the two late herbicide treatments on boneseed seedling numbers (Table 5.8), the elimination of all boneseed seedlings in plots sprayed with the late metsulfuron-methyl herbicide application was a highly desirable result. By the end of the experiment (September 1999) there were significantly more seedlings in plots that had been sprayed with the early herbicide application of metsulfuron-methyl, than with the later application timing (Table 5.8) although numbers of seedlings were low.

There was no difference between the number of first year boneseed plants remaining in control plots and plots where all first year flowering boneseed plants had been hand-pulled (Table 5.8). However, there were fewer seedlings in plots where metsulfuron-methyl herbicide had been sprayed prior to the hand-pulling of remaining seedlings (Table 5.8).

At the species rich site, manual distribution of seed of the native C3 grass *P. sieberiana* to the post-fire ash-bed led to the growth of dense, continuous swards of *P. sieberiana* (Figure 5.1a). These plots had a trend towards increased total plant cover (Figure 5.8) and less light reached the emerging boneseed seedlings across all treatments in which *P. sieberiana* was sown. There was no statistically significant reduction in the number of boneseed seedlings in subplots due to the distribution of seed of the native grass *P. sieberiana* at the species rich site (P>0.05, Table 5.8). However, very few boneseed seedlings survived in plots sprayed with herbicide (P<0.05, Table 5.8, Figure 5.1), regardless of the distribution of native grass seed (treatment level P>0.05, Table 5.8). No boneseed seedlings survived in subplots where seed of *P. sieberiana* was distributed and which were also treated with metsulfuron-methyl herbicide application in the first growth season after burning (Figure 5.1b), or in plots treated with metsulfuron-methyl herbicide in the second growth season after burning with or without distribution of *P. sieberiana* (Table 5.8). Grass addition subplots in glyphosate herbicide plots were not sprayed as grass death would have occurred. Fewer boneseed seedlings survived in plots treated with the later glyphosate treatment where grass was distributed, compared with control plots (P<0.05, Table 5.8). Where boneseed seedlings existed in herbicide treated plots, they provided negligible ground cover (Figure 5.3a, Table 5.10a), were shorter than seedlings in unsprayed plots (P<0.05, Figure 5.3b, Table 5.10b) and none were in flower (Figure 5.3c,

Table 5.10c). The reduction of boneseed seedling numbers to zero was a biologically significant weed reduction, as no boneseed re-establishment would occur in these subplots.

Whilst there was no difference in the number of boneseed seedlings found in the control treatments with or without the distribution of *P. sieberiana* seed (Table 5.8), a 24% reduction in ground cover of boneseed seedlings occurred (P>0.05, Figure 5.3a). At the species rich site there was no difference in average maximum height of boneseed plants in control plots due to *P. sieberiana* (P>0.05, Figure 5.3b). In control plots, there was no difference between the number of boneseed seedlings in flower in subplots with and without *P. sieberiana* seed: 1.34 and 1.86 seedlings m^{-2} respectively (P>0.05, Figure 5.3c).

The number of boneseed seedlings at the species rich site in unsprayed plots where the only additional weed control was pulling of flowering boneseed plants was similar to control plots (Table 5.8). At the species rich site, ground cover by boneseed seedlings in plots where flowering boneseed was pulled, but with no grass previously having been distributed was similar to that in control plots with no grass distributed (P>0.05, Figure 5.3a). However, when grass was distributed and the dominant first year flowering plants had been hand-pulled, the remaining seedlings provided only 10% cover. Although not statistically significant (P>0.05), this was the largest decrease in boneseed ground cover due to distributing grass seed across all treatments. *P. sieberiana* had no effect on boneseed seedling height, even in plots where the first year flowering plants were hand-pulled (P>0.05, Figure 5.3b). At the species rich site, there was no difference in the number of boneseed plants in flower in plots where flowering boneseed had been hand-pulled, with or without *P. sieberiana*; 0.28 and 0.14 plants m^{-2} respectively (P>0.05, Figure 5.3c).

Table 5.2 Sequential comparison of anti-dependence structures for boneseed seedling numbers over time at the species rich site.

	Unadjusted Chi-square statistic	Adjustment factor	Adjusted Chi-square statistic	d.f.	Prob.
Order 0 v order 1	293.73	0.571	167.59	3	<0.001
Order 1 v order 2	27.32	0.554	15.14	2	<0.001
Order 2 v order 3	1.70	0.546	0.93	1	0.336

Table 5.3 Comparison of ante-dependence structures with max order for boneseed seedling numbers over time at the species rich site.

	Unadjusted Chi-square statistic	Adjustment factor	Adjusted Chi-square statistic	d.f.	Prob.
Order 0 v order 3	322.75	0.561	181.01	6	<0.001
Order 1 v order 3	29.02	0.551	16.00	3	0.001
Order 2 v order 3	1.70	0.546	0.93	1	0.336

Table 5.4 Tests of PlotTMT assuming ante-dependence structure of order 2 for boneseed seedling numbers over time at the species rich site.

	Test for change at each time			**Overall test up to each time**		
Time	**Statistic**	**d.f.**	**Prob.**	**Statistic**	**d.f.**	**Prob.**
1	3.339	4	0.503	3.339	4	0.503
2	115.988	4	<0.001	120.871	8	<0.001
3	23.665	4	<0.001	142.781	12	<0.001
4	167.6629	4	<0.001	314.657	16	<0.001
Overall test using data from all the times						
Statistic 314.657	d.f. 16	Probability <0.001	Significant difference between treatments			

Table 5.5 Tests of subplTMT assuming ante-dependence structure of order 2 for boneseed seedling numbers over time at the species rich site.

	Test for change at each time			**Overall test up to each time**		
Time	**Statistic**	**d.f.**	**Prob.**	**Statistic**	**d.f.**	**Prob.**
1	1.173	3	0.759	1.173	3	0.759
2	2.611	3	0.456	3.803	6	0.703
3	1.940	3	0.585	5.745	9	0.765
4	4.924	3	0.177	10.776	12	0.548
Overall test using data from all the times						
Statistic 10.776	d.f. 12	Probability 0.548	No significant difference between subplot treatments			

Table 5.6 Tests of PlotTMT.SubplTMT assuming ante-dependence structure of order 2 for boneseed seedling numbers over time at the species rich site.

	Test for change at each time			**Overall test up to each time**		
Time	**Statistic**	**d.f.**	**Prob.**	**Statistic**	**d.f.**	**Prob.**
1	13.045	12	0.366	13.045	12	0.366
2	15.275	12	0.227	28.349	24	0.246
3	9.884	12	0.626	38.038	36	0.377
4	18.925	12	0.090	57.174	48	0.171
Overall test using data from all the times						
Statistic 57.174	d.f. 48	Probability 0.171	No significant interaction between plot and subplot treatments			

Table 5.7 Analysis of Variance (adjusted for covariates) for boneseed seedling numbers over time at the species rich site.

Source of variation	**d.f.(m.v.)**	**s.s**	**m.s.**	**v.r.**	**cov.ef.**	**F pr.**
Transect stratum						
Covariates	2	5.5299	2.7649	7.62		0.067
Lo98	1	4.8595	4.8595	13.39		0.035
Lm99	1	0.6703	0.6703	1.85		0.267
Residual	3	1.0885	0.3628	0.64	3.64	
Transect.PlotTMT stratum						
PlotTMT	4	136.3889	34.0972	60.01	0.34	<.001
Covariates	2	3.0816	1.5408	2.71		0.095
Lo98	1	1.1206	1.1206	1.97		0.178
Lm99	1	1.9610	1.9610	3.45		0.081
Residual	17(1)	9.6600	0.5682	3.01	1.18	
Transect.PlotTMT.SubplTMT stratum						
SubplTMT	3	0.9583	0.3194	1.69	0.98	0.177
PlotTMT.SubplTMT	12	3.8165	0.3180	1.68	0.96	0.091
Covariates	2	11.2863	5.6431	29.86		<.001
Lo98	1	10.0459	10.0459	53.16		<.001
Lm99	1	1.2403	1.2403	6.56		0.013
Residual	67(6)	12.6622	0.1890		1.84	
Total	112(7)	239.6409				

La98 =log(timeAug98boneseed seedling numbers+1)
Lo98 =log(timeOct98boneseed seedling numbers+1)
Lm99 =log(timeMay99boneseed seedling numbers+1)
Ls99 =log(timeSept99boneseed seedling numbers+1)

Table 5.8 Boneseed seedling numbers over time at the species rich site in treatment subplots with and without seed of *P. sieberiana* distributed two weeks after burning (in March 98).

	Mean number of boneseed seedlings m^{-2*}			
	August 98	**October 98**	**May 99**	**September 99**
Control + grass	29.29^{a}	23.65^{a}	24.34^{a}	22.42^{a}
Control	29.57^{a}	25.99^{a}	25.99^{a}	23.65^{a}
Early gly-Late pull	35.42^{a}	0^{b}	0.35^{b}	0.46^{b}
Early met-Late pull + grass	26.70^{a}	2.07^{b}	0^{b}	0^{b}
Early met-Late pull	32.55^{a}	0.46^{b}	0.23^{b}	0.23^{b**}
Late pull + grass	(37.54)^{a}	(18.29)^{a}	(32.18)^{a}	19.67^{a}
Late pull	(33.56)^{a}	(31.49)^{a}	(24.62)^{a}	31.91^{a}
Late gly + grass	(45.02)^{a}	(39.65)^{a}	(35.07)^{a}	0.58^{c}
Late gly	(24.76)^{a}	(22.69)^{a}	(22.69)^{a}	0.12^{c}
Late met + grass	(22.00)^{a}	(17.08)^{a}	(18.34)^{a}	0^{c}
Late met	(23.73)^{a}	(21.55)^{a}	(21.44)^{a}	0^{c**}

* Letters denote differences between treatments at a particular time (column), not across collection times (rows)(P<0.05).
** Although there was no difference between herbicide treatments at each application time, there was a difference between the early and the late metsulfuron-methyl treatments (P<0.001).
Treatments yet to be undertaken are shown in brackets.

Table 5.9 Percentage change in boneseed seedling numbers after post-burn seedling emergence at four months after fire and after boneseed seedling control treatments at the species rich site.

Post burn boneseed seedling control treatments[AB]	First post-burn growth season up to 7 months post-burn (Aug to Oct)	First summer post-burn from 7 to 13 months post-burn (Oct to May)	Second post-burn growth season from 13 to 17 months post-burn (May to Sept)
Control	-12.1 [a]	0 [a]	-9.00 [a]
G98P99	-100 [b]	Na	+33.3 [b]
M98P99	-98.6 [b]	-50.0 [b]	0 [a]
P99	(-6.2) [a]	(-21.8) [a]	+29.6 [b]
G99	(-8.3) [a]	(0) [a]	-99.5 [c]
M99	(-9.2) [a]	(-0.5) [a]	-100 [c]

[A] Control; G98P99, First growth season glyphosate herbicide (August 1998), then hand-pulling of first year flowering boneseed plants (June 1999); M98P99, First growth season metsulfuron-methyl herbicide (August 1998), then hand-pulling of first year flowering boneseed plants (June 1999); P99, Hand-pulling of first year flowering boneseed plants (June 1999); G99, Second growth season glyphosate herbicide (May 1999); M99, Second growth season metsulfuron-methyl herbicide (May 1999). [B] Treatments yet to be undertaken are shown in brackets.

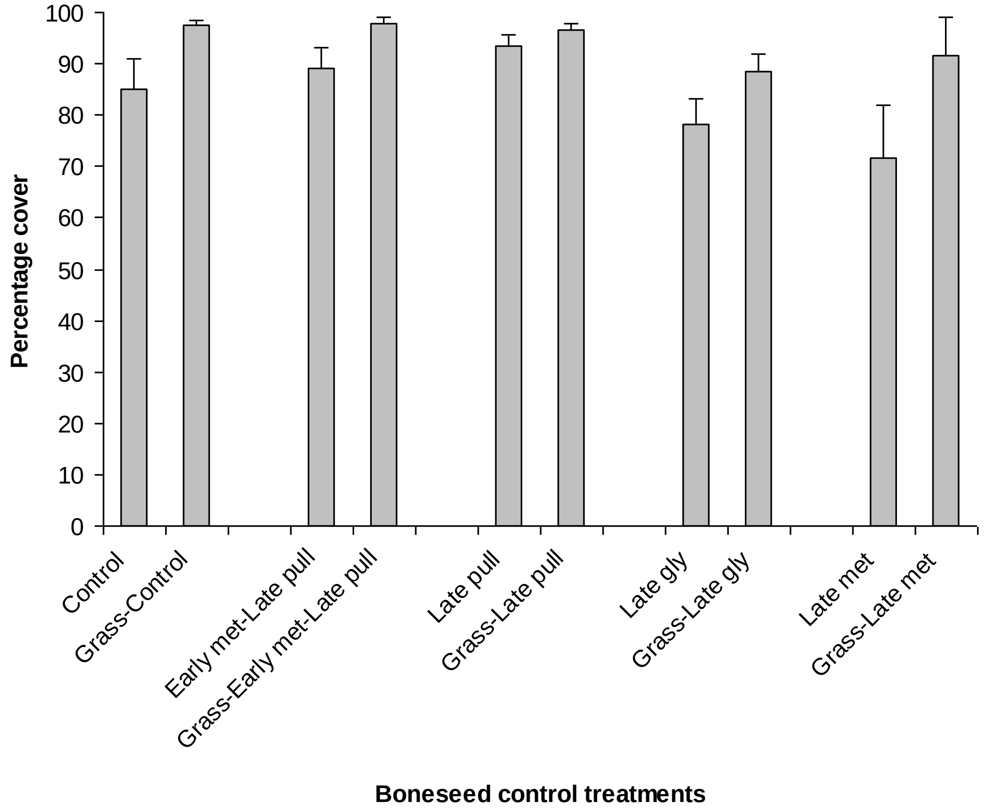


Figure 5.2 Comparison of total ground cover of all species in herbicide and hand pull treatments where seed of *P. sieberiana* was and was not distributed.

Table 5.10a Split-plot ANOVA with randomized blocking of percentage of ground cover provided by boneseed seedlings in control and handpull plots only* at the species rich site in September 1999, after burning and weed control treatments had been applied (Figure 5.3a).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Transect stratum	5	8713.1	1742.6	8.43	
Transect.Treatment stratum					
Treatment	1	361.5	361.5	1.75	0.256,ns
Residual	4(1)	826.5	206.6	0.81	
Transect.Treatment.Supplottmt stratum					
Subplottmt	1	1214.5	1214.5	4.73	0.061,ns
Treatment	1	258.7	258.7	1.01	0.345,ns
Residual	8(2)	2053.0	256.6	0.88	
Transect.Treatment.Subplottmt.Units stratum	20(4)	5856.7	292.8		
Total	40(7)	13521.9			

ns, not significant, P>0.05.

* Data for all other treatments contained too many zero‟s for meaningful inclusion in this analysis.

Table 5.10b Split-plot ANOVA with randomized blocking of boneseed plant heights at the species rich site in September 1999, after burning and weed control treatments had been applied (Figure 5.3b).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Transect stratum	5	3.6774	0.7355	0.34	
Transect.Treatment stratum					
Treatment	3	298.2263	99.4088	46.14	<.001
Residual	14(1)	30.1633	2.1545	2.55	
Transect.Treatment.Supplottmt stratum					
Subplottmt	1	4.8430	4.8430	5.74	0.028,ns
Treatment	3	0.4161	0.1387	0.16	0.919,ns
Residual	18(2)	15.1898	0.8439	0.94	
Transect.Treatment.Subplottmt.Units stratum	46(6)	37.8178	0.9004		
Total	86(9)	345.9761			

ns, not significant, P>0.05.

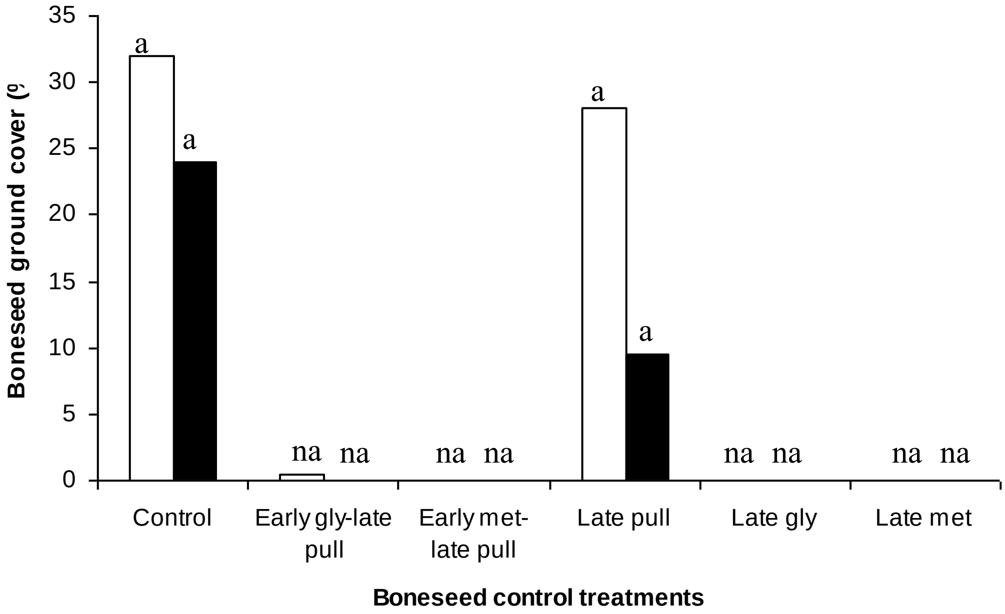
Table 5.10c Split-plot ANOVA with randomized blocking of flowering boneseed plants in control and handpull plots only* at the species rich site in September 1999, after burning and weed control treatments had been applied (Figure 5.3c).

Source of variation	**d.f.(m.v.)**	**s.s.**	**m.s.**	**v.r.**	**F pr.**
Transect stratum	4(1)	1.4974	0.3743	0.57	
Transect.Treatment stratum					
Treatment	1	1.1906	1.1906	1.8	0.251,ns
Residual	4(1)	2.6453	0.6613	5.95	
Transect.Treatment.Supplottmt stratum					
Subplottmt	1	0.0174	0.0174	0.16	0.703,ns
Treatment	1	0.0721	0.0721	0.65	0.444,ns
Residual	8(2)	0.8889	0.1111	0.29	
Transect.Treatment.Subplottmt.Units stratum	20(4)	7.6480	0.3824		
Total	39(8)	13.7440			

ns, not significant, P>0.05.

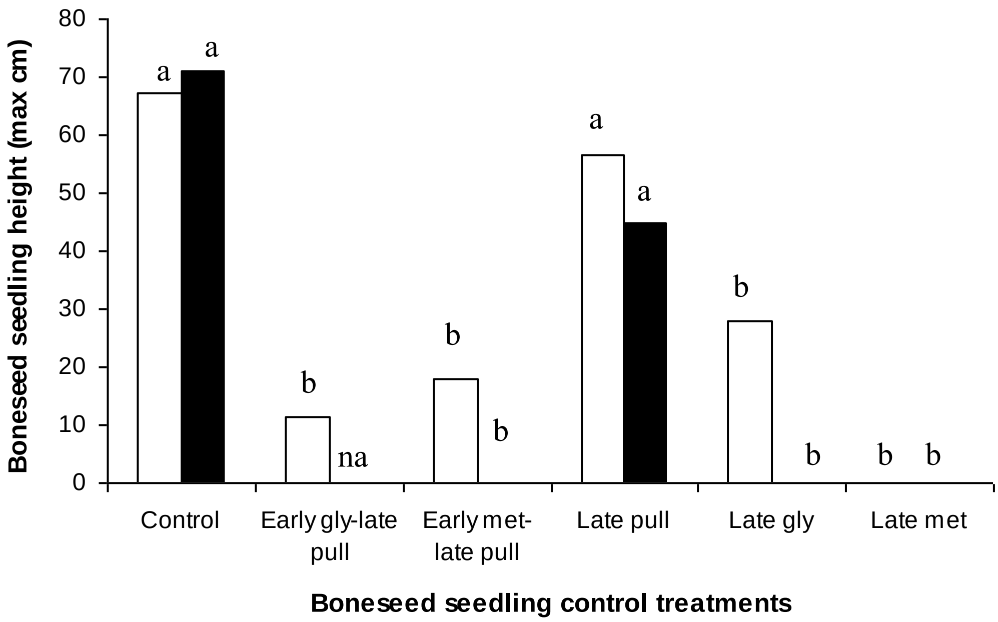
* Data for all other treatments contained too many zero‟s for meaningful inclusion in this analysis.

a)



35
30
25
20
15
10
5
0
Boneseed ground cover (%
a
a
na na
na na
a
a
na na
na na
Control
Early gly-late pull
Early met-late pull
Late pull
Late gly
Late met
Boneseed control treatments

b)



80
70
60
50
40
30
20
10
0
Boneseed seedling height (max cm)
a a
b na
b b
a a
b b
b b
Control
Early gly-late pull
Early met-late pull
Late pull
Late gly
Late met
Boneseed seedling control treatments

c)

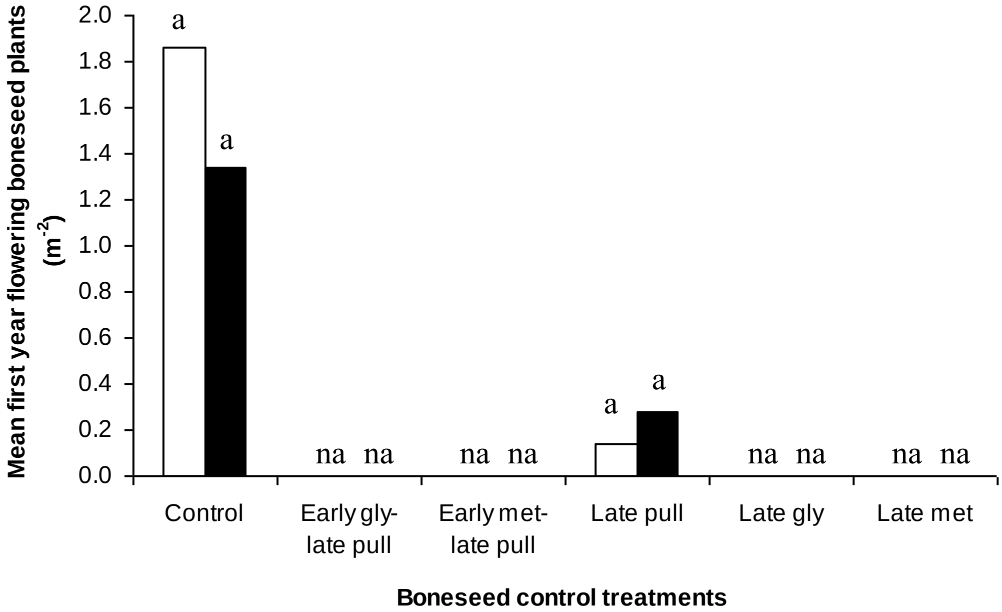


Figure 5.3 Boneseed population vigour and reproductive capacity in September 1999, after burning and boneseed seedling control treatments and sub-plot treatments of increasing native grass density at the species rich site: **a)** the percentage of cover provided by boneseed seedlings, **b)** the average maximum boneseed seedling height and **c)** the number of flowering boneseed plants m^{-2}, in plot and sub-plot treatments at the species rich site at the end of experimental duration, where no grass seed was added (open bars), and where seed of the native grass *P. sieberiana* was added (solid bars). Different letters above bars indicate statistically significant differences from control treatments (P<0.05).

5.3.2.2 Effect of herbicide and hand-pulling treatments on reducing numbers of post-fire boneseed seedlings and boneseed seedling growth at the degraded site

At the degraded site boneseed seedlings were counted on five occasions, June 1997, October 1997, April 1998, December 1998 and September 1999 during the three years following controlled burning (Table 5.15). The anti-dependence test showed that four previous measurements needed to be used as covariates when analysing this data set ($p<0.001$, Table 5.11 and 5.12) (Kenward 1987; Hancock 2000; Lorimer 2001). The profile (relative graphical position) of boneseed seedling numbers within all treatments changed significantly between each measurement time after June 1997 ($p<0.001$), except between measurements taken in October 1997 and April 1998 (Tables 5.13, 5.14 and 5.16). There was a significant difference between one or more treatments at each time after June 1997 (ante-dep $p<0.001$), after accounting for the boneseed numbers at up to four previous times for each treatment (Table 5.14). However, if five outliers (all where boneseed seedling numbers = 0) were removed from the ante-dependence analysis, then there was no significant difference between treatments at April 1998. There was a greater influence of the covariates (that is, the number of seedlings present in October 1997 and June 1997), in April 1998 than of the treatments (treatment m.s.=1.8466, while covariates m.s.=16.7352)(data not shown – September 1999 analyses shown in table 5.14) (Lorimer 2001).

Boneseed seedlings that had emerged by three months after controlled burning at the degraded site reached densities of up to 1461 seedlings m^{-2}, with an average of 856 seedlings m^{-2} across the whole degraded site (Table 5.1, Figure 5.1c). At three months after the fire, no further control treatments had yet been applied and, as expected, there was no significant difference between numbers of seedlings in treatment plots (Table 5.15).

Eight weeks after the application of metsulfuron-methyl and glyphosate herbicides in the first growing season after the fire (October 1997), the herbicide treatments had caused a significant reduction ($P<0.001$, Table 5.15) in seedling numbers (87%, Table 5.16), compared with the control and other, as yet untreated, plots. There was no significant difference between the numbers of boneseed seedlings in plots treated with either glyphosate or metsulfuron-methyl herbicide at the early application time (Table 5.15), with means of 152 and 99 seedlings m^{-2} remaining, respectively.

A year after controlled burning and eight months after the first growth season herbicide application (April 1998), the number of boneseed seedlings in treated plots remained significantly lower than in untreated plots (Table 5.15). There was no difference in the number of seedlings in plots treated with the glyphosate or metsulfuron-methyl herbicides treatments (Table 5.15). Natural seedling mortality apparently caused by summer water deficiency stress (Bureau of Meteorology 2007) and infection by fungal pathogens (*Itersonilia perplexans* Derx, *Pythium* spp. possibly *P. polymastum* Drechsler and *Sclerotinia minor* Jagger) had caused a 51% reduction of boneseed seedlings in control plots by this time (Table 5.16), to an average of 105 seedlings m^{-2} (Figure 5.1c, Table 5.15). When compared with the natural decline in seedling numbers in control plots over the summer period (October to April, Table 5.16), the average of 56 seedlings m^{-2} remaining in both early herbicide treated plots indicated a poor effect of the early herbicide treatments (Table 5.15).

Sixteen months after the early herbicide application, and four months after the later herbicide application and hand-pulling treatment (December 1998), the late herbicide treatments had significantly fewer seedlings than the control plots (Table 5.15, Figure 5.1d). There were also fewer seedlings in the late glyphosate treatments (2.4 seedlings m^{-2}) than in the late metsulfuron-methyl treated plots (87 seedlings m^{-2}, Table 5.15). During the second growing season after the fire, from April 1998 to December 1998, the number of seedlings in plots that received the early herbicide application increased (Table 5.16), despite all first year flowering plants having been hand-pulled in September of that same year. There was no difference between the number of boneseed seedlings in control plots compared to plots where first year flowering plants were hand-pulled without having had prior herbicide application (Table 5.15). Likewise, hand-pulling first year flowering plants had no impact on boneseed seedling reduction compared to plots where either herbicide was applied prior to hand-pulling the first year flowering plants (Table 5.15). However, the time taken to hand-pull first year flowering plants in plots that had previously been sprayed with herbicide was less than half that taken to pull the first year flowering plants in unsprayed plots (Table 5.17). Although the numbers of first year flowering plants m^{-2} were similar between these three treatment groups (Table 5.17), there were more non-flowering plants m^{-2} in unsprayed plots compared to those that had been sprayed (Table 5.17, Table 5.15), resulting in smaller and more difficult to locate first year flowering plants in the unsprayed plots.

At the end of the experiment, glyphosate or metsulfuron-methyl herbicide when applied at the end of the second growing season, were equally effective in controlling boneseed seedlings (Table 5.15, Figure 5.1d and e). There were fewer boneseed seedlings in these late herbicide treated plots compared with control plots and all other treatments (Table 5.15). The number of seedlings in the control treatments remained reasonably constant over the last half of the experiment at around 100 seedlings m^{-2} (Table 5.15) and there was no significant difference to the hand-pull or early herbicide followed by hand-pulling treatments (Table 5.15).

At the degraded site, the late herbicide treatments were the most successful treatments for reducing both the number and growth of boneseed seedlings. The late glyphosate sprayed plots (with 7.3 boneseed seedlings m^{-2}) had less ground cover (1%) and fewer boneseed plants in flower (0.06 m^{-2}) than the control and all other treatment plots except the late metsulfuron-methyl treatment plots ($P<0.05$, Figure 5.4a and c, Table 5.18a and c). The late metsulfuron-methyl sprayed plots also had fewer boneseed seedlings (6.8 m^{-2}), less ground cover (5%) and fewer boneseed seedlings in flower (1.28 m^{-2}) than controls and all other treatment plots except late glyphosate treated plots ($P<0.05$, Table 5.15, Figure 5.4a and c). The average maximum height of boneseed seedlings at the degraded site was similar across all treatment plots ($P>0.05$, Figure 5.4b, Table 5.18b). More flowering seedlings were present in early metsulfuron-methyl treated plots than in control plots ($P<0.05$, Figure 5.4c).

When only the larger, flowering boneseed seedlings were hand-pulled, with no additional herbicide treatment, the boneseed population density was higher than in control plots. Boneseed in plots where flowering seedlings were hand-pulled provided a higher level of boneseed ground cover than any other treatment plots ($P<0.05$), but a similar level of cover to control plots ($P>0.05$, Figure 5.4a). Where flowering boneseed seedlings were hand-pulled more flowering seedlings were present (16 m^{-2}) than in any other treatment plots except the early metsulfuron-methyl treated plots ($P<0.05$, Figure 5.4c).

Table 5.11 Sequential comparison of anti-dependence structures for boneseed seedling numbers over time at the degraded site.

	Unadjusted Chi-square statistic	**Adjustment factor**	**Adjusted Chi-square statistic**	**d.f.**	**Prob.**
Order 0 v order 1	328.52	0.817	268.29	4	<0.001
Order 1 v order 2	45.98	0.810	37.26	3	<0.001
Order 2 v order 3	39.64	0.806	31.94	2	<0.001
Order 3 v order 4	6.61	0.803	5.31	1	0.021

Table 5.12 Comparison of ante-dependence structures with max order for boneseed seedling numbers over time at the degraded site.

	Unadjusted Chi-square statistic	**Adjustment factor**	**Adjusted Chi-square statistic**	**d.f.**	**Prob.**
Order 0 v order 4	420.76	0.811	341.27	10	<0.001
Order 1 v order 4	92.24	0.807	74.48	6	<0.001
Order 2 v order 4	46.26	0.805	37.22	3	<0.001
Order 3 v order 4	6.61	0.803	5.31	1	0.021

Table 5.13 Tests of TMT assuming ante-dependence structure of order 4 for boneseed seedling numbers over time at the degraded site.

	Test for change at each time			**Overall test up to each time**		
Time	**Statistic**	**d.f.**	**Prob.**	**Statistic**	**d.f.**	**Prob.**
1	11.879	5	0.036	11.879	5	0.036
2	70.203	5	<0.001	82.469	10	<0.001
3	12.713	5	0.026	94.669	15	<0.001
4	147.173	5	<0.001	245.216	20	<0.001
5	77.996	5	<0.001	323.791	25	<0.001
Overall test using data from all the times						
Statistic 323.791	d.f. 25	Probability <0.001	Significant difference between treatments			

Table 5.14 Analysis of Variance (adjusted for covariates) to boneseed seedling numbers over time at the degraded site.

Source of variation	**d.f.(m.v.)**	**s.s**	**m.s.**	**v.r.**	**Cov.ef.**	**F pr.**
Block stratum						
Covariates	4	11.1632	2.7908			
Lj97	1	1.5939	1.5939			
Lo97	1	0.0448	0.0448			
La98	1	5.8231	5.8231			
Ld98	1	3.7014	3.7014			
Block.Plot stratum						
TMT	5	60.0145	12.0029	6.55	0.28	0.002
6 vs 2,4	1	5.5653	5.5653	3.04	0.33	0.101, ns
1 vs 3,5	1	44.2210	44.2210	24.12	0.20	<.001
1 vs 6	1	0.6183	0.6183	0.34	0.75	0.570, ns
4 vs 2	1	0.0991	0.0991	0.05	0.85	0.819, ns
3 vs 5	1	2.1355	2.1355	1.16	0.42	0.297, ns
Covariates	4	46.3576	11.5894	6.32		0.003
Lj97	1	22.1660	22.1660	12.09		0.003
Lo97	1	15.1290	15.1290	8.25		0.011
La98	1	3.3775	3.3775	1.84		0.194
Ld98	1	5.6851	5.6851	3.10		0.097
Residual	16	29.3391	1.8337	3.15	2.06	
Block.Plot.Quadrat stratum						
Covariates	4	131.1178	32.7794	56.24		<.001
Lj97	1	58.2253	58.2253	99.89		<.001
Lo97	1	42.2709	42.2709	72.52		<.001
La98	1	8.5655	8.5655	14.69		<.001
Ld98	1	22.0561	22.0561	37.84		<.001
Residual	140(6)	81.6045	0.5829		2.53	
Total	173(6)	614.5301				

Table 5.15 The number of boneseed seedlings present over time at the degraded site after burning and the application of post-fire weed control treatments.

	Mean number of boneseed seedlings m^{-2*}				
Post burn boneseed seedling control treatments[A]	**June 97**	**October 97**	**April 98**	**December 98**	**September 99**
Control	**736**[a]	**214**[a]	**105**[a]	**105**[a]	**95**[a]
Gly97-pull98	**1296**[a]	**152**[b]	**56**[b]	**63**[b]	**59**[a]
Met97-pull98	**728**[a]	**99**[b]	**56**[b]	**57**[b]	**46**[a]
Pull98	**(845)**[a]	**(442)**[a]	**(192)**[a]	**192**[a]	**167**[a]
Gly98	**(879)**[a]	**(284)**[a]	**(131)**[a]	**2**[c]	**7**[b]
Met98	**(649)**[a]	**(250)**[a]	**(124)**[a]	**87**[c]	**7**[b]

[A] Control; G97P98, First growth season glyphosate herbicide (August 1997), then hand-pulling of first year flowering boneseed plants (September 1998); M97P98, First growth season metsulfuron-methyl herbicide (August 1997), then hand-pulling of first year flowering boneseed plants (September 1998); P98, Second growth season hand-pulling of first year flowering boneseed plants (September 1998); G98, Second growth season glyphosate herbicide (August 1998); M98, Second growth season metsulfuron-methyl herbicide (August 1998).

[B] (numbers in brackets) = treatments had not yet been applied.

Table 5.16 Percentage changes in boneseed plant numbers between seedling counts, after post-burn seedling emergence after fire and boneseed seedling control treatments at the degraded site.

	First post-burn growth season	First summer post-burn	Second post-burn growth season	Second summer & third growth season
Post burn boneseed seedling control treatments[AB]	**3 to 7 months post-burn (June to Oct)**	**7 to 13 months post-burn (Oct to April)**	**13 to 21 months post-burn (April to Dec)**	**21 to 30 months post-burn (Dec to Sept)**
Control	-70.94 [a]	-50.98[a]	-0.19 [a]	-9.08 [a]
Gly97-pull98	-88.26 [b] (pull98)	-62.98 [a]	+11.72 [b]	-5.72 [a]
Met97-pull98	-86.44 [b] (pull98)	-43.67 [a]	+3.24 [b]	-19.69 [a]
Pull98	(-47.72) [a]	(-56.52) [a]	-0.10 [a]	-12.98 [a]
Gly98	(-67.74) [a]	(-53.91) [a]	-98.16 [c]	+204.17 [b]
Met98	(-61.43) [a]	(-50.68) [a]	-29.47 [c]	-92.19 [c]

[A] Control; G97P98, First growth season glyphosate herbicide (August 1997), then hand-pulling of first year flowering boneseed plants (September 1998); M97P98, First growth season metsulfuron-methyl herbicide (August 1997), then hand-pulling of first year flowering boneseed plants (September 1998); P98, Second growth season hand-pulling of first year flowering boneseed plants (September 1998); G98, Second growth season glyphosate herbicide (August 1998); M98, Second growth season metsulfuron-methyl herbicide (August 1998). [B] (numbers in brackets) = treatments had not yet been applied.

Table 5.17 A comparison of the total number of first year flowering boneseed plants present, number of boneseed plants m^{-2} and the time taken to hand-pull all first year flowering boneseed plants present in the hand-pulling treatments with and without prior herbicide application in December 1998.

	Number of non-flowering boneseed seedlings m^{-2} [A]	**Number of flowering seedlings m^{-2}**	**Mean time taken to hand-pull all flowering boneseed seedlings per plot (minutes)**
Pull only 98	191.9	1.58	43
Gly97 Pull98	62.9	1.33	24
Met97 Pull98	57.4	1.66	15

[A] Measured in December 1998

Table 5.18a One-way ANOVA with randomized blocking of percentage of ground cover provided by boneseed seedlings at the degraded site in September 1999, after burning and weed control treatments had been applied (Figure 5.4a).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
BlockTran stratum	4	137.8	34.45	0.65	
BlockTran.Units stratum					
Treatment	5	5244.55	1048.91	19.78	<.001
Residual	20	1060.54	53.03		
Total	29	6442.89			

ns, not significant, P>0.05.

Table 5.18b General ANOVA with randomized blocking of boneseed plant heights at the degraded site in September 1999, after burning and weed control treatments had been applied (Figure 5.4b).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
BlockTran stratum	2(2)	81.59	40.79	0.56	
BlockTran.Units stratum					
Treatment	5	1956.93	391.39	5.39	0.018
Residual	8(12)	580.54	72.57		
Total	15(14)	1598.94			

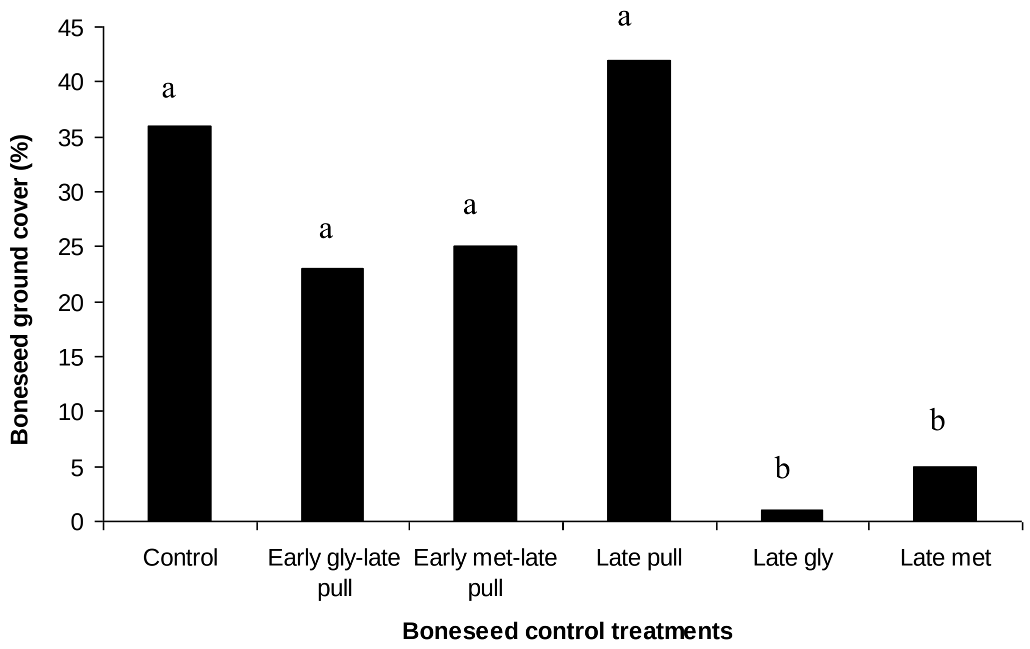
ns, not significant, P>0.05.

Table 5.18c One-way ANOVA with randomized blocking of flowering boneseed plants at the species rich site in September 1999, after burning and weed control treatments had been applied (Figure 5.4c).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
BlockTran stratum	2(2)	0.4848	0.2424	0.61	
BlockTran.Units stratum					
Treatment	5	28.6697	5.7339	14.44	<.001
Residual	10(10)	3.9714	0.3971		
Total	17(12)	21.6594			

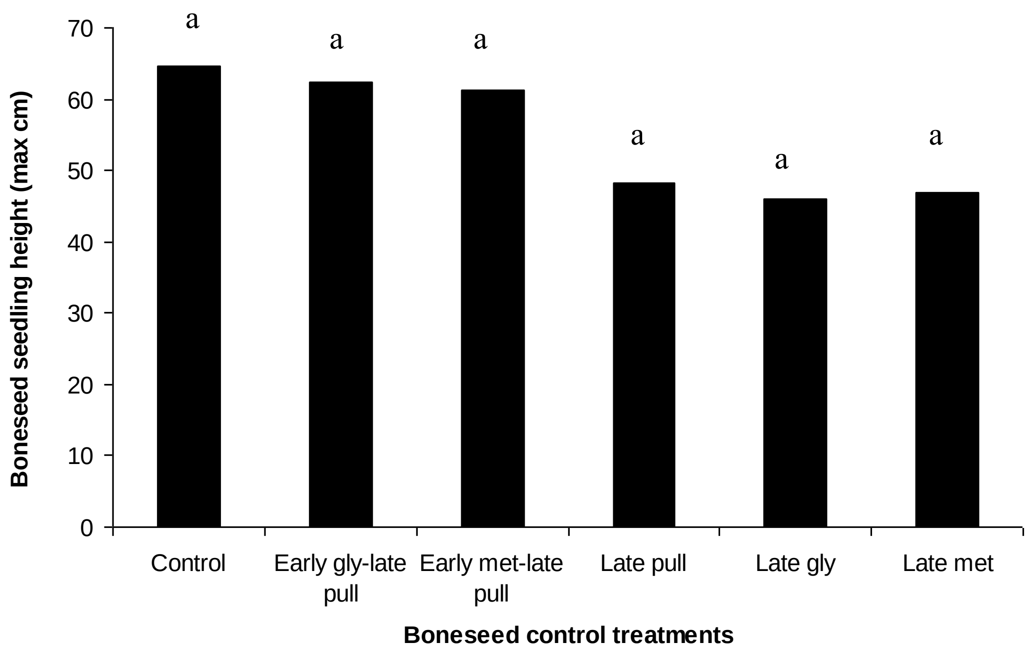
ns, not significant, P>0.05.

a)



Boneseed ground cover (%)
45
40
35
30
25
20
15
10
5
0
a
a
a
a
b
b
Control
Early gly-late pull
Early met-late pull
Late pull
Late gly
Late met
Boneseed control treatments

b)



Boneseed seedling height (max cm)
70
60
50
40
30
20
10
0
a
a
a
a
a
a
Control
Early gly-late pull
Early met-late pull
Late pull
Late gly
Late met
Boneseed control treatments

c)

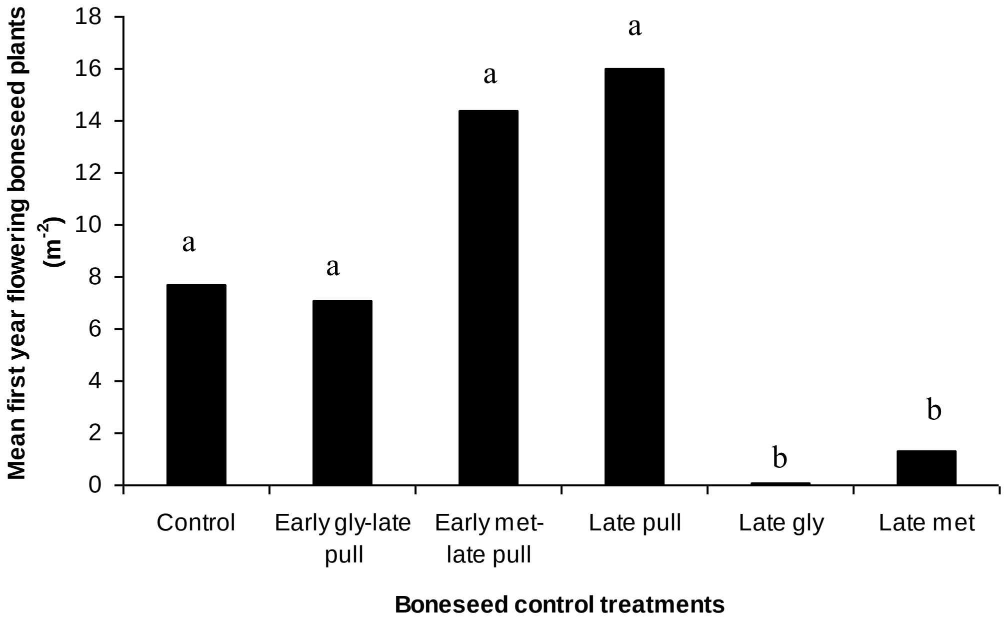


Figure 5.4 Post-fire boneseed population vigour and reproductive capacity after burning and weed control treatments at the degraded site: **a)** the percentage of cover provided by boneseed seedlings (P<0.001), **b)** the average maximum boneseed seedling height (P<0.001) and **c)** the mean number of flowering boneseed plants m^{-2} (P<0.002) at the end of the experiment. Different letters above bars indicate statistically significant differences from control treatments (P<0.05).

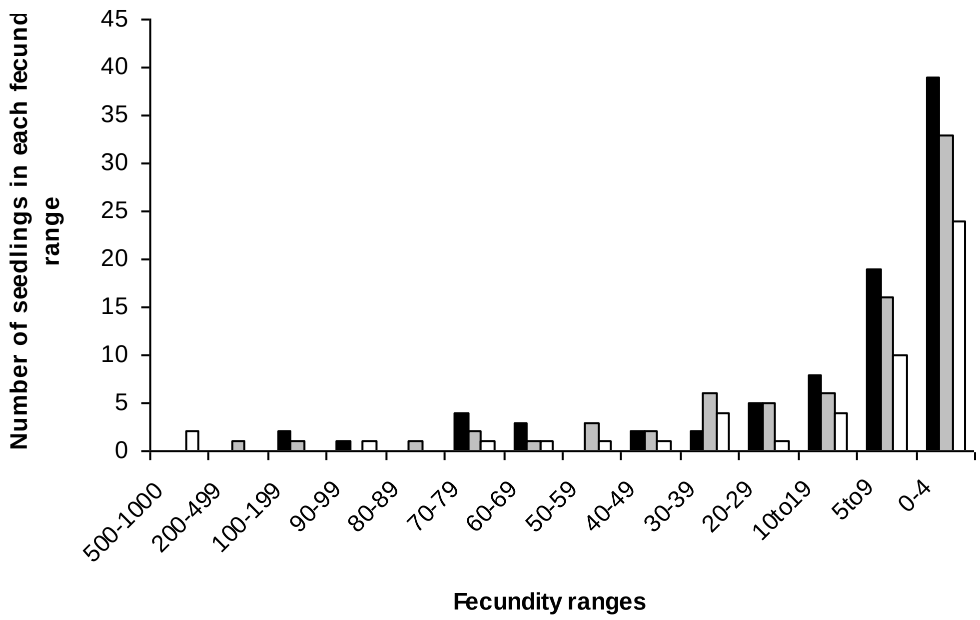
5.3.3 Early herbicide treatment effect on boneseed seedling biomass and fecundity ratio at the degraded site

At the degraded site, the effect of herbicide application on seedling biomass and potential seedling fecundity (the sum of flowers, buds, developing ovules and seeds present on individual seedlings) was compared between plots where flowering seedlings had been hand-pulled either with or without having previously been sprayed with either of glyphosate or metsulfuron-methyl herbicides. The flowering boneseed seedlings that were hand-pulled from these treatment plots were also compared in terms of their ratios of biomass (dry weight) to fecundity, assuming all developing ovules and buds developed into seeds. Total fecundity was lower in plots where either glyphosate or metsulfuron-methyl herbicide had been applied (Figure 5.5a). There were 75% and 36% of the developing, or developed seeds present in metsulfuron-methyl and glyphosate sprayed plots, respectively compared with those found in unsprayed plots.

There were fewer seedlings of all size classes in herbicide sprayed plots. There were around half the number of small seedlings weighing from five to 19 grams in sprayed compared to unsprayed plots (Figure 5.5b). The lower fecundity in herbicide treated plots corresponded with the lower average individual seedling biomass for plots sprayed with metsulfuron-methyl (14.76 g) or glyphosate (13.71 g) compared with unsprayed plots (17.44 g), (Figure 5.5b).

Herbicide treatment had no effect on fecundity per seedling of a given biomass, as shown by regression analysis that showed that slopes were parallel (P<0.001, Table 5.19 and Figure 5.6). Herbicides were found to reduce overall fecundity by killing seedlings of various sizes rather than reducing seed production on surviving or new plants.

a)



b)

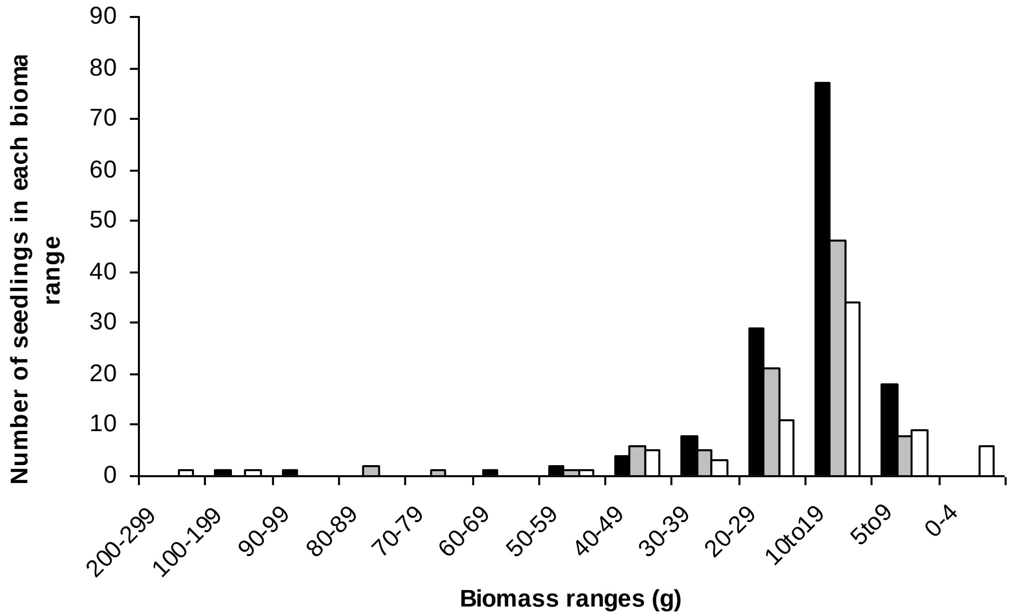


Figure 5.5 Frequency of boneseed seedling **a)** fecundity and **b)** biomass in September 1998 at the degraded site in plots where first year flowering plants had been hand-pulled either with, or without having previously been sprayed with glyphosate or metsulfuron-methyl herbicide. Treatments were hand-pulling of first year flowering plants (black bars), application of metsulfuron-methyl followed by hand-pulling of first year flowering plants (grey bars), or application of glyphosate followed by hand-pulling of first year flowering plants (white bars).

Table 5.19 Summary of regression analysis for biomass v fecundity of boneseed at degraded site in September 1998 in plots where first year flowering boneseed plants had been hand-pulled either with, or without having previously been sprayed with glyphosate or metsulfuron-methyl herbicide (see Figure 5.6).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Regression	6	206457	34409.5	101.07	<.001
Residual	293	99753	340.5		
Total	299	306210	1024.1		
Change	-2	-4814	2407.2	7.07	0.001*

Response variate:Fecundity
Explanatory: Biomass
Percentage variance accounted for 66.8
* Significant value indicates parallel slopes of lines.

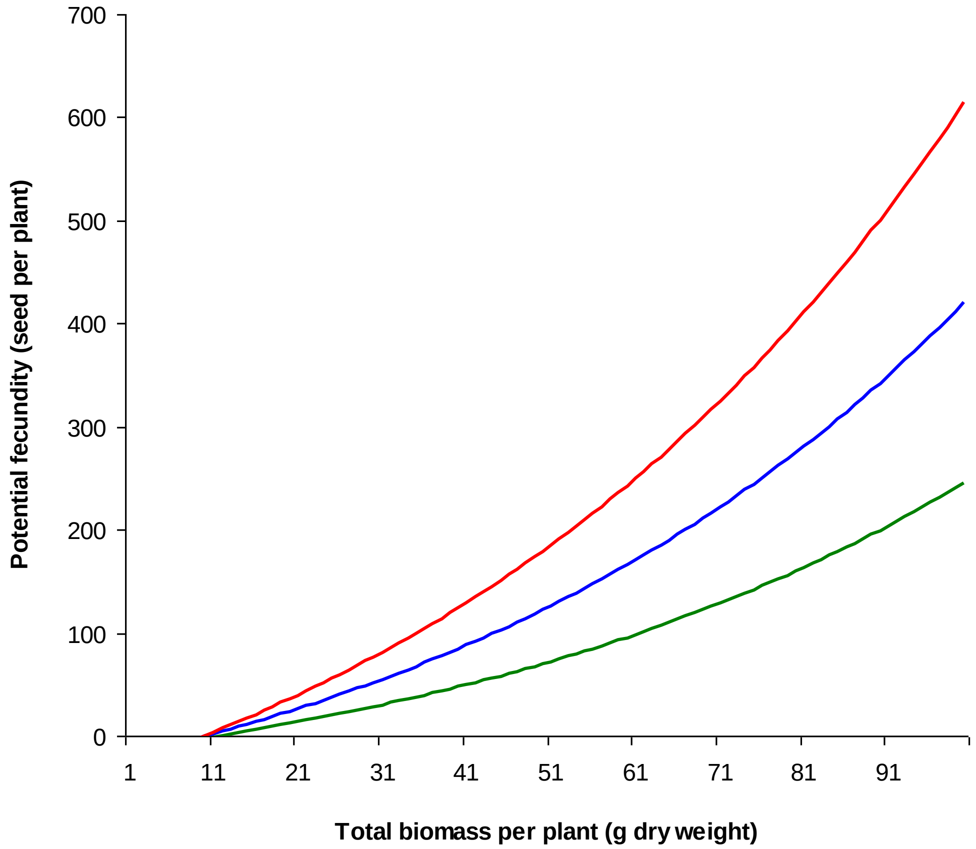


Figure 5.6 Biomass (g dry weight) compared with potential fecundity for individual boneseed plants in September 1998 in plots where first year flowering boneseed plants had been hand-pulled either with, or without having previously been sprayed with glyphosate or metsulfuron-methyl herbicide at the degraded site. Treatments were **a)** hand-pulling of first year flowering plants (green line), **b)** application of metsulfuron-methyl followed by hand-pulling of first year flowering plants (blue line) or **c)** application of glyphosate followed by hand-pulling of first year flowering plants (red line).

5.3.4 New boneseed seed input into the soil across all treatments after three growth seasons

In successfully treated plots at the species rich site, no seedlings were available to produce new seed (for example Figure 5.1b). In untreated areas of the species rich site an average of only 5.3 new seeds m^{-2} had entered the soil seed bank by the end of the experiment (Table 5.20). There was a median of no new seeds across the site, which indicated that the average of 1.86 flowering plants m^{-2} (control plots) had produced very few seeds by this time and in only a few locations.

At the degraded site the late metsulfuron-methyl treatment was the most effective treatment for reducing new seed input into the soil seed bank. No seedlings in these treatment plots were vigorous enough to have produced any new seed 13 months after the herbicide application (Table 5.20, Figure 5.1e). By contrast, plots treated with glyphosate herbicide at the same time (end of the second growth season), appeared to have produced more seed by 13 months after treatment (Table 5.20). These glyphosate treated plots had an average of 84 $\pm$ 188 new seeds m^{-2}. However, the median number of new seeds in these plots was zero m^{-2}, which indicated that large amounts of seed were produced by a few large seedlings (0.06 m^{-2}), while no seed entered the soil across most of the plot area (Table 5.20).

The greatest amount of new seed appeared to have been produced in plots treated with the early glyphosate and the later hand-pulling of flowering boneseed seedlings (307 $\pm$ 225 new seeds m^{-2}), and the control plots (320 $\pm$ 239 new seeds m^{-2}, Table 5.20). The average input of seeds from the early glyphosate treated plots also appeared similar to the whole degraded site average of old seeds (396 m^{-2}, Table 5.1).

Table 5.20 Number of new viable boneseed seeds on the ground 30 months after fire at the degraded site and 18 months after fire at the species rich site, after both fire and post-fire weed control treatments had been applied [D].

Site and treatment	Boneseed seedlings m^{-2}	New boneseed seeds on soil surface m^{-2}		New boneseed seeds per flowering seedling
	Average number of flowering seedlings $m^{-2} \pm$ s.d.[E]	**Average $\pm$s.d.**	**Median**	**Average**
Degraded site				
Control	$7.67^{a} \pm 3.12$	320 ± 239	358	41.72
First growth season[A] glyphosate application, then second growth season[B] PFB[C]	$7.11^{a} \pm 3.5$	307 ± 225	421	43.18
First growth season metsulfuron-methyl application, then second growth season PFB	$14.39^{a} \pm 4.07$	116 ± 53	105	8.06
Second growth season PFB only	$16.0^{a} \pm 15.35$	114 ± 68	147	7.12
Second growth season glyphosate application	$0.06^{b} \pm 0.11$	84 ± 118	0	1400
Second growth season metsulfuron-methyl application	$1.28^{b} \pm 1.78$	0	0	N/A
Species rich site				
Control[D]	1.78 ± 2.9	5.3	0	2.85

[A] End of first growth season = 5 months after controlled burning at the degraded site. [B] End of second growth season = 17 months after controlled burning at the degraded site. [C] PFB = Pulled Flowering Boneseed treatment. [D] Soil cores (and therefore counts of new seeds) were taken from outside treatment plots at the species rich site and are therefore representative of control treatment plots. [E] One-way ANOVA, see Figures 5.7c and 5.8c.

5.4 Discussion

Follow-up boneseed control treatments were highly successful in controlling boneseed seedlings that had emerged after the burn. Follow-up treatments were particularly successful at the species rich site where no boneseed individuals remained after three different control options were applied; sowing of seed of the native perennial grass *P. sieberiana* to the post-fire ash-bed followed by the application of a low dose of metsulfuron-methyl five months after an autumn burn, or the application of the label rate of either glyphosate or metsulfuron-methyl 12 months after an autumn burn. As the boneseed soil seed bank was also eliminated by fire at this site (Chapter 4), the achievement of complete seedling post-fire mortality resulted in the elimination of the boneseed population. At the degraded site, post-fire seedling control by applying herbicide 17 months after fire reduced the number of boneseed seedlings remaining to a level (7 m^{-2}) feasible for manual removal (hand-pullling). The removal of flowering boneseed plants successfully delayed the input of new seed into the previously fire-reduced soil seed bank.

In Australian temperate ecosystems, autumn burns have been found to favour the growth of herbaceous species over shrubs (Baird 1977 cited in (Christensen et al. 1981)). Whether native herbaceous species receive any advantage by burning boneseed populations in autumn will depend on the density of the post fire boneseed seedling flush. After burning at the degraded site there was negligible space remaining for species other than boneseed to grow. The faster growing boneseed seedlings emerged before the native species at the degraded site. The early herbicide treatments attempted to quickly rid the area of these small boneseed seedlings and thereby give the native species a chance to emerge and survive post-fire. However, this control strategy was found to be completely ineffectual at the degraded site. At the species rich site, herbaceous species had space on the post fire ash bed to grow. By contrast, at the degraded site, native herbaceous species would have benefited from the longer growth period between an autumn burn and the onset of summer and potential water stress conditions. In the temperate Australian environment, spring burns have often been found to favour post-fire resprouting shrubs over obligate seeder shrubs. The survival disadvantage experienced by the seeder shrubs after a spring burn is due to establishing seedlings often not having sufficient root development to survive the summer drought (Baird 1977 cited in (Christensen et al. 1981)). This suggests that in situations where it is necessary to undertake burning in spring, an obligate seeding woody weed, such as boneseed, would suffer similar high levels of seedling mortality as occurred after autumn burning.

5.4.1 Boneseed seedling emergence after fire

Burning at both the species rich and degraded boneseed invaded ecosystems caused the death of the majority of seed in the soil (Chapter 4) and stimulated much of the remaining seed to germinate. At the species rich site, this combined effect resulted in no seed remaining in the soil seed bank. In the heterogeneous vegetation structures, with their resultant heterogeneous burn temperatures (Chapters 3 and 4), the effect on both seed death and the stimulation of seedling emergence was variable.

Burning boneseed was found to be more successful at killing plants of all age classes and causing *en masse* seedling germination, than has been found for other woody weeds in Australia. Burning invasive *A. nilotica* in northern Australia only killed one-year-old seedlings, whilst older plants resprouted from branches (Radford et al. 2001). Likewise bitou bush can resprout after fires of low intensity (Vranjic and Groves 1999; Weiss et al. 2008). Burning weedy *Acacia* species often produces conflicting results: fire kills mature plants of some species while in others it increases the plant and stem density. Higher vegetation density occurs when fire causes plant coppicing and seed germination *en masse* (Radford et al. 2001). Resprouting after burning occurs for most woody weeds in the U.S.A. (DiTomaso 2006).

Burning caused high rates of boneseed seed germination from the soil seed bank. Heat, rather than smoke, is the most likely trigger for germination in hard seeded species (Enright 2001). Fire acts to scarify weedy *A. nilotica* seeds in northern Australia, thus promoting germination (Radford et al. 2001). In contrast, hard boneseed seed coats readily break into thirds with age or pressure, suggesting that fire acts on those fissure lines to open up the seed for germination. The fracturing of seed coats by fire occurs in the Fabaceae, Rhamnaceae, Mimosaceae and Proteaceae families ((Enright 2001) and references therein). High rates of germination after fire have been shown for the soil seed banks of many Australian *Acacia* spp. (Auld 1986; Auld 1996; Bell 1999), which require high temperatures for germination (Shea et al. 1979). Auld (1986) found that the optimal temperatures for germination were „between 60-80^{o}C for any duration, or up to 100^{o}C for durations less than 1 hr" for the woody shrub *A. suaveolens*. In this species seeds were left dormant and viable in the soil after experiencing temperatures less than 60^{o}C. In Africa too, the seed banks of the weedy Australian *Acacia* species *A. mearnsii*, *A. longifolia* and *Acacia sieberiana* DC. germinate *en masse* after fire (Pieterse and Cairns 1988; Sabiiti and Wein 1988; Pieterse and Boucher 1997). Amongst the woody species in Californian chaparral around a quarter of the species have been found to be stimulated to germinate by heat treatments of up to 120^{o}C for 5 min and another quarter to be stimulated to germinate by the addition of charate (powdered charred wood) (Keeley 1987). Other species were stimulated to germinate by wetting only and Keeley (1987) proposes that the mix of species in the chaparral ecosystem is maintained by a variety of burning regimes.

Many southeastern Australian Fabaceae species have their highest germination rates when heated to between 80-100^{o}C (Auld and O'Connell 1991), and the same occurs for species of Fabaceae in South African fynbos (Cocks and Stock 1997). In temperate South Australian woodlands a germination rate of 30 to 60% was found for the woody legume *G. monspessulana* in burnt stands compared to a rate of less than 10% in unburnt or cleared stands (Lloyd 2000). After fire, seeds of the legumes *Acacia farnesiana* (L.) Willd., *Kennedia rubicunda* Vent. and *Acacia pulchella* R.Br. have been found to germinate from depths of 1 to 5 cm (and none below 6 cm), 0 to 6.5 cm, and 1 to 4.5 cm singly or 3 to 6.5 cm clumped (none below 9 cm) respectively ((Auld 1986) and authors therein). The post fire seedling flush of *Cistaceae* sp. in Spain was found to come from seed down to 5 cm in the soil profile (Ferrandis et al. 1999). Boneseed seed was also mostly located in the top two centimetres of the soil profile, especially in the hard clay soils of the species rich site. After a hot fire of around 300^{o}C on the soil surface, boneseed seeds on the soil surface were killed and seeds were found to have germinated from depths of 5 cm. However, similarly to the examples above, cooler fires of between 50 to 200^{o}C resulted in *en masse* germination of boneseed seeds.

5.4.2 Similarities and differences between boneseed control treatments at the species rich and degraded sites

Assessment of the numbers of boneseed seedlings, their percentage ground cover, maximum height, the number in flower and the amount of new seed produced showed the most effective post-fire control treatments at the species rich and degraded sites. Burning boneseed populations in autumn was found to eliminate large portions of the soil seed bank (see Chapter 4), kill and remove many mature plants and stimulate large quantities of seed to germinate at both sites. At the species rich site herbicide treatments appeared to be more successful in reducing boneseed population vigour than at the degraded site after burning (Tables 5.8 and 5.15). There appeared to be fewer boneseed plants, both non-flowering and flowering, and less cover by boneseed seedlings in all herbicide treated plots at the species rich site compared with herbicide treated plots at the degraded site (Tables 5.8 and 5.15, Figures 5.3 and 5.4). Boneseed seedlings appeared to be shorter in early herbicide treated plots at the species rich site compared with the degraded site (Figure 5.3b and 5.4b). No flowering seedlings were present in any herbicide treated plots at the species rich site, which was biologically significant for boneseed control. At the species rich site all herbicide treatments resulted in no or very few seedlings being present and successfully prevented any boneseed flowering occurring for at least 17 months after the controlled burn occurred.

Metsulfuron-methyl applied during the second year was the most effective treatment for reducing the number of post-fire emergent boneseed seedlings to zero at the species rich site and to seven seedlings m^{-2} at the degraded site. This treatment also reduced the reproductive capacity of the boneseed populations at both sites, as most seedlings were only a few centimetres tall and were unlikely to produce seed for at least another 12 months following the end of the experiment. At the species rich site, seedlings in all herbicide treated plots averaged only 2 cm in height, as opposed to 40 cm high reproductively mature plants in unsprayed plots. Similarly, at the degraded site most of the few remaining seedlings in the plots treated with herbicide in the second year were less than 5 cm tall. In contrast, at the end of the experiment at the degraded site the boneseed plants present in unsprayed plots were over one metre tall and setting seed. Therefore, an additional benefit of herbicide application across all boneseed impact levels at both sites was the extra time gained for follow up seedling control, before remaining boneseed plants set seed. Burning and metsulfuron-methyl herbicide applied in the second year inhibited the input of fresh boneseed seed into the soil seed bank at both sites. The only seed source in these areas was mature plants surrounding the treated area. Follow up monitoring was required to remove seedlings resulting from dispersed seed.

Volunteer groups often remove boneseed seedlings from native vegetation by hand-pulling. This study showed that hand-pulling first year flowering boneseed plants after a fire would appear to be more satisfactory for shorter term boneseed control than is pulling seedlings without having previously burnt the area, as indicated by anecdotal descriptions by weed control volunteers.. This is due to the fact that burning caused a significant depletion of the amount of boneseed seed in the soil. This depletion would reduce the time taken to eliminate boneseed from an area via hand pulling, from about ten years to around three years at the degraded site and 18 months at the species rich site, assuming all flowering plants were removed each year. Fewer plants appeared to be in flower in the species rich site plots where flowering boneseed was hand-pulled (0.14 plants) than in the degraded site control plots (1.86 plants m^{-2}; Figures 5.3c and 5.4c). The level of cover provided by boneseed at the species rich site in plots where flowering boneseed was hand-pulled (28%) was also similar to control plots at that site (32%), and both appeared similar to their respective plots at the degraded site (42 and 36%; Figure 5.3a and 5.4a). There appeared to be no differences in average maximum boneseed plant height between the degraded and species rich site plots where flowering boneseed was hand-pulled (Figures 5.3b and 5.4b).

There appeared to be fewer or no boneseed seedlings in all species rich site treatment and control plots compared with the degraded site treatment and control plots at the end of the experiments (Tables 5.8 and 5.15). There appeared to be no difference in the percentage ground cover provided by boneseed seedlings in the degraded site control plots (36%) and species rich site control plots (32%, Figures 5.3a and 5.4a). There appeared to be no difference between the average maximum boneseed height in control plots at the species rich (67 cm) and degraded sites (65 cm, Figures 5.3b and 5.4b). Despite the similar boneseed seedling heights (Figures 5.3b and 5.4b), fewer seedlings appeared to be in flower at the species rich site (1.86 seedlings m^{-2}) compared with degraded site (7.67 seedlings m^{-2}).

Burning boneseed without controlling the emergent seedlings before they set new seed will result in the boneseed population retaining or regaining its dominant status over the native vegetation during the post-fire years. In dry schlerophyll forest in temperate Australia, the highest diversity of species is present immediately after burning has occurred and decreases from that point onwards (Noble and Slayter 1981). In these ecosystems, the composition of species present before a fire and the adaptive traits they possess will largely determine post-fire species succession (Christensen et al. 1981; Noble and Slayter 1981). Given the large numbers of mature boneseed plants present at infested sites, the high numbers of viable boneseed seed produced by them prior to burning and the vigorous growth of seedlings on the post fire ash bed, boneseed would be expected to continue to dominate the temperate Australian ecosystems it has invaded after burning. Indeed the degraded site infestations dominated all available ground space from the first post-fire seedling flush. At the species rich site, boneseed seedlings were not immediately dominant, but were a fast growing component of the post-fire emergent vegetation and the first species to emerge after the burn. Therefore, the effectiveness of post-fire control measures for boneseed infestations are boneseed population density dependent.

5.5 Conclusion

The experiments described in this chapter found that the weed control methods of herbicide application with or without the addition of competitive native grass species could be used either alone or in combination to control post-fire emergent boneseed seedlings. The success of these methods varied depending upon the initial bonseed soil seed bank, the number of seeds killed by the fire and the number of seedlings that emerged after burning. The weed control method of hand-pulling of flowering boneseed plants did not result in successful seedling control and in most cases there were too many seedlings for all to be removed by hand. Handpulling all post-fire emergent seedlings would be more effective in areas with an initial low number of boneseed seeds in the soil, where fire killed most seeds and where consequently, few seedlings emerged after burning.

This study also found that applying weed control treatments after the first or the second growth season after burning caused differing levels of post-fire seedling mortality depending on the intial boneseed soil seed bank density and the consequent number of seedlings that emerged after burning. It was found to be important to time herbicide and handpulling weed control ttreatments to occur prior to plants setting seed and, in turn, optimal treatment timing was found to be dependant upon favourable rainfall and growth conditions in a particular region.

Where diverse native vegetation still existed, where there was abundant fine fuel for fire, where there were less than 500 viable boneseed seeds m^{-2} in the soil, and where an even burn with surface temperatures between 250 and 300^{o}C was achieved, levels of post-fire seedling emergence were found to be around 30 seedlings m^{-2}. Under these circumstances three treatment combinations were found to eliminate (or reduce to one seedling m^{-2}) all boneseed seedlings by two years after the burn: boom spraying with a low dose of either of glyphosate or metsulfuron-methyl herbicides at the end of the first winter growth season (5 months) after the burn (one seedling m^{-2}); distributing native grass seed onto the ash bed two weeks after the burn then boom spraying as above (0 seedlings m^{-2}); or spot spraying flowering boneseed plants with either herbicide at the recommended rate 12-17 months aftr the burn (0 seedlings m^{-2}).

Where there was a dense boneseed infestation in severely degraded native vegetation there were few native species and the area was predominantly a boneseed monoculture with little fine fuel available at ground level to carry a fire. Seed density was found to measure between 2000 to 19,000 viable boneseed seeds m^{-2} and, even when brushcutting of boneseed occurred in late spring prior to controlled burning in autumn, the resultant burn was patchy across the site. Boneseed soil seed was significantly reduced to around 230 viable seeds m^{-2} by fire, and between 216 and 1461 boneseed seedlings m^{-2} emerged after burning. Under these circumstances any weed control treatment after the first winter growth season was completely ineffectual. Successful seedling control resulted in around seven boneseed plants remaining at two and a half years after the burn, and was achieved by spot spraying flowering boneseed plants with either herbicide, at the recommended rate, at the end of the second winter growth season (17 months) after the burn. Boneseed weed control treatments, including choice of glyphosate or metsulfuron-methyl herbicides, were found to have differential effects on the native vegetation and this will be discussed in the next chapter.

Chapter 6: Effects of boneseed control methods on secondary weeds and native species

6.1 Introduction

In natural ecosystems, there is potential for a secondary weed species to dominate an area after the principal weed has been controlled. The population dynamics of other weeds occurring in an area where a woody weed is brought under control are important to consider when controlling weeds as part of a process of restoring native vegetation. Without ecological weed control focusing on overall ecosystem restoration, boneseed could potentially be replaced at the species rich site by another South African shrub, *Polygala myrtifolia* L. (Groves 1991), or by the climber, *B. heterophylla* (see Chapter 3, Figure 3.3), or by the highly invasive Mediterranean bramble *Rubus* spp. (blackberry). *B. heterophylla* is found in increasing densities at the species rich site (Melland pers. obs.) and is a woody climbing plant native to Western Australia, with blue fleshy berries that are dispersed by birds. The species grows over native vegetation in dense clumps (Blood 2001). In California, *B. heterophylla* is found over a wide range of the state, and a warning regarding its invasiveness has been given for South Africa (Randall and Lloyd 2002). At the degraded site, the South African grasses *Ehrharta* spp. (Groves 1991), *Arctotheca calendula* (L.) Levyns, *Nassella trichotoma* (Nees) Hack. ex Arechav., the thistles *Onopordum* spp., or the herbaceous weed horehound *Marrubium vulgare* L. are all present and are known invasive species in Australia and therefore, in combination, could potentially replace controlled boneseed.

The management of boneseed requires techniques that simultaneously control other weeds in the area as well as encourage native plant regeneration and survival. This regeneration could occur if controlled burning regimes were beneficial to native plant populations and if herbicide application and other control techniques gave native species a competitive advantage over boneseed and any other weed populations. This chapter gives results from the section of the study that tested the hypothesis that boneseed control treatments could simultaneously control secondary weeds, as well as enable the partial restoration of the diversity and density of native plants.

6.2 Methods

6.2.1 Native vegetation and secondary weed parameters recorded and methods of recording for both sites

Experimentation sought to determine whether applying a low dose of glyphosate to the post-fire emergent boneseed seedlings, prior to the emergence of native species, would enable the native plant species to survive. Although metsulfuron-methyl only targets dicotyledonous species, and therefore should be tolerated by native grass species, it is soil active, and so the influence of an early low dose application was investigated. Both herbicides were also spot sprayed onto older boneseed seedlings after the second growth season in order to identify whether this timing and reduced direct herbicide contact would improve native seedling survival.

Quadrat counting frames and placement within the plots (degraded site) and transects (species rich site) are the same as for boneseed plant counts over time, as described in Chapter 3, Section 3.2.8, 3.2.8.1, 3.2.8.2, and 3.2.8.4.

The number of seedlings of the invasive climber *B. heterophylla* (see Chapter 3, Figure 3.3) and woody native species (*Acacia* spp., *Eucalyptus* spp. and *Prostanthera nivea* A.Cunn. ex Benth.) were counted as the number of growing tips present per quadrat. At the degraded site, grasses, herbaceous species including annuals and other weeds, bryophytes (mosses) and the native rock fern *Cheilanthes austrotenuifolia* H.M. Quirk & T.C. Chambers were all recorded as present or absent in a square rather than as cover, due to their small size. Additional notes were made of large *A. calendula* diameters and/or if a particular plant covered other squares in addition to the one in which it was recorded as being present. At the species rich site, there were a greater number and cover of species other than boneseed than at the degraded site. As well as this greater natural abundance of other species, native grass seed had been distributed on three of the four subplots per plot. Consequently, grasses, herbaceous species, annuals and the bracken fern *Pteridium esculentum* (G.Forst.) Cockayne were recorded as a percentage cover. Grasses were recorded as a percentage cover at the earlier recording dates. However, due to vigorous plant growth at this site, by the later recording dates, the cover of individual grass species, total grass cover, and other species cover, was recorded as a percentage cover for the whole quadrat. Grass height and density were also recorded later in the experiment.

6.2.2 Statistical analyses

The number of *B. heterophylla* plants in treatment plots and subplots at the species rich site were analysed using a split-plot ANOVA (Genstat 2002; Quinn and Keough 2002). Data were square-root transformed in order to fit the assumptions of normality as ascertained by normal and residual plots (Quinn and Keough 2002). Transformation of data was required for this test as the residuals from an initial application of ANOVA (GENSTAT 2002) did not have homogeneous variance and normal distribution as is required in order for the results of an ANOVA to be considered valid (Sokal and Rohlf 1981). Data was transformed in order to produce homogeneous and normal residuals when the ANOVA was applied to the transformed data.

The percentage ground cover of *A. calendula* at the degraded site was analysed for control and all treatment plots using a one-way ANOVA with randomised blocking (Genstat 2002) (Quinn and Keough 2002). Data were untransformed as they fitted the assumptions of normality as ascertained by normal and residual plots, and therefore the results of an ANOVA using these data could be considered valid (Sokal and Rohlf 1981).

Both the above ANOVAs are as described in Chapter 3, Section 3.2.9.3. No other counts of individual species or plant functional groups contained enough statistical power for analysis, and trends are indicated. No other counts of individual species or plant functional groups contained enough statistical power for analysis and trends are indicated.

6.3 Results

6.3.1 Effects of treatments on secondary weeds

6.3.1.1 Species rich closed woodland

The main secondary weed present at the species rich site was *B. heterophylla* (Figure 3.3). *B. heterophylla* was observed climbing on boneseed plants prior to burning. Other secondary weeds at the species rich site were a number of small *Rubus* spp. plants and some pasture grasses such as *Phalaris* spp. The woody Australian trees *Acacia sophorae* (Labill.) R.Br. and *L. laevigatum* are native to the coastal region south-east of Melbourne, but had moved inland to the higher altitude of the species rich site. A few individuals of *A. sophorae* were found towards the upper slope of the site, while a patch of *L. laevigatum* was found encroaching on the lower edge of the site. Only *B. heterophylla* was present in high enough numbers across the whole site for statistical inferences to be made regarding treatment effects on secondary weeds.

One of the most effective treatment and sub-treatment combinations for reducing the numbers of *B. heterophylla* plants was to distribute *P. sieberiana* seed within two weeks of burning and then spray with metsulfuron-methyl herbicide five months after burning. This combination resulted in only 0.5 *B. heterophylla* seedlings m^{-2} remaining (treatment Met98-pull99, Table 6.1, Figure 6.1). *P. sieberiana* reduced the number of *B. heterophylla* seedlings in control plots, plots where flowering boneseed seedlings had been hand-pulled and plots sprayed with glyphosate at the later application time (P>0.001), compared with control plots without *P. sieberiana* (Table 6.1, Figure 6.1). The non-significant reduction of *B. heterophylla* seedlings in metsulfuron-methyl treated plots following additional grass distribution was likely due to the large reduction in *B. heterophylla* seedling numbers caused by the application of the herbicide (Figure 6.1). Distributing *P. sieberiana* seed to the post fire ash bed with no subsequent herbicide application reduced the number of *B. heterophylla* individuals by half in control plots and by two thirds in hand-pulled flowering boneseed treatment plots (Figure 6.1). After burning, unsprayed *B. heterophylla* grew into a mass of climbing stems containing mature fruits, whereas all herbicide sprayed *B. heterophylla* was still vegetative and stems were less than 30 cm in length.

Without the addition of native grass seed, application of metsulfuron-methyl herbicide five months after burning was one effective plot treatment (one *B. heterophylla* seedling m^{-2}). Another effective herbicide treatment, metsulfuron-methyl herbicide application at 12 months after burning, also reduced the number of *B. heterophylla* seedlings remaining (3 m^{-2}); however, the number of seedlings was further reduced by adding *P. sieberiana* seed to the post fire ashbed (to 1.3 *B. heterophylla* seedlings m^{-2}; Figure 6.1).

6.3.1.2 Degraded open woodland site

Secondary weeds found to emerge after fire and boneseed control treatments at the degraded site were the winter annual *A. calendula*, occasional *N. trichotoma* plants, the fireweed *Senecio quadridentatus* Labill. and occasional patches of *M. vulgare*. *A. calendula* was the only weed species, other than boneseed, present in high enough numbers across the whole site for statistical inferences to be made regarding treatment effects on the species.

The cover of *A. calendula* at the degraded site was least (Table 6.2, Figure 6.2) where the cover of boneseed seedlings was greatest (Figure 5.3b). There was a greater ground cover of *A. calendula* in plots treated with glyphosate or metsulfuron-methyl at the later application time compared with control plots (P<0.05, Table 6.2, Figure 6.2). There was no difference in ground cover of *A. calendula* in the two later applied herbicide treatment plots (P>0.05, Figure 6.2). A similar level of ground cover of *A. calendula* occurred in control plots and all other treatment plots (P>0.05, Figure 6.2). In treatments that provided effective boneseed control *A. calendula* grew in areas left bare by controlled boneseed.

Table 6.1 Split-plot ANOVA with randomized blocking of the number of *B. heterophylla* plants in treatment plots and subplots at the species rich site (SR) site (Figure 6.1).

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Transect stratum	5	35.5724	7.1145	1.52	
Transect.Treatment stratum					
Treatment	5	87.4825	17.4965	3.73	0.012
Residual	24(1)	112.6576	4.6941	4.29	
Transect.Treatment.Supplottmt stratum					
Subplottmt	1	6.3284	6.3284	5.79	0.023
Treatment.Subplot	5	30.2851	6.0570	5.54	0.001
Residual	28(2)	30.6036	1.0930	1.65	
Transect.Treatment.Subplottmt.Units stratum	68(4)	45.1732	0.6643		
Total	136(7)	315.1969			

ns, not significant, P>0.05.

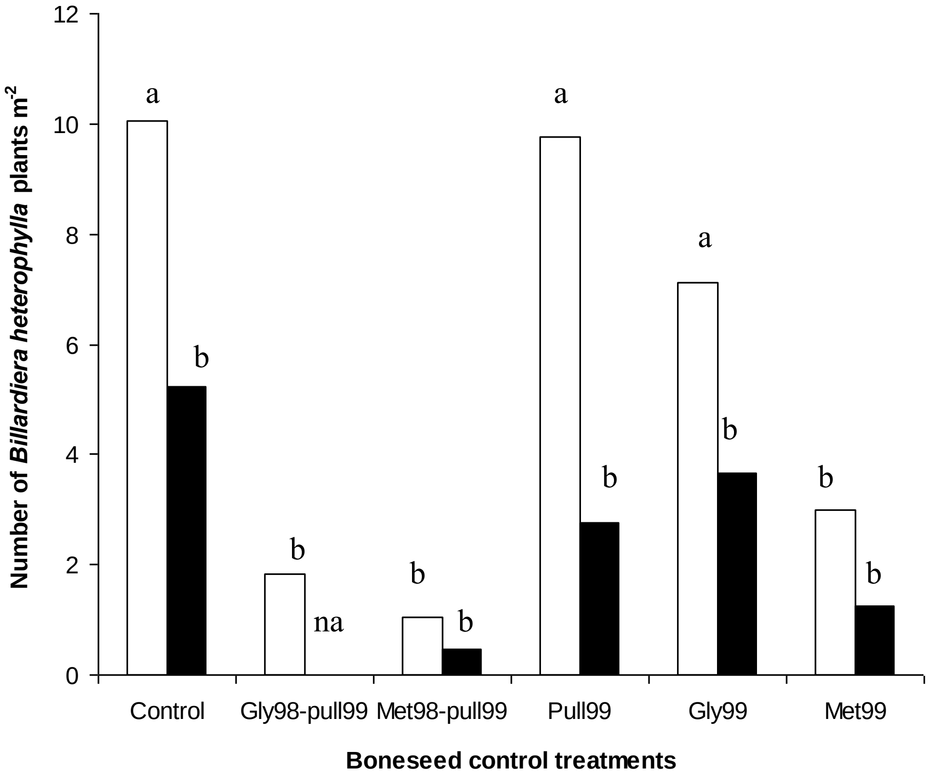


Figure 6.1 Number of *B. heterophylla* plants in treatment plots in September 1999, without (open bars) and with (solid bars) *P. sieberiana* seed distributed two weeks after fire at the species rich site. Treatments were as follows: control; early glyphosate herbicide (August 1998), followed by hand-pulling of first year flowering boneseed plants (May 1999)(Met98-pull99); early metsulfuron-methyl herbicide (August 1998), followed by hand-pulling of first year flowering boneseed plants (May 1999)(Met98-pull99); late hand-pulling of first year flowering boneseed plants (May 1999)(Pull99); late glyphosate herbicide (May 1999)(Gly99); late metsulfuron-methyl herbicide (May 1999)(Met99). Letters indicate treatment and grass combinations that caused a significant reduction in *B. heterophylla* compared with control plots.

Table 6.2 One-way ANOVA with randomized blocking of the percentage ground cover of *A. calendula* at the degraded site was analysed for control and all treatment plots at the degraded (D) site (Figure 6.2).

Source of variation	**d.f.(m.v.)**	**s.s.**	**m.s.**	**v.r.**	**F pr.**
BlockTran stratum	4	741.9	185.5	1.77	
BlockTran.Units stratum					
Treatment	5	4452.8	890.6	8.51	<.001
Residual	20	2092.3	104.6		
Total	29	7287.0			

ns, not significant, P>0.05.

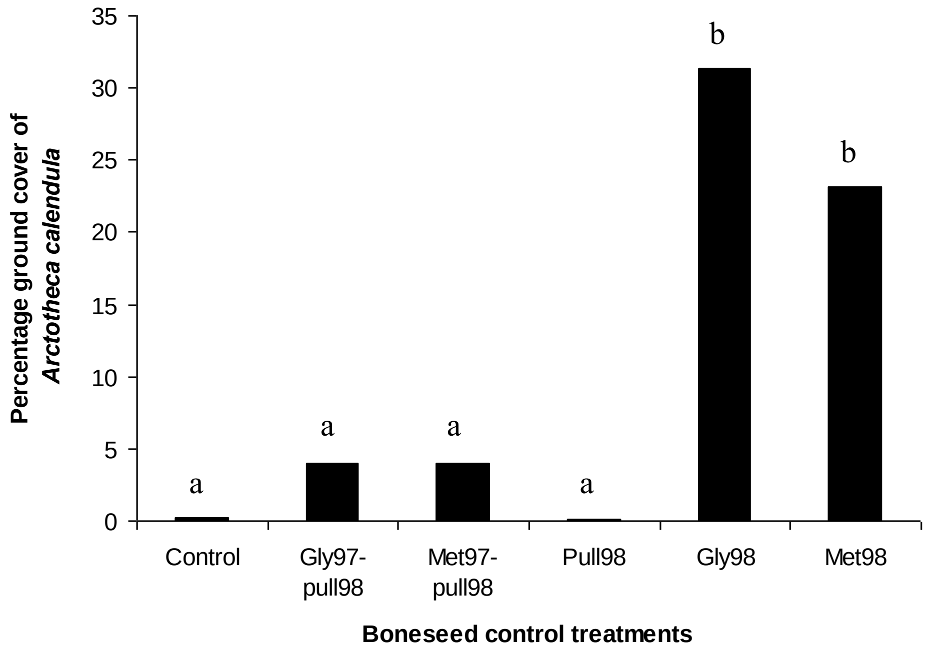
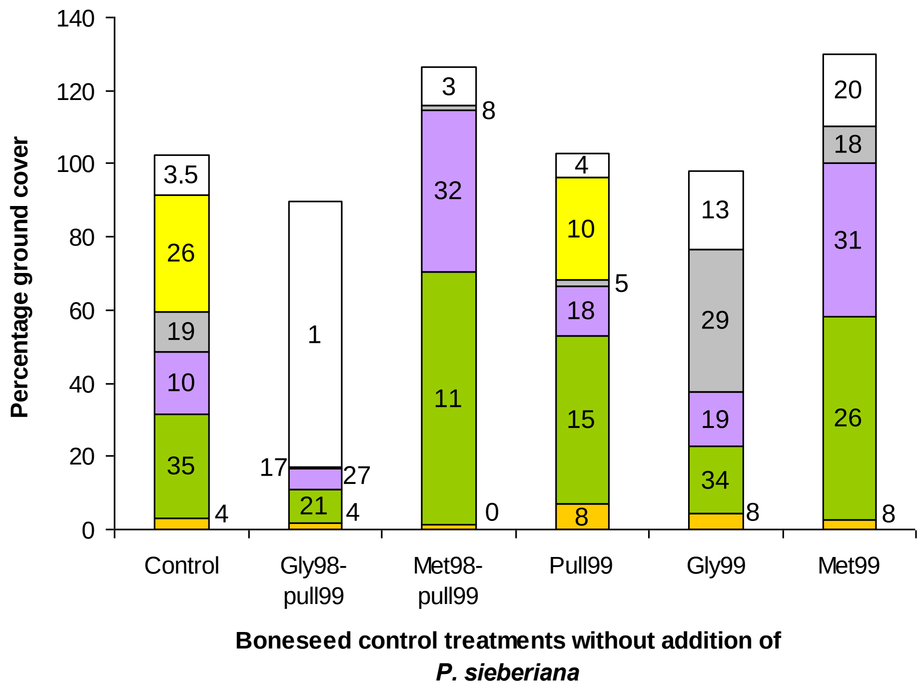


Figure 6.2 Proportion of ground cover by *A. calendula* after boneseed control treatments at the degraded site in September 1999. Treatments were as follows: control; early glyphosate herbicide application (August 1997), followed by hand-pulling of first year flowering boneseed plants (September 1998)(Gly97-pull98); early metsulfuron-methyl herbicide (August 1997), followed by hand-pulling of first year flowering boneseed plants (September 1998)(Met97-pull98); late hand-pulling of first year flowering boneseed plants (September 1998)(Pull98); late glyphosate herbicide (August 1998)(Gly98); late metsulfuron-methyl herbicide (August 1998)(Met98). Letters indicate treatment and grass combinations that caused a significant reduction in *A. calendula* compared with control plots.

6.3.2 Treatment effects on native species at both experimental sites

The differing quality of the native vegetation remaining after boneseed invasion at the species rich site compared with the degraded site was evident in the differing responses to fire and post-fire boneseed control treatments. An abundant and diverse flora established after the fire at the species rich site (Figure 6.3a), with emergent boneseed seedlings present amongst the native species. At the degraded site the post-fire vegetation was dominated by boneseed over the experimental duration (Figure 5.3b, Figure 6.4) and, where this was controlled, there was a predominance of bare ground, annual weeds or grass cover (Figure 6.4). The occurrence of large areas of bare ground after weed control is an undesirable outcome, as it is within these gaps that new weeds are likely to establish. The establishment of a range of native species that cover the ground is a more desirable outcome. The grass cover that emerged at the species rich site was in the form of thick swards, while at the degraded site small plants were present, many of which were only 5 cm in diameter (Table 6.3).

a)



b)

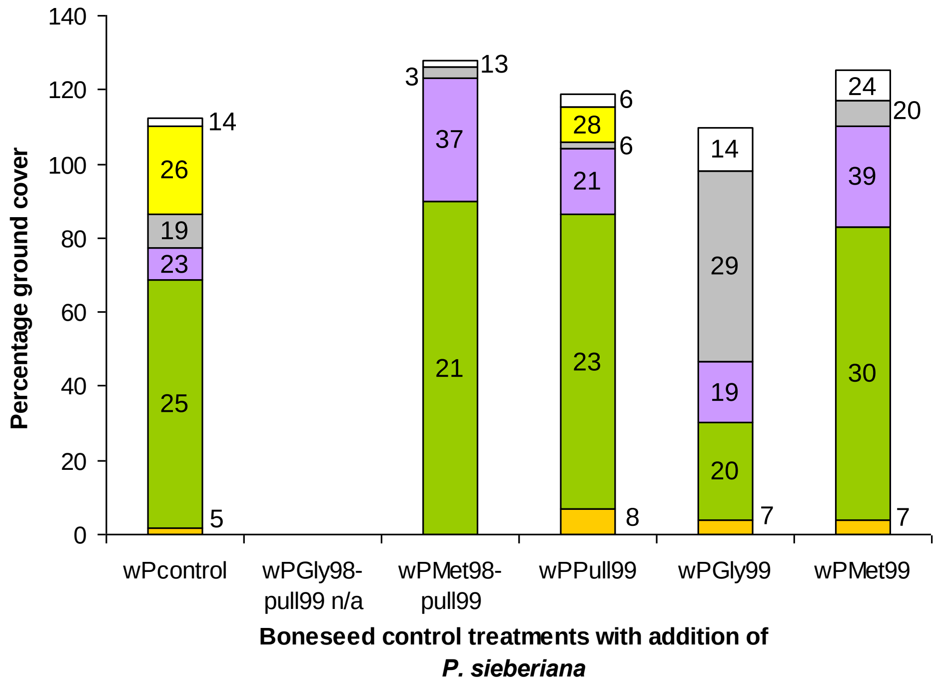


Figure 6.3 Proportion of the ground covered by the native bracken fern *P. esculentum* (G.Forst.) Cockayne (orange), native grasses, mostly *Microlaena stipoides* (Labill) R.Br. (green), native annual and other herbaceous species including *Arthropodium* spp. and *Kennedia* spp. (lilac), dead plants (grey), boneseed (yellow) and bare ground (white), after boneseed control treatments at the species rich site **a)** where no extra native grass seed was added to plots after fire, and **b)** where seed of the native grass *P. sieberiana* was added to plots after fire. Data labels are ± standard deviations from the mean.

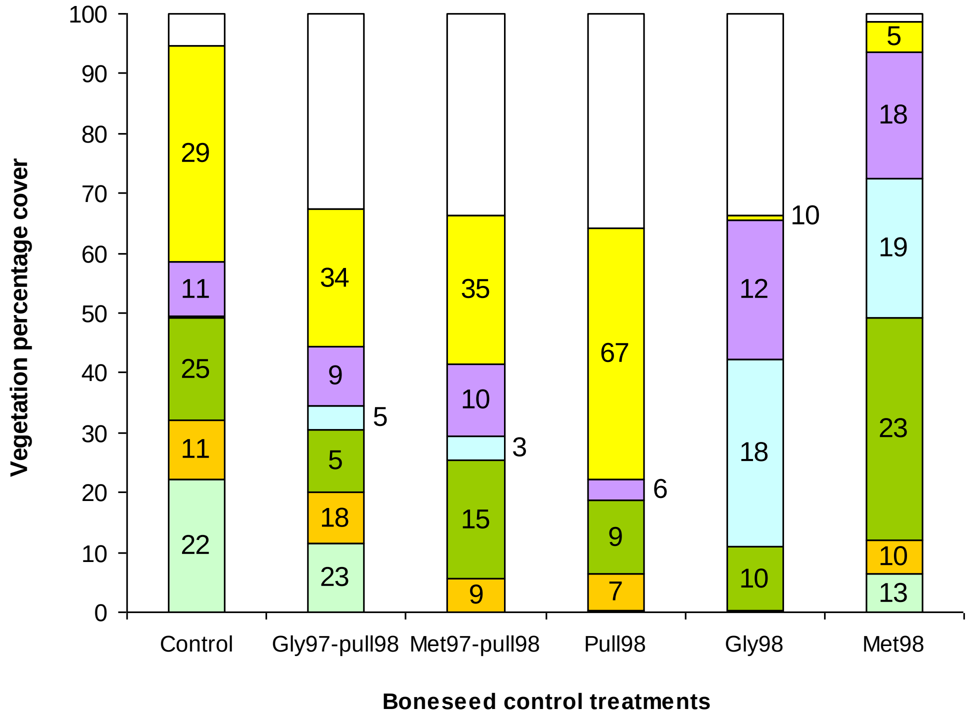


Figure 6.4 Proportion of the ground covered by native bryophytes (pale green), *C. austrotenuifolia* (native rock fern)(orange), native *Danthonia* spp., *M. stipoides* and *Stipa* spp. grass (green), *A. calendula* (weedy)(pale blue), other small native and weedy annuals (lilac), boneseed (yellow), and bare ground (white) at the degraded site. Cover provided by *A. mearnsii* was negligible and is not included on this graph. Data labels are $\pm$ standard deviations from the mean.

Table 6.3 Total grass cover at the degraded site and the percentage of grass cover made up of small grass plants less than 5 cm in diameter in September 1999.

	Total grass cover (% $\pm$ s.e.)	**Proportion of grass cover consisting of plants less than 5 cm in diameter.** (Means $\pm$ s.e.)
Control	38.9 $\pm$ 18.2	40.0 $\pm$ 16.0
Early gly - late pull	37.4 $\pm$ 11.4	56.8 $\pm$ 15.6
Early met - late pull	32.8 $\pm$ 7.1	35.9 $\pm$ 15.2
Late pull	28.5 $\pm$ 11.6	39.3 $\pm$ 15.7
Late gly	18.3 $\pm$ 3.84	46.0 $\pm$ 16.1
Late met	67.9 $\pm$ 10	40.7 $\pm$ 15.3

6.3.2.1 Effect of distributed native grass seed (subplot treatments) on native species at the species rich site

The addition of *P. sieberiana* seed increased the proportion of the ground that was covered by *P. sieberiana* rather than other native grass (Figure 6.5) and herbaceous species (Figure 6.3). This reduction in abundance of other native species in subplots where *P. sieberiana* seed was added exceeded the level of the overall increase in ground cover. Therefore, *P. sieberiana* effectively replaced some of the native species that naturally re-established in subplots where *P. sieberiana* was not distributed after the fire (Figure 6.3).

6.3.2.2 Effect of herbicide, hand-pulling, and distributed native grass seed treatments on plant species and functional groups at the species rich site

Spraying with metsulfuron-methyl herbicide at both five and 12 months after fire, or hand-pulling all first year flowering plants after fire, were the most successful boneseed control strategies for maintaining an abundant and diverse cover of native species at the species rich site. Although the cover of native species was higher when metsulfuron-methyl was applied at five rather than 12 months after burning, there was no apparent difference in cover of any plant species or functional group between these two treatment groups (Figure 6.3). At the species rich site, fire followed by metsulfuron-methyl application resulted in more ground cover of native herbaceous species and native grasses than any other treatment. Plots treated with metsulfuron-methyl maintained the same level of native bracken fern cover as all other plots and had less dead plant cover or bare ground than all other plots.

Adding seed of *P. sieberiana* to the early metsulfuron-methyl treatment increased total ground cover from 89 to 98% (Chapter 5, Figure 5.2) and total grass cover from 69 to 90% (Figure 6.5). Cover of *P. sieberiana* increased from 35 to 72% (Figure 6.5). The percentage cover of herbaceous dicotyledonous species decreased from 19 to 5% (Figure 6.3a and b). Therefore, in plots treated „early" with metsulfuron-methyl, the distribution of *P. sieberiana* seed increased the percentage cover of *P. sieberiana*, but not other species. Where *P. sieberiana* seed was not distributed, a diverse composition of native species occurred naturally after burning and the total plant cover was high (89%). Even in the absence of herbicide treatment, a decrease in ground cover of herbaceous dicotyledonous species as a consequence of distributing *P. sieberiana* seed was found across all treatment groups (Figure 6.3a and b).

Native plants were naturally abundant after fire in hand-pull-only plots at the species rich site; however, without the addition of the competitive native grass *P. sieberiana,* boneseed seedlings overshadowed the native plant cover in these plots (Chapter 5, Figure 5.3b). Manually removing boneseed, without spraying with herbicide, increased total grass cover without reducing the cover of herbaceous native species or the cover of the native fern (Figure 6.3a and b). This hand pulling of flowering boneseed seedlings treatment also successfully reduced the cover of boneseed seedlings (Figure 6.3a and b).

In plots treated with the early glyphosate application, total plant cover was low compared with the control and all other treatments (Chapter 5, Figure 5.2). Approximately half the plant cover in late glyphosate plots was dead (Figure 6.3a and b). In subplots where *P. sieberiana* seed had been added after the fire and that were then sprayed with glyphosate herbicide, a greater proportion of the total cover was dead (Figure 6.3a and b). The dead plant material in these plots was predominantly a thick mat of *P. sieberiana* (data not shown). However, a higher level of live vegetation was maintained when glyphosate was applied at 17 months after fire compared to 5 months after fire at the species rich site (Figure 6.3a). This was due to the spot spraying application method used at the later date, rather than hand-held boom spray method that was used for the early application. Spot spraying enabled spray contact with native species to be minimised.

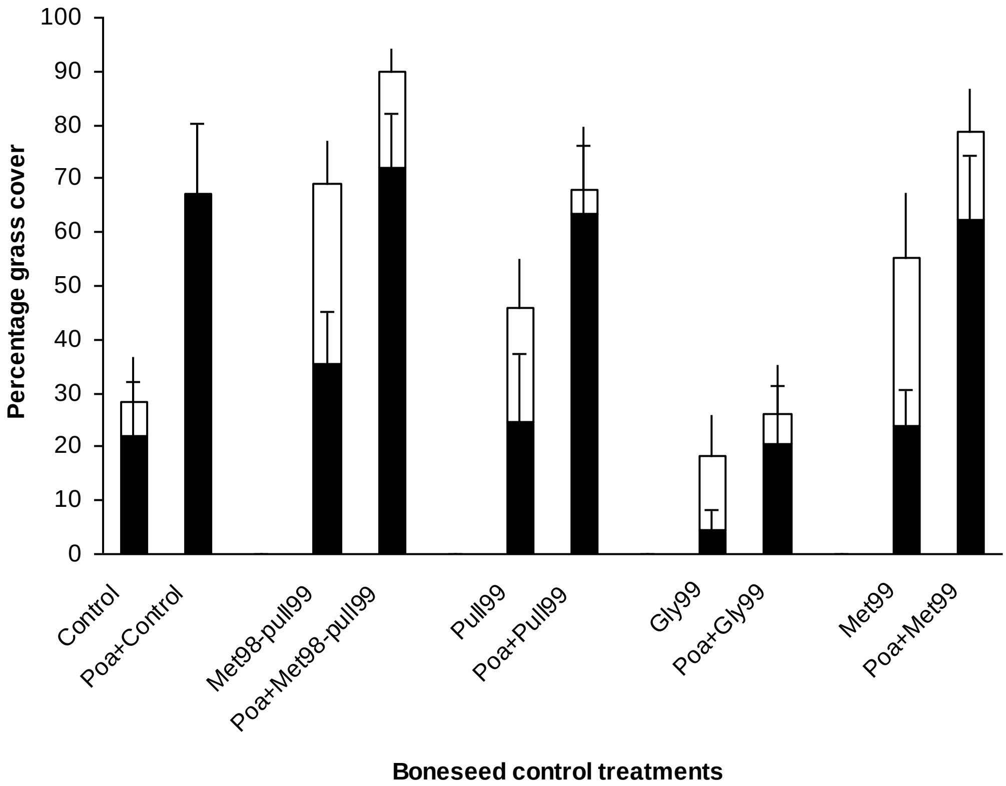


Figure 6.5 Grass cover (entire bars) and proportion of that grass cover that was *P. sieberiana* (solid portion of bars) across boneseed control treatments with and without distribution of seed of *P. sieberiana* onto the post-fire ashbed at the species rich site.

6.3.2.3 Treatment effects on plant species and functional groups at the degraded site

At the degraded site, spraying boneseed seedlings with metsulfuron-methyl 17 months after the fire was the most beneficial overall weed control treatment for maintaining ground cover of a range of plant functional groups (Figure 6.4). Plots subjected to this treatment had the greatest cover of native grasses and a low number and cover of boneseed seedlings (see Chapter 5). Plots treated with the late application of metsulfuron-methyl had less bare ground exposed, although they also had more *A. calendula* than all other treatments (P<0.05, Figure 6.2), except where glyphosate was applied late (P>0.05, Figure 6.2). This late application of metsulfuron-methyl enabled the survival of more bryophytes than the early application of the same herbicide, the hand-pull only treatment and the late application of glyphosate, in which all bryophytes were killed; but less than were found in control plots and slightly less than in plots sprayed with glyphosate at the earlier time (Figure 6.4). The late application of metsulfuron-methyl resulted in the presence of more of the small native fern, *C. austrotenuifolia,* than the late glyphosate treatment (in which all *C. austrotenuifolia* was killed) and similar amounts of fern cover as were found in all the other treatments. Mature individuals and some post-fire seedlings of the native woody species *P. nivea* and *Eucalyptus* spp. were also present across the degraded site, but not in sufficient numbers for statistical analysis of treatment effects.

6.3.2.4 Treatment effect on the woody native *A. mearnsii* at the degraded site

Although represented across most of the degraded site, *A. mearnsii* seedlings were present in too few numbers to be analysed statistically; however, certain trends were apparent. There was a tendency for more *A. mearnsii* seedlings (2.22 m^{-2}) to be present in plots treated with metsulfuron-methyl herbicide at five months after fire, than in controls or any other treatment plots (Figure 6.6). *A. mearnsii* seedlings in these early metsulfuron-methyl treated plots also appeared to be the tallest across all treatments, except in plots that had not been sprayed with herbicide where flowering boneseed seedlings had been hand-pulled (Figure 6.6). There appeared to be more and taller *A. mearnsii* seedlings in plots where metsulfuron-methyl herbicide was applied than after the use of glyphosate, although *A. mearnsii* seedlings appeared shorter when either herbicide was applied at the later application time (Figure 6.6).

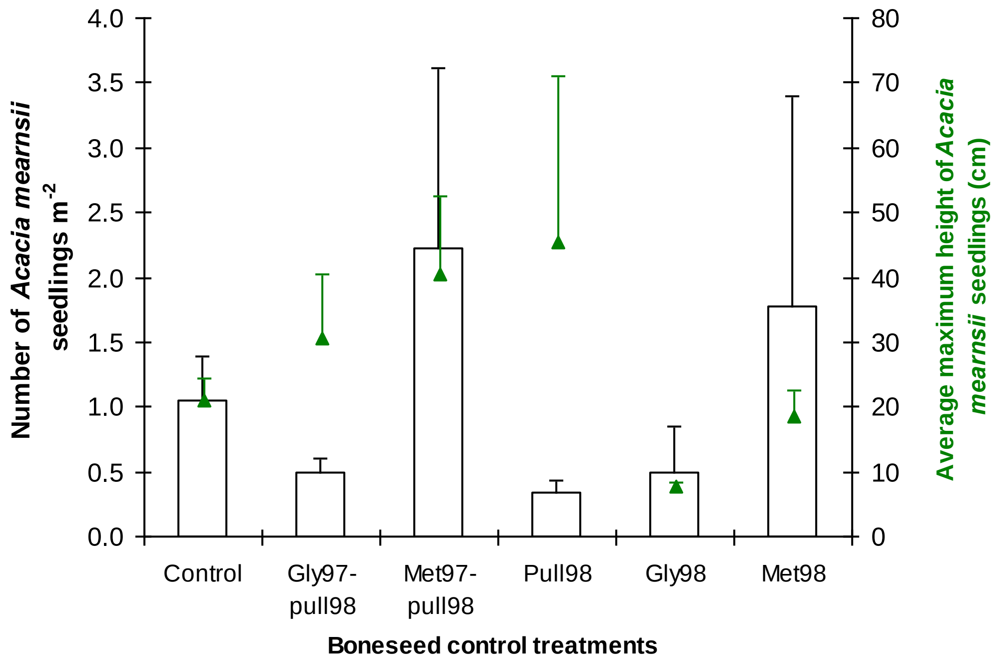


Figure 6.6 The number (open bars) and average maximum height (green triangles) of *A. mearnsii* seedlings present in treatment plots at the degraded site. Data is taken from blocks 2, 3 and 5, where mature *A. mearnsii* trees were located. Error bars show standard errors of means.

6.4 Discussion

Several successful integrated boneseed control options were found in this study (see previous chapters); however, only some of them would be recommended for use where ecosystem restoration was a goal, along with weed control per se. The choice of herbicide had a large impact on native species survival, as did the timing of application in pre-fire degraded versus species rich vegetation. Distributing native grass was also an effective aid to weed control; however, this too was found to impact upon the density of other native species.

In Australia, the long-term abundance of native species after a fire event is dependent upon the pre-fire abundance of that species and upon the immediate post-fire abundance of the species (Gill 1999). Negative impacts on native species establishing after fire would therefore be expected when an exotic woody species that was not only dominant pre-fire is also dominant immediately after fire. At the species rich site, native species had a higher survival rate and caused greater ground cover if weed reduction occurred in the first year following planting using methods that did not kill the native species. However, at the degraded site boneseed control in the first year after fire was ineffective and many post-fire emerging native species were smothered by dense boneseed cover. Therefore in degraded habitats, stimulation of native seed to emerge after fire would not benefit native species in the long term. Conservation strategies involving fire regimes need to recognize the importance of post-fire woody weed control. Native species that have been stimulated to germinate by fire need to reach reproductive maturity and be vigorous enough to replenish the native seed pools to levels above the pre-fire levels.

Considering that most areas at both sites had a canopy of boneseed, the increase in native species density after fire was partly due to the extra space made available when mature boneseed and boneseed seedlings were removed. An increase in species diversity necessarily came from native seed banks that had survived the boneseed infestation, or from propagules dispersed from nearby native plants. Where boneseed was controlled, native species density did not increase in areas where control methods resulted in bare ground. This occurred in glyphosate treated plots and in areas where few native propagules were available, as was evident at the degraded site. In South African fynbos, in contrast to the work presented in this thesis, research warns against using the „fell and burn" technique for woody weed control as the intensity of those fires resulted in low native plant guild survival, favouring only the non-mycorrhizal graminoides (predominantly myrmecochores – plants with ant buried seed) (Holmes et al. 2000). The alternative burn techniques, „burn standing‟ and „fell, remove and burn‟, both resulted in cooler burns and higher survival of native plant guilds in South Africa (Holmes et al. 2000). The „fell and burn‟ technique used in this study resulted in successful emergence of native species where native propagules where present. Rather than creating a fire that was too hot, the fell method was necessary in order to maintain fire in the boneseed infestations.

Native species and secondary weeds were affected differently when herbicides were applied after different periods of time since the fires. Native species abundance increased at both sites when metsulfuron-methyl herbicide was applied during the second growth season after burning. However, at the species rich site, the application of metsulfuron-methyl herbicide in the first growth season after fire provided the best control of *B. heterophylla* and also was the most beneficial to native plant species groups. At the degraded site, the application of metsulfuron-methyl herbicide in the first growth season after fire benefited growth of the native tree *A. mearnsii*, but not other native plant species. However, both metsulfuron-methyl treatments appeared to be most beneficial for the survival of *A. mearnsii* seedlings than any other treatment, regardless of the application being in year one or year two, although this result was variable. In the degraded system, boneseed control methods applied in the first growth season after burning were completely ineffectual in controlling boneseed and resulted in greater competition for native species. Application of metsulfuron-methyl in the first growth season after burning resulted in the lowest percentage of the ground being covered by *A. calendula* at the degraded site; however, this was only due to the higher cover of boneseed seedlings present after this treatment. In this latter scenario, the native ecosystem was more degraded than it had been prior to the burn, as the native soil seed bank reserves had been depleted. The survival of perennial grasses at the degraded site was greatest when metsulfuron-methyl was applied in the second rather than the first year following burning. At the degraded site, the second year metsulfuron-methyl treatment resulted in the highest percentage of grass cover remaining. Prior to these treatments native grasses had been outshaded by boneseed for many years, so few tussocks were available to survive and resprout after burning. Seed was required from nearby areas that were sparsely populated, making recolonisation slow. This also meant that grasses and boneseed seedlings were commencing growth at the same time, rather than mature grass tussocks regrowing after fire. Resprouting grass tussocks would be less likely than new seedlings to be overshadowed by fast growing boneseed.

The two herbicides tested, glyphosate and metsulfuron-methyl, impacted differently upon native plant species. As expected, the application of glyphosate was detrimental to the abundance and diversity of native species and groups of native plant species at both sites. However, while the use of metsulfuron-methyl herbicide caused some off target damage, many affected plants recovered and all native species benefited from the successful control of boneseed seedlings achieved by metsulfuron-methyl herbicide. The advantage of using metsulfuron-methyl instead of glyphosate, even when the latter was used after the second growth season, was evident by the greater cover of all native species and a reduction in bare ground at the species rich site. At the degraded site there was greater survival of *A. mearnsii*, native grass species and the *C. austrotenuifolia*. If, as commonly occurs in practice, glyphosate spraying were to be undertaken in highly degraded vegetation that had little surviving native seedbank, then reseeding with natives would be required following the herbicide application. Established native shrubs, including some species of Acacia on the NSW. coast, showed relatively little detrimental effect of glyphosate application at 1440 g ha^{-1} in winter (Toth et al. 1996); however, the current study found glyphosate applied in spring had a severe effect on seedlings of *A. mearnsii*. Matarczyk et al. (2002) raise the concern that it is unknown whether all native plant populations are able to withstand the application of glyphosate or metsulfuron-methyl. Work by Matarczyk et al. (2002) in NSW shows that seedlings and young plants of the rare and endangered native species *Pimelia spicata* R.Br. are killed by glyphosate spraying applied to the incumbent bitou bush. These authors found that the slow growth rate of some other Australian native species, as occurred when water was deliberately limited in glasshouse trials, gave those species a degree of glyphosate tolerance. They note that this occurs especially for *A. sophorae* and *T. triandra*. Rosette forming forbs and orchid species could also be adversely affected by metsulfuron-methyl (Matarczyk et al. 2002). Metsulfuron-methyl herbicide would be recommended for boneseed control where management goals included restoration of the boneseed-invaded native ecosystem. It is necessary to avoiding spraying at times of the year when sensitive native species are above ground.

Artificially increased densities of *P. sieberiana* caused an increase in the proportion of the ground cover that was *P. sieberiana* rather than other native grass and herbaceous species.

This increase occurred beyond the level of the overall ground cover increase. In other words *P. sieberiana* grew instead of some of the native species that established after fire where *P. sieberiana* seed was not distributed. Distributing *P. sieberiana* seed effectively controlled, but did not eliminate, post-fire seedlings of the secondary weed *B. heterophylla*, especially where herbicide was not applied. Without the use of herbicide, adding *P. sieberiana* seed was a more effective strategy for reducing *B. heterophylla* than boneseed. Therefore, *P. sieberiana* increased boneseed seedling control to 100% and simultaneously increased control of *B. heterophylla*, but caused a decrease in native species diversity. The broadcasting of seed of native grasses as a post-fire weed control strategy would only be recommended for patchy use in healthy vegetation, focusing on areas where *B. heterophylla* was present within a boneseed population.

Hand pulling of dominant, flowering boneseed seedlings at the species rich site caused an increase in native species abundance; however, the opposite occurred at the degraded site. The tallest *A. mearnsii* seedlings were found in plots where no herbicide had been applied but flowering boneseed seedlings had been hand-pulled 17 months after fire, indicating that those plants that survived competition with boneseed at a young age were later able to sustain faster growth rates than *A. mearnsii* seedlings treated with herbicide. However, the hand-pulling of flowering boneseed seedlings at the degraded site also resulted in the lowest abundance of other native species and could not be a recommended control treatment in a severely degraded ecosystem. Hand pulling is best employed in species rich vegetation where the use of herbicides is considered undesirable.

After the dominant weed infestation has been reduced in an area, the landscape is often open to invasion by other weedy species (Gillespie 1991). Other weeds can often colonise the newly created gaps faster than the slower growing native species. At Arthurs Seat, weedy species that were present within the existing boneseed infestation included the woody climber *B. heterophylla*, a few seedlings of *Rubus* spp. and several species of annual grasses. *Rubus* is a horticultural species with origins in the Mediterranean region, whilst *B. heterophylla* is an Australian native species, indigenous to Western Australia.

At the species rich site, treatments used to control the boneseed population needed to simultaneously control *B. heterophylla*. This was due to the vigour of *B. heterophylla* plants and their ability to grow in areas where boneseed was controlled. It would also be more cost effective to control two woody weeds with the same control techniques. The survival, growth of new seedlings and size of *B. heterophylla* plants after treatment showed that the control of both weeds was possible, albeit with the requirement for constant follow up removal of small numbers of seedlings of both species. *B. heterophylla* plants can resprout after low intensity burning ((Groves 2001), Melland pers. obs.). Many resprouted plants or seedlings were present after the burn at the species rich site. By the end of the experiment, 17 months after burning, all plots treated with either of the two herbicides contained only 30 cm juvenile single stemmed *B. heterophylla* seedlings. However, plots with no herbicide treatment contained mature, multi-stemmed *B. heterophylla* in dense clumps, which would set seed that season. While distributing *P. sieberiana* seed after burning significantly reduced the numbers of *B. heterophylla* seedlings present after 17 months, the plants remaining were larger and sexually mature. Follow up removal of the small *B. heterophylla* plants remaining in herbicide treated plots would be needed. It is unknown whether hand pulling would be sufficient to stop resprouting or whether local application of more herbicide would be required. The successful control of another perennial woody climber that has become weedy in Australia, *Lonicera japonica* Thunb., has also been achieved using herbicides rather than physical methods. Mowing, grazing or hand-pulling produces resprouting from remaining *L. japonica* stems (Williams et al. 2001).

Most boneseed infestations in Australia occur in native vegetation. Therefore the majority of boneseed control strategies in this country will have a companion restoration aim ranging from causing the least damage, to actively restoring the invaded native vegetation. An exception would be pasture land that has been closed to grazing for revegetation purposes. This is this only situation where the impact on existing native species is of a lower concern, as it is likely not many native species are present. Regardless of historical land use, populations of other plant species will be in a state of decline beneath a boneseed infestation and control measures for boneseed and secondary weeds should aim to boost native plant populations rather than become another degrading pressure. Likewise, as most weed control measures are disturbances and as they occur for weed control purposes at a faster frequency than the lifecycles of most native plant species, they need to be minimised. An exception of course is slow hand weeding using least disturbance techniques. Ideally therefore, the same few disturbances would be used to both control all weeds in the area, and stimulate the natural regeneration or manual restoration of the native plant community. That has been achieved in this study for the two boneseed infestations investigated. Of the several control options for boneseed found in this study, the only ones recommended are those that also controlled secondary weeds in the area and that resulted in the highest density and diversity of native species. Although commonly used, the results of this study suggest that glyphosate should not be recommended for use as the preferred herbicide to control boneseed and other weeds after fire. Result from this study would instead suggest that metsulfuron-methyl be recommended for use soon after a fire on low numbers of boneseed seedlings that have emerged faster than native seedlings; however, targeting individual boneseed and other weed seedlings in the second growth season after burning also caused minimal damage where native plant species were plentiful. Where a dense flush of boneseed seedlings occurred after fire, post fire emergent native plants could not be aided by prompt weed control measures. Highly degraded systems are always going to be more difficult to restore; however, a good cover of native grasses and tree seedlings was achieved when control was left until the second growth season after the fire. Active restoration via distributing native grass seed increased grass densities to levels that effectively reduced boneseed seedling survival; however, their use in species rich systems should be limited, as the practice also caused a reduction of post-fire native species that would have grown in those locations had grass not been distributed. The results suggest that distributing native grass seed would be advantageous in degraded areas where the growth of grass largely relies on the natural dispersal of propagules from nearby areas. Grass seed distribution has the beneficial effect of reducing large areas of bare ground after weed removal however it should always be done in a patchy manner across the site, to ensure the distributed species does not smother other emerging native plant species.

6.5 Conclusion - Control of Secondary Weeds

This chapter found that certain boneseed control treatments could simultaneously control the principle secondary weeds found in infestation areas, as well as enable the partial restoration of the diversity and density of native plants in invaded areas. Boneseed weed control treatments using glyphosate or metsulfuron-methyl herbicides were found to have differential effects on the native vegetation. As a result of this study, the spot spray application method using metsulfuron-methyl herbicide just prior to first year flowering boneseed plant developing seeds would be recommended for use on post-fire boneseed seedlings, due to the lower impact observed on native plant species of this treatment, by comparison to other control methods tested. All weed control treatments tested reduced the size and number of the perennial weed *B. heterophylla* plants, with herbicide application reducing both the size and reproductive capacity of plants. Notably the addition of competitive native grass seed without prior herbicide application appeared to have a greater impact on the reduction of *B. heterophylla* (around a 50% decrease) than on boneseed seedlings where no handpulling occurred (Tables 5.2 and Figure 6.1). The combination of handpulling of flowering boneseed plants along with the prior addition of native grass seed appeared to reduce the number of plants of boneseed and *B. heterophylla* by around 40 and 65% respectively (Table 5.2 and Figure 6.1). By contrast a greater ground cover of the secondary annual weed *A. calendula* was present where boneseed control treatments were most successful (Table 5.5, Figure 6.2), however, as boneseed is considered the worse weed, this result remained a successful one.

Chapter 7: General discussion

The research described in this thesis has shown that boneseed can be eliminated from Australian temperate woodlands using fire followed by herbicide application, with or without broadcasting of seed of the native grass *P. sieberiana*. Field experiments demonstrated effective integrated boneseed control strategies for two contrasting woodlands. One woodland had been highly degraded by long-term boneseed invasion. The predominant features of the degraded woodland were a large soil seed bank of boneseed containing 2000 to 19,000 viable seed m^{-2} and the presence of few, highly dispersed native plant species. There was also little fine fuel to carry a fire and a thick layer of boneseed seeds that merged with the litter soil interface. The other woodland contained high native species diversity amongst a boneseed invasion. Features of this site were a boneseed seed bank containing less than 500 viable seeds m^{-2}, abundant fine fuel for burning at ground level and the presence of a woody climbing weed *B. heterophylla*. Brushcutting and drying boneseed prior to burning was found to be essential to maintaining fire where levels of the fuel at ground level were below 4.5 kg m^2, as occurred at much of the degraded site. Fire surface temperatures of between 250 and 300^{o}C were most effective at causing boneseed seed death during autumn burning at both sites. Fire temperatures were most variable at the degraded site where the burn profile resembled a mosaic of areas that experienced high burn temperatures (above), areas exposed to cooler (0 to 250^{o}C) temperatures (effect caused boneseed germination) and unburnt areas. By contrast, the species rich site experienced an even burn that resulted in consistent bonseed control. It should be noted, however, that whilst the burn at the species rich site most effectively reduced boneseed numbers, the homogeneity of the burn did not allow for a variety of native plant responses.

In the species rich vegetation, the two most effective treatments resulted in the elimination of the boneseed soil seed bank and the above ground boneseed population. The first effective strategy for controlling boneseed and suppressing secondary weeds was to distribute seed of *P. sieberiana* within two weeks of burning followed by spraying with metsulfuron-methyl herbicide five months after burning. The second effective boneseed control strategy involved applying metsulfuron-methyl or manually removing boneseed seedlings in the second growth season after burning. In addition, spraying with metsulfuron-methyl five months after burning, without the distribution of grass seed, eliminated the boneseed soil seed bank and controlled the above ground boneseed population.

In the dense, mature boneseed infestation that occurred at the degraded site, one of the most effective treatments for the control of boneseed seedlings was spraying with metsulfuron-methyl 17 months after a warm autumn controlled burn. Follow-up manual removal of the few remaining seedlings was required. In addition to controlling boneseed, this method was also the most beneficial to the survival of desired plant groups.

7.1 Using broad scale disturbance mechanisms to manage woody weeds

Weed invasion is an ecosystem disturbance that has the potential to eliminate vast areas of native vegetation if no control is implemented. Most woody weed populations have been shown to drastically reduce or eliminate the biodiversity of the area they have invaded (Vranjic et al. 1999; Rejmanek 2000; Coutts-Smith and Downey 2006), with some exceptions where flora or fauna have utilised the new resource (Lawrie 2002). Significantly, many weed control measures including fire, broad scale physical removal and broad scale herbicide application are disturbances in their own right. As such, these control measures need to be carefully managed to ensure they do not exacerbate the problem they have been employed to combat. Indeed, some studies have reported that natural or anthropogenic disturbances, including disturbance associated with woody weed control techniques, can cause an increase in woody weed invasion (Duggin and Gentle 1998; Rees and Hill 2001; Ansley et al. 2006; Stokes and Cunningham 2006). However, single managed disturbance events do not always cause an increase in the weed population. For example, several methods of physical removal of boneseed were found not to increase the germination of boneseed seed from the soil (Thomas et al. 2000). Typically, follow-up control after disturbance is required to prevent an increase in weed distribution, density and biomass (Duggin and Gentle 1998), particularly where these increases pose further threats to the native vegetation. It is important that research into effective woody weed control techniques test how natural and imposed disturbance mechanisms can be used to both effectively control weeds, as well as to benefit native species.

7.1.1 Fire

This study has shown that, unlike most other woody weeds, boneseed plants are killed by fire. Many woody weeds re-sprout after fire, or fire will only kill first year seedlings but not mature plants. This is the case for most woody weeds studied in the USA, with the exception of a few in the Mediterranean climate of California (DiTomaso et al. 2006). In temperate Western Australia, populations of the indigenous *A. saligna* and *Agonis flexuosa* Lindl. are enhanced by frequent fire regimes. Both species are weedy in other temperate locations around the globe, such as South Africa (Keighery 2002). Similarly, in tropical Australia the worst woody weeds are difficult to kill with prescribed fire. Healthy *M. pigra* is difficult to burn, in part because it often grows in areas that flood for many months of the year. After burning, many mimosa plants re-sprout. Mimosa seeds survive in the soil after fire, then germinate and require follow-up control (Paynter and Flanagan 2002). In sub-tropical Australia, nearly 30% of mature bitou bush individuals re-sprout after fire (Weiss et al. 2008). The finding here that a variety of temperatures of prescribed burns kill mature boneseed plants presents an uncommon advantage for the control of this woody weed.

The varying boneseed vegetation structures and densities of the boneseed soil seed bank were measured in degraded and species rich native vegetation and found to influence boneseed population management (Chapters 3, 4, 5 and 6). This study found that it was only possible to sustain a controlled burn through a large boneseed population (Chapter 4) when at least 4.5 kg m^{-2} of fine fuel (less than 6 mm in diameter) was present at ground level. However, it was uncommon for sufficient boneseed fine fuel to be present at ground level where few other species were present. Therefore, further research into integrated control strategies for boneseed using fire in highly degraded ecosystems should investigate the most effective way in which to create a ground layer of fine fuel greater than 4.5 kg m^{-2} as preparation for a successful burn. Possibilities include slashing or hand-pulling mature plants, herbicide application to mature plants and artificially increasing grass, straw or other litter density prior to burning. Further research into the efficacy of burning other woody weeds should also include the quantification of weed density, biomass and fine fuel availability, within the weed infestation.

Control measures should be tailored to suit the weed density, which may vary across a site and therefore require a combination of control techniques. The successful use of fire, with or without prior herbicide application to brown off plants, for either killing mature plants, reducing their biomass, killing seeds or causing seed to germinate appears possible for several woody weeds (Lloyd 2000; Wardill et al. 2002; Vitelli and Madigan 2004; DiTomaso et al. 2006). The use of fire will not usually control woody weeds when used in isolation. However, when combined with herbicides, manual weed removal, plant competition and biological control (see below), fire appears to be a key component of successful woody weed removal.

This study found that controlled burning depleted the soil of more viable seeds than did natural mortality, seedling emergence or any secondary effects of seedling control treatments at both experimental sites. For differing population structures and densities within boneseed infestations (Chapter 3), fire at temperatures between 250 and 300°C effectively killed boneseed seeds in the top 2 cm of the soil and stimulated the emergence of seeds that were buried below 2 cm in depth (Chapter 4). Fire at temperatures between 50 and 250°C caused some seed death, but also stimulated the mass germination of boneseed seeds, mainly from the top 2 cm of soil (Chapter 4).

Control measures that do not directly kill sufficient numbers of boneseed seeds in the soil are unlikely to be successful over a period of two to three years in dense boneseed infestations. In vegetation that had been highly degraded by boneseed infestation, the large quantity of seed remaining in the soil 2.5 years after burning would readily allow a new and dense boneseed population to re-establish. Replenishment of the weed population would occur even if weed control treatments killed all seedlings during the years after the burn and no fresh seed entered the soil seed bank. Similarly, for *U. europaeus* in New Zealand, burning caused a temperature increase of 237°C in the top 2 cm of soil, but no significant temperature increase any deeper in the soil. Fire in the gorse population only reduced the soil seed bank from 2600 to 1000 seeds m^{-2}; therefore sufficient seed was still available to re-establish the population (Rolston and Talbot 1980).

7.1.2 Other disturbances for use in weed control

Aerial herbicide spraying and mechanical methods are other broad scale disturbances that are used for woody weed control. Aerial spraying has been employed to control mature bellyache bush in grasslands in Queensland, using a range of herbicides including triclopyr/picloram, glyphosate, fluroxypyr, metsulfuron and metsulfuron/glyphosate, followed by fire (Vitelli and

Madigan 2002). Aerial spraying has also been used to control woody weeds in native vegetation on Australian rangelands, and in dense bitou bush infestations in native vegetation on the New South Wales coast (Toth et al. 1996). However, aerial spraying is difficult in hilly terrain and mixed vegetation types due to inaccurate and incomplete contact of the spray with weed populations. For example, aerial spraying of boneseed after wildfires at the You Yangs in 1983 was an ineffective control measure because only one third of boneseed plants received herbicide treatment, as the plane was unable to fly sufficiently low (Adair pers. com.). Mechanical methods can effectively remove large stands of woody weeds, eg. *M. pigra* (Paynter and Flanagan 2004) and *L. camara* (Goodchild 1951); however, they are generally only suitable for ex-pasture land and already disturbed edges of native vegetation, as they destroy remaining native vegetation, the soil surface layer and soil structure.

7.2 Integrated control: fire and follow up control prior to new seed set

The use of fire in combination with follow-up control measures, to prevent new seed from entering the soil, can be effective in controlling woody weeds irrespective of the chosen method of follow-up control. For example, herbicide application followed by bulldozing then fire, successfully removed stands of *M. pigra* in the Northern Territory and caused seeds to germinate (Paynter and Flanagan 2002). However, heterogeneous fire temperatures often have differing impacts on uniform or differing densities of woody weed seed banks, even within a small area, as was found in this study. Also, Zabkiewicz (1978) reported that fire at temperatures below 100^{o}C stimulated the germination of gorse seed, while a hotter burn killed about a third of the *U. europaeus* soil seed bank. These results highlight the variable effects of fire on woody weed seed banks and that a variety of tailored follow-up control measures will be needed to reflect the varying post fire weed population dynamics. Fire preparation and follow-up techniques have varying impacts on native vegetation, which need to be considered when designing an integrated control strategy using fire. For example, the use of herbicide to „brown off" *U. europaeus* plants prior to burning (Rolston and Talbot 1980) may restrict the use of herbicides for immediate post-fire control if mature native species were adversely affected by both the first herbicide application and the fire. Indeed in most cases, fire itself cannot be used as a follow-up control technique for weed seedlings that have emerged after one fire. Effective weed control requires that weeds be killed before they reach reproductive maturity and set new seed into the soil seed bank. The interval between two fires used to kill weeds before weed maturity would be most likely shorter than that required for many native species to reach reproductive maturity.

In this study, broadcasting seed of native grass species after fire had the advantage of suppressing seedlings of both boneseed and the secondary weed *B. heterophylla*. Furthermore, when metsulfuron-methyl was applied to the few seedlings that emerged through the grass cover, both weed species were eliminated. A similar strategy has been successfully used to suppress *L. camara* re-growth after bulldozer and fire treatments on infested pasture-lands (Goodchild 1951). However, in native vegetation, the distribution of native grass seed reduced the native plant diversity and, as a consequence, this technique would be counter-productive to restoration aims if used continuously over a large area. Therefore, it is recommended that grass seed be distributed only in patches. Elsewhere, follow-up hand weeding or herbicide control could provide a variety of conditions conducive to regeneration of native species.

The use of herbicides to control woody weed seedlings in the second year after fire allows the use of spot spraying instead of boom spraying in order to target larger seedlings, which in many cases will be taller than the surrounding native species. Boom spraying has the advantage of providing rapid coverage of a dense mat of newly emerged post-fire seedlings; however, native species cannot be avoided with this method. After fire, some weed species emerge more quickly and grow faster than native species. Spraying can therefore be undertaken when weeds have emerged, but most native species have not. The greatest limitation when boom spraying seedlings after a fire is that the large soil seed bank will result in more seedlings emerging the following year. Spraying where large boneseed seed banks exist should therefore be undertaken later when seedlings have emerged. The choice of herbicide for later spray applications will be important, as native species will also have emerged and will be exposed to the herbicide. Both glyphosate and metsulfuron-methyl killed boneseed and *B. heterophylla* seedlings with similar efficacy; however, metsulfuron-methyl was the preferred herbicide as it was less detrimental to the survival of native species. Indeed, glyphosate application typically resulted in bare ground that proved to be ideal for rapid re-colonisation by boneseed and secondary weeds.

The manual removal of boneseed seedlings after fire, whilst labour intensive, resulted in the least off-target damage. However, this control method was not feasible where a high density of boneseed seedlings was present. Up to a few weed seedlings m^{-2} is often considered feasible for manual weed removal particularly where seedlings are very small and not deep rooted. Where the initial boneseed soil seed bank levels were low, several integrated control strategies resulted in no seedlings remaining. By contrast, where boneseed soil seed banks were larger prior to burning, the most effective integrated control strategies resulted in some weed seedlings remaining in treated areas. The remaining seedlings were typically a mixture of a few larger plants and more very small seedlings, all of which were easy to remove by hand prior to their setting seed. The research highlights the importance of monitoring and removing isolated weeds following investment in a control program.

The integrated control of woody weeds using various combinations of fire, herbicides, competitive native species and mechanical or manual weed removal techniques can be effective over a large area. However, the weed control techniques are sometimes cost prohibitive (Cacho et al. 2008). Biological control is often the preferred and most cost effective option (Page and Lacey 2006) for woody weed control, particularly in difficult to access terrain, due to its sustainability over the long-term. The costs associated with weed control need to be addressed with targeted funds for control programs, research and investment in measures to prevent new weed incursions. Despite the costs, there are situations where integrated control using „disturbance" methods is warranted, such as where effective biological control agents are not yet established, effective or possible for particular weeds. Integrated weed control is also useful in areas of high flora and fauna values where faster weed control is needed and where people are willing and able to volunteer for weed control activities. These conditions apply to many woody weed invasions in Australia.

7.3 A protocol for an adaptive mosaic of several integrated weed control strategies

This study is one of only a few that have specifically investigated the use of integrated control methods against woody weeds (see also (Lloyd 2000; Paynter and Flanagan 2004; DiTomaso et al. 2006)). Many woody weeds cannot be controlled using a single type of control measure, even if that technique is used repeatedly. In native ecosystems, weed control strategies are typically aimed at conserving or restoring the biodiversity of the ecosystem. While this is often the overarching purpose of weed control activities, the strategies themselves often focus on eliminating a single species and do not take account of the responses of native species and other weeds in the area of control.

From this study it is clear that the implementation of a series of integrated weed control and native vegetation restoration strategies in a mosaic across an infested site will be of benefit to the native ecosystem. Depending on the density of the weed infestation and the diversity and structure of the surrounding native vegetation, the use of a disturbance event such as fire, to control weeds can result in all post-fire emergent species growing onto a clear, open ash bed or into disparate patches of varying weed density and open space. Different weed control strategies with the dual aims of weed control and ecosystem restoration should be undertaken in a patchy manner across the landscape. This will allow for differing densities and age structures of various native species depending upon species responses to differing weed control treatments. In this way, a high level of native ecosystem diversity can be achieved across the landscape. The application of control techniques in a mosaic pattern across the landscape provides an opportunity for native species intolerant of control methods to recolonise from nearby areas. The use of a mosaic of control strategies could be of benefit where two or more woody weeds grow together and where each is controlled more or less effectively by one or more control measures. Where gorse and boneseed grow together in New Zealand, boneseed is considered the worse weed as it will completely outshade all native species, while native species are eventually able to grow through the more open canopy of gorse plants (McAlpine and Timmins 2002). Preliminary tests have shown that a cool burn will cause the faster growing and larger boneseed seedlings to become dominant, causing an increase in abundance of this weed (McAlpine and Timmins 2002). In this case, a heterogeneous mosaic of integrated woody weed control techniques would need to be undertaken to benefit native species. This would mean that in some areas purposefully cool or no burns would be implemented and boneseed would dominate and require follow-up control. Post-fire weed control measures should be implemented when they will cause the greatest reduction to the weed population and when juvenile native species are least affected. This can present something of a dilemma, as post-fire growth responses of all native species are not fully understood and further work is required in this area.

Using a mosaic of several integrated weed control strategies should fit well with differing resource availability. For example, funds may be available to spray some patches while people may be available for hand pulling adjacent areas. Usually neither resource is plentiful enough to be used across the whole area. As a result of the research conducted here, a single integrated weed management strategy for the control of boneseed cannot be recommended for all infestations. Rather a series of successful boneseed control strategies should be used in a mosaic across infested areas. In doing so, different types of weed control resources need to be purposefully allocated to plans for controlling boneseed.

7.4 The economic and policy implications of this research

The economic cost of weeds in Australia has been conservatively estimated as being 3.9 billion dollars per annum in the agricultural sector, 116.4 million dollars per annum spent by State and local governments on State and council land and 19.6 million dollars per year in other natural environment areas (Sinden et al. 2004). The monetary costs and costs to biodiversity of boneseed and bitou bush invasion in Australia are considerable. Combined, boneseed and bitou bush cover 3% of the Australian land mass (Thorp and Lynch 2000). The total cost of control activities for boneseed and bitou bush are unknown and involve herbicide costs, workers‟ salaries, volunteer labour time and the cost of the current biological control program. The cost of that program for the period 1990 to 2004/05 was estimated at $7.1 million (Page and Lacey 2006). The same report projected that a successful biological control program for bitou bush and boneseed would result in a benefit of $53 million by 2030. That figure is comprised of savings in direct costs of weed control of $7.2 million, an increase in the value of amenities of $4.4 million and an increase in the value of biodiversity of $41.5 million (Page and Lacey 2006). The calculated costs of weeds do not include the cost of volunteer labour which governments increasingly rely upon for weed control (Sinden et al. 2004) and is a cost that is difficult to ascertain and quantify.

Specific implications for fire management policies flow from this work. Whilst weed control is usually a component of wildfire recovery plans, funds that can be directed towards weed control are often the remaining funds after other infrastructure has been rebuilt. Given the great gains to be had by controlling woody weeds after fire, it is essential that sufficient money be available for weed control at this time. Following a fire, the weed population will either increase dramatically by making use of the plentiful resources of space, light, nutrients and lack of competition or it will be greatly reduced due to plant and seed death in the fire. In either scenario there will be a lack of reproductively mature weeds in existence for a short time after the fire. Policy planning and funds need to enable a quick response to eliminate weed seedlings that emerge after wildfire. Similarly, post-fire weed control should occur after controlled burns for fuel reduction and other ecological purposes.

7.5 Future research directions for boneseed research in Australia

Factors other than a lack of effective weed control are predicted to increase the negative impact of woody weeds on Australia"s temperate ecosystems. The impact of woody weeds on Australia"s temperate ecosystems is predicted to worsen and the distribution of weeds predicted to increase as a consequence of increasing global atmospheric temperatures (Kriticos et al. 2006). Increasing habitat fragmentation due to urbanization and land-clearing can also be expected to increase weed spread by way of the construction of more roads, along which weeds are spread (Lonsdale 1999), and closer proximity of native vegetation to existing weed populations in urban areas (Rouget et al. 2003). In addition to the aforementioned factors, there will be a corresponding increase in the costs of weed control. Therefore, it is important that research into effective weed control measures at both the landscape and small site scale be maintained in Australia. Several findings from the field experiments described in this thesis warrant further investigation.

7.5.1 Integrating biological control with 'disturbance' control methods

Many woody Weeds of National Significance (WoNS) in Australia (Thorp and Lynch 2000) are subject to a biological control program (Briese 1999) and it has been estimated that investment in biological control for weeds in Australia returns a benefit of 23.10 dollars for every dollar invested (Page and Lacey 2006). Biological control can take many years to implement successfully; however, biological control remains the single most sustainable and cost effective control method for woody weed control in Australia. Although very few studies have been undertaken into integrated control strategies for woody weeds (Rees and Hill 2001), Paynter (2004) has found that in the tropical Northern Territory of Australia, the use of fire, chemical or mechanical means to fragment large *M. pigra* infestations into smaller stands increases the establishment of biological control as agents prefer to colonise the edges of *M. pigra* stands. Biological control agents for boneseed have been very difficult to establish in the field (Meggs 1995; Weiss et al. 2008) and as yet no agents have reduced boneseed population density or spread. In the event that a biological control agent that has been released for boneseed establishes successfully in the field, there will be a need to research how best to incorporate the biological control of boneseed into the integrated control strategies described in this thesis.

7.5.2 Integration of revegetation measures

Research in this thesis found that broadcasting seed of native grass aided the control of boneseed and *B. heterophylla,* but reduced species diversity in a species rich ecosystem. Further research should aim to take advantage of the potential of the seed of native species to grow competitively with boneseed and other weeds when broadcast onto a post fire ash bed. Further research should also aim to optimise the use of competitive native species for woody weed control without reducing naturally occurring species richness. The maintenance of natural post fire species diversity is particularly important since native seeds banks may already be exhausted following both weed infestation and fire. Weed control measures could potentially use a representative mix of competitive indigenous species in a mosaic across the site, leaving other areas where no additional seed is to be distributed. Research also needs to occur in degraded ecosystems where seed of native species may need to be distributed for revegetation rather than competitive weed control purposes.

7.6 Future research needs for woody weeds in Australia

An ecosystem approach to single or multiple woody weed infestation needs to be maintained, expanding upon the work described in this thesis and other work (Rees and Hill 2001; Alston and Richardson 2006; Brown et al. 2008). Multiple integrated control strategies need to be developed for all woody weed species occurring in Australia. These integrated control strategies need to be able to be implemented in a mosaic across a landscape where multiple woody weeds exist and strategies need to address the control of monoculture woody weed infestations as well as situations where several woody weeds occur together. Integral to these weed control strategies is the need to assess the impact of control measures on a wide range of functional groups of native plant species and the indigenous fauna.

The control of woody weeds also needs to have the least negative impact possible upon native vegetation. However, it must be understood that where no weed control is undertaken most weed invasions will result in the destruction of the native ecosystem. It is important that the negative impacts of using fire are minimised by ensuring that a single burn event has the greatest restorative effect on a given ecosystem, thereby reducing the need for an additional burn in the future. Similarly, the cost of herbicides, transport, labour and any negative off target effects of herbicide use need to be minimised and this is best done by continued research into the effective use of herbicides in multi woody weed infestations in various native ecosystems.

A successful mosaic of weed control practices could give effective woody weed control and restoration of native ecosystems by allowing the expression of a variety of weed and native species responses to each control measure and differences in timing of control measures. The implementation of different woody weed control measures within a mosaic and within a time span where effective weed control and native species germination and growth rates occur, will create areas where more or less of the weed was controlled and more of certain native species may be present than others. When undertaken in a mosaic, weed control can gradually be achieved across the whole site and a range and abundance of differing plant propagules can be maintained and promoted. These propagules would then be available for dispersal into nearby areas where control methods may not have been as favourable for a particular species. In order to design an optimal mosaic of integrated control strategies for woody weeds in a particular area, a knowledge of the size and impact of soil seed banks of woody weeds, effective measures for controlling differing numbers of post fire emergent seedlings and effective techniques for restoring native vegetation are vital.

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Appendices

Appendices 1 a) b) and c) Current weed lists for Australia

a) The current and potential distribution of the most serious environmental weeds in Australia – the Weeds of National Significance (WONS) (Department of Environment and Heritage Australian Government 1999; Australian Bureau of Statistics 2001) redrawn from (Lindenmayer and Burgman 2005).

Scientific name	Common name	Origin of weed	Current distribution (x1000 square kilometres)	Potential distribution (x1000 square kilometres
Alternanthera philoxeroides (Martius) Grisebach	Alligator weed	Argentina	30	500
T. aphylla	Athel pine	North Africa, Arabia, Iran and India	80	3646
C. monilifera	Bitou bush/boneseed	South Africa	231	1258
Rubus spp.	Blackberry	Europe	691	1425
A. asparagoides	Bridal creeper	South Africa	385	1244
Cabomba caroliniana Gray	Cabomba	USA	35	181
Nassella neesiana Trin. & Rupr. Barkworth	Chilean needle grass	South America	14	242
U. europaeus	Gorse	Europe	233	870
Hymenachne amplexicaulis (Rudge) Nees	Hymenachne	Central America	73	415
L. camara	Lantana	Central America	389	1052
Prosopis spp.	Mesquite	Central America	410	5110
M. pigra	Mimosa	Tropical America	73	434
P. aculeata	Parkinsonia	Central America	950	5302
Parthenium hysterophorus L.	Parthenium	Caribbean	427	2007
A. glabra	Pond apple	North, Central and South America and West Africa	27	181
A. nilotica	Prickly acacia	Africa	173	2249
C. grandiflora	Rubber vine	Madagascar	592	2850
S. molesta	Salvinia	Brazil	383	1376
N. trichotoma	Serrated tussock	South America	171	538
Salix spp.	Willows	Europe, America and Asia	63	135

b) National Environmental Alert List (Department of Environment and Heritage Australian Government).

Scientific Name	Common Name
Acacia catechu (L.f.) Willd.	Cutch Tree
Acacia karroo Hayne	Karroo Thorn
Asystasia gangetica (L.) T.Anderson ssp. *micrantha*	Chinese Violet
Barleria prionitis L.	Barleria
Bassia scoparia (L.) A.J.Scott *subsp. densiflora*	Kochia
Calluna vulgaris (L.) Hull	Heather
Chromolaena odorata (L.) R.M.King & H.Rob.	Siam Weed
Cynoglossum creticum Mill.	Blue Hound‟s Tongue
Cyperus teneristolon Mattf. & Kuk.	Cyperus
Cytisus multiflorus (Aiton) Sweet	White Spanish Broom
Dittrichia viscose (L.) Greuter	False Yellowhead
Equisetum spp. L.	Horsetails
Gymnocoronis spilanthoides DC.	Senegal Tea Plant
Hieracium aurantiacum L.	Orange Hawkweed
Koelreuteria elegans subsp. Formosana (Hayata) F.G.Mey.	Chinese Rain Tree
Lachenalia reflexa Thunb.	Yellow Soldier
Lagarosiphon major (Ridl.) Moss	Lagarosiphon
Nassella charruana (Arechav.) Barkworth	Lobed Needle Grass
Nassella hyalina (Nees) Barkworth	Cane Needle Grass
Pelargonium alchemilloides (L.) L‟Hér	Garden Geranium
Pereskia aculeata Mill.	Leaf Cactus
Piptochaetium montevidense Parodi	Uruguayan Rice Grass
Praxelis clematidea (Griseb.) R.M.King & H.Rob.	Praxelis
Retama raetam Webb & Berthel.	White Weeping Broom
Senecio glastifolius Hook.f.	Holly Leaf Senecio
Thunbergia laurifolia Lindl.	Laurel Clock Vine
Tipuana tipu (Benth.) Kuntze	Rosewood
Trianoptiles solitaria (C.B.Clarke) Levyns	Subterranean Cape Sedge

c) Priority Sleeper Weeds (Department of Environment and Heritage Australian Government)

Scientific Name	Common Name
Aeschynomene paniculata (Vog.) Willd.	Pannicle Jointvetch
A. gangetica spp. *micrantha*	Chinese Violet, Philippine Violet, Coromandel, Karikamonga, Ganges Primrose
Baccharis pingraea Nutt.	Chilquilla
Brillantaisia lamium Benth.	-
Centaurea eriophora Forssk.	Mallee Cockspur, Wild Sand Heath
Crupina vulgaris (Pers.) Cass.	Common Crupina, Bearded Creeper
Cuscuta suaveolens (Reiche) Lechler	Dodder, Lucerne Dodder, Fringed Dodder, Chilean Dodder, Chile Dodder
Eleocharis parodii Barros	Parodi Spike Rush
Froelichia floridana (Nutt.) Moq.	Snake Cotton, Plains Snake Cotton, Prairie Snake Cotton, Prairie Froelichia, Cotton Weed, Field Snake Cotton, Florida Snake Cotton, Cotton Tails
Gmelina elliptica Sm.	Badhara Bush, Bulany, Bulangan
Hieracium aurantiacum L.	Orange Hawkweed, Devil's Paintbrush, Missionary Weed, Fox-and-cubs
Hypericum tetrapterum Fries	Square-stalked St John's-wort, Square-stemmed Hypericum, Golden Red, St Peter's Wort, Winged St John's Wort
N. charruana	Lobed Needle Grass, Uruguay Needle Grass, Silver Needle Grass
Oenanthe pimpinelloides Sm.	Meadow Parsley, Water Dropwort, Corky Fruit
Onopordum tauricum Willd.	Taurian Thistle
P. montevidense	Uruguayan Ricegrass, Pasto Pampa
Rorippa sylvestris (L.) Besser	Creeping Yellow Cress, Yellow Field Cress, Creeping Yellow Field Cress

Appendix 2 Herbicides registered for use on boneseed in Australia (from Brougham 2006). The Australian Pesticides and Veterinary Medicines Authority website contains current registration and permit information – www.apvma.com.au.

NOTE:
This table is included on page 217-218 of the print copy of the thesis held in the University of Adelaide Library.

Appendix 3 Shrub, tree and vine weeds in Australia for which biological control projects exist prior to or up until 1999. The habit invaded by each weed and the status of agent impact are given (Redrawn from Briese (1999), *with additional bridle creeper information from Virtue pers.comm.).

NOTE:
This table is included on page 219-220 of the print copy of the thesis held in the University of Adelaide Library.

Category definitions from Briese (Briese 1999)
[A] Shrub = generally woody and multi-stemmed plant, Tree = woody plant greater than 4m with single main stem, Vine = climbing or sprawling plant.