THE IMPACTS OF THE ENVIRONMENTAL WEED *ASPARAGUS ASPARAGOIDES* AND THE ECOLOGICAL BARRIERS TO RESTORING INVADED SITES FOLLOWING BIOLOGICAL CONTROL

By

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ABSTRACT

Weeds which invade native communities can have major impacts on biodiversity and ecosystem processes. However, these impacts are rarely quantified, and the mechanisms behind these impacts are rarely investigated. *Asparagus asparagoides* (L.) Druce (Asparagaceae; common name: bridal creeper), a plant native to southern Africa, is a significant environmental weed in southern Australia. Bridal creeper can invade both disturbed and undisturbed native ecosystems and then dominate native communities. As is the case for many environmental weeds, there has been little work conducted on the impacts of this plant. This lack of knowledge has hampered restoration efforts of invaded areas because very little is known about the potential for invaded communities to recover prior to undertaking weed management.

There is a need to improve our understanding of how to manage ecosystem recovery during and after weed control. This can be achieved by (i) determining the impacts caused by the weed; (ii) assessing the condition of invaded communities; and (iii) predicting the impacts that weed management itself will have on the native communities. These three prerequisites to environmental weed control have been determined across sites invaded by bridal creeper in southern Australia. The impacts of this invasive geophyte have been determined through multi-site comparisons, weed removal experiments and controlled glasshouse and laboratory experiments. The impacts on plant and ant communities were investigated as well as the impact on nutrient cycling. Invaded communities were assessed and included soil nutrient measurements and the determination of the readily germinable seed bank. Removal experiments were undertaken to predict the successionary pathways that could occur after bridal creeper control. In addition, as a biological control programme for bridal creeper has commenced in Australia, predictions of the likely benefits and other changes that will occur following biological control were investigated.

Bridal creeper reduces plant diversity. The main impact is expressed through a change in the structure of the community, with native understorey shrubs and trees that bridal creeper uses as supports, being most heavily impacted. Bridal creeper has had a limited impact on invertebrate communities; however the biggest impact of bridal creeper has

been on ecosystem processes. Bridal creeper has transformed native communities by increasing the availability of soil phosphorus through changes in nutrient cycling. Although bridal creeper appears to be a poor competitor at the seedling stage, bridal creeper can invade intact native vegetation. It allocates more resources to its belowground tubers in the first year if faced with high competition. Once bridal creeper has produced a large tuberous mat, bridal creeper occupies a large area of space in the top-soil, which excludes other plants. With changes to soil nutrients and possible allelopathic impacts, these impacts have contributed to the bridal creeper monocultures found within Australian native ecosystems.

The biological control programme for bridal creeper is already being considered as one of the most successful in Australia. In less than two years there has been a dramatic decrease in the cover of bridal creeper at my study sites. Following biological control, there will be a suite of native and exotic plants that will benefit from this control. Without additional restoration, we will see those species that readily germinate and those that respond positively to increased soil fertility, replacing bridal creeper after control. This will be dominated by other weeds as the invaded sites have large exotic seed banks that will readily germinate. The tuberous mats of older bridal creeper plants will also leave a legacy as they will remain many years after control and still impact on vegetation, even if control has killed the plant. These impacts will be highest at sites where bridal creeper has dominated over the longer term.

Environmental weeds, such as bridal creeper, that are capable of altering ecosystem functions can lead to substantial declines in biodiversity. Therefore, it was fortunate that bridal creeper became a target for biocontrol in Australia even though the impacts of the weed were not quantified when this decision was made. There are areas in southern Australia that are still free of bridal creeper or have sparse populations, and it is highly likely that this biological control programme has lead to the protection of these areas. This protection would not have been possible if other control measures were chosen over biological control, given that biocontrol agents can self-disperse and are able to give continuous control. This means that biological control of weeds in conservation areas can be very effective and is the only economically viable option for the control of widespread environmental weeds such as bridal creeper.

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Much of my field work was carried out six and half hours drive south from my Perth office in Fitzgerald River National Park. I would like to acknowledge the friendship and hospitality that Karin and Carsten Richelmann gave me while staying adjacent to the park at Quaalup Homestead. To access to these study sites, this research would also not have been possible without the access to the 4 Wheel Drive vehicles from CSIRO.

PUBLICATIONS ARISING FROM THIS THESIS

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Turner, P.J., Spafford, H. & Scott, J.K. (2008) The ecological barriers to the recovery of bridal creeper (*Asparagus asparagoides* (L.) Druce) infested sites: impacts on vegetation and the potential increase in other exotic species. *Austral Ecology*, 33, 713-722. (Chapter 3 in full).

Turner, P.J. & Virtue, J.G. (in press) Ten year post-fire response of a native ecosystem in the presence of high or low densities of the invasive weed, *Asparagus asparagoides*. *Plant Protection Quarterly.* (Chapter 7 in full).

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Turner, P.J., Scott, J.K. & Spafford, H. (2008) Implications of successful biological control of bridal creeper (*Asparagus asparagoides* (L.) Druce) in south west Australia. In *Proceedings of the Sixteenth Australian Weeds Conference* (eds R.D. van Klinken, V.A. Osten, F.D. Panetta & J.C. Scanlan), pp. 390-92. Queensland Weeds Society, May 2008 – Brisbane, Australia. (Part of Chapter 8).

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STATEMENT OF CANDIDATE CONTRIBUTION

The research presented in this thesis is an original contribution to the management and restoration of native areas invaded by bridal creeper. This thesis is also an original contribution to the field of environmental weed management, especially in the areas of managing the impacts from an invasive geophyte and the barriers that must be overcome to restore invaded sites.

A broad range of techniques is needed to determine the impact of weeds on biodiversity, ecosystem functions and successional consequences (Adair and Groves, 1998). Although components of this project have been undertaken in the past on other weed species, I am not aware of other studies that have incorporated all three methods of investigating the impacts of weeds through glasshouse experiments, multi-site comparisons and manipulative field studies. Few have combined the effects of weeds on both plant and animal communities and even fewer studies have assessed if these impacts have been reduced following weed control.

This thesis is presented in a series of research papers, preceded by a general introduction and followed by a general discussion. As some of these research papers (Chapters) have been accepted for publication, there may be a small amount of repetition between Chapters.

The design and conduct of experiments were carried out by me, Peter John Turner, after consultation with my supervisors, Dr John Scott and Dr Helen Spafford. This thesis was prepared by myself, after discussions with and review by my supervisors. It is estimated that I contributed to 90% of all the Chapters (except Chapters 2 and 7) and that my supervisors, contributed each approximately 5% towards this research. Chapters 2 and 7 describe long-term trends following weed control. These sites where initially established by Dr John Virtue. I confirm that I, Peter John Turner contributed to 50% of the field vegetation surveys when these sites were re-sampled for my PhD project, between 2004 and 2007. I have also contributed to 80% of the field soil and root measurements at these sites, as well as 90% of the data analysis and writing of these Chapters. Other people have also assisted with discussions on experimental design and

others have also provided reviews of specific Chapters/papers. These people have been acknowledged for their contribution at the end of each Chapter.

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Peter John Turner 9/6/08

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CHAPTER ONE

THE IMPACTS OF ENVIRONMENTAL WEEDS AND THE RECOVERY OF NATIVE BIODIVERSITY AND ECOSYSTEM FUNCTION FOLLOWING WEED CONTROL

Introduction

Exotic plant invasions are a threat to both managed and native ecosystems (Prieur-Richard and Lavorel, 2000). Plant species that are undesirable from an ecological perspective and invade native ecosystems other than those in which they have evolved are referred to as environmental weeds (Adair and Groves, 1998; Humphries et al., 1991; Richardson, 2001; Williams and West, 2000; Willis et al., 2003). Impacts caused by these invasive alien plants include eliminating native species and altering ecosystem processes (Richardson, 2001; Vitousek, 1990; Williams and West, 2000). Environmental weeds threaten biological diversity, by not only out-competing native vegetation, but also by impacting on native animals, by altering the availability of food, nesting sites and cover from predators (Brown et al., 1991). Environmental weeds not only infest disturbed areas; many of these species have the ability to invade undisturbed native ecosystems and as such present a serious ecological problem (Vranjic et al., 2000a).

An environmental weed, growing within native vegetation, is difficult to control since the range of control measures are limited when compared to weeds growing in an agricultural setting, leading Groves (1986) to suggest that biological control was an appropriate tool to control environmental weeds. However, biological control of environmental weeds may not be desirable if it does not result in the restoration of native diversity or if other environmental weeds increase instead of the desirable species following control (Lesica and Hanna, 2004). To improve the role of environmental weed management, especially when undertaking biological control, a better understanding of the impacts of weeds is required (Thomas and Reid, 2007). The success of a widespread environmental weed control programme must be measured against the reduction of the weed's impacts, not just a reduction in the weed's density,

and thus the ultimate success of environmental weed control must be measured on the level of replacement of the targeted weed with other vegetation (Adair, 1995).

In an attempt to control environmental weeds, there has been an assumption that weed control will eventually allow the re-establishment of a balanced system dominated by native species, yet it has been acknowledged for some time that this assumption is not guaranteed (for example see Humphries et al., 1993; Luken, 1997). Environmental weeds can alter biodiversity, but removal of these weeds in isolation can also result in unexpected changes to ecosystem components (Zavaleta et al., 2001), with weed management practices themselves altering biodiversity (Grice, 2004). Even the control of one weed may lead to its replacement by another (McEvoy and Coombs 2000).

Management of environmental weeds is essential, given that these weeds are a major threat to a large number of rare and threatened native species (for example see Coutts-Smith and Downey, 2006; Turner et al., 2007), and without urgent control actions, some of these species will not survive (Turner et al., 2008a). However, many land managers focus their weed management simply on reducing the presence of weeds, with limited regard for the existing or resulting plant community (Sheley and Rinella, 2001). Yet, successful management of communities containing environmental weeds should include:

- assessing whether the invaders have significantly altered the ecosystem,
- quantification of the character and magnitude of the biological problem posed by the invader by recognising and measuring properties that have been altered,
- estimation of the magnitude of the likely environmental benefit of limiting the invader, and
- developing strategies that return communities and ecosystem processes towards a similar pre-invasion state (Walker and Smith, 1997).

This thesis will explore the above issues and investigate the impacts caused by and management of an environmental weed, bridal creeper, *Asparagus asparagoides* (L.) Druce (Asparagaceae). This southern African geophyte has invaded southern Australia. The research described within this thesis explores the impacts of bridal creeper, not just on biological diversity, but also on changes to ecosystem functioning at study sites in

South Australia and southern Western Australia. Given that a biological control programme for bridal creeper has commenced in Australia (Morin et al., 2006b), predictions of the likely benefits and other changes that will occur following biological control are also investigated.

Impacts of environmental weeds

Environmental weeds can have a range of impacts on native ecosystems (see Williams and West, 2000), yet studies on the impacts of environmental weeds in Australia are still relatively rare (Adair and Groves, 1998; Grice et al., 2004). Therefore, there is a need to document these impacts as well as the mechanisms that drive them, such as resource competition, allelopathy or the alteration of ecosystem processes (Levine et al., 2003).

Adair and Groves (1998) recommended the use of multi-site comparisons for the assessment of the impacts of widespread and well established weeds. This involves sample units which are located within a particular habitat, or vegetation type, at sites where the weed is present and in comparable areas where the weed is absent (control). No manipulations are undertaken. However, an assumption to this approach is that the community composition in the invaded areas was the same as or similar to the control areas prior to invasion. Also, the analyses used for multi-site comparisons are usually undertaken with correlation statistics and therefore lack the power of manipulative studies (Adair and Groves, 1998). Woods (1997) has argued that this could lead to difficulty in management as there is a need for a clear distinction between correlation and causation.

Examples of previous multi-site comparison studies include that undertaken by Mullet and Simmons (1995). They found the cover and abundance of native (indigenous) species to be negatively correlated with increasing cover of *Pittosporum undulatum* Vent. across four sites in south east Australia. Mullet and Simmons (1995) measured vascular plant species, cover and abundance as well as recording aspect, slope, soil pH and light levels, leading to the conclusion that reduced light infiltration caused by the weed led to the displacement of native species. Kedzie-Webb et al. (2001) measured cover and biomass of all plant species along a gradient of spotted knapweed (*Centaurea*

maculosa Lam.). At two sites in the US, five transects were located through an infestation and permanent plots were placed along each transact. Native cover, richness and diversity were inversely related to the weed's cover. Also in the US, Hobbs and Mooney (1986) studied community changes following shrub invasion of a grassland. At one site, quadrats were placed in shrub stands and age of the shrubs determined. Quadrats were harvested and aboveground dry weight of each herbaceous species determined. Biomass of herbaceous species decreased after shrubs were 2-3 years old and formed a closed canopy. Similarly, Lee et al. (1986) aged gorse (*Ulex europaeus* L.) plants within plots in New Zealand. At 60% of the plots with gorse younger than 25 years, native species were not establishing.

Another approach to determine the impacts of a well established invader is through removal experiments (D'Antonio et al., 1998). Partridge (1992) in an eight year study in New Zealand, found removal of broom (*Cytisus scoparius* (L.) Link) and bracken (*Pteridium esculentum* (G.Forst.) Cockayne) at one site caused a switch to a grassland. However, when bracken only was removed it resulted in the invasion of grasses and forbs, and bushier broom plants, while the removal of broom alone resulted in a bracken dominated area. Numerous factors may confound interpretations from removal experiments, including the speed of response (Aarssen and Epp, 1990), disturbance due to the removal technique and the residual impact of the invader remaining after its removal (Adair and Groves, 1998). Unless removal experiments are conducted prior to the widespread establishment of the invader, the experiment may only measure the residual effect of the invader and the response of species with strong dispersal abilities and growth rates (Adair and Groves, 1998). Even so, the removal technique will still identify the likely successional responses of communities to weed control efforts (Woods, 1997).

Recovery of native biodiversity and ecosystem function following weed control

Management of environmental weeds is a vital aspect of protecting native biodiversity and normal ecosystem processes (Byers et al., 2002). However, if ecosystem processes or structure have been altered significantly by environmental weeds, weed management will not necessarily restore the native ecosystem (Hobbs and Humphries, 1995). Therefore, there is a need to improve our understanding of how to manage ecosystem

recovery (Richardson and van Wilgen, 2004; Witkowski and Garner, 2008) as very little is known about the potential for communities to recover prior to undertaking weed management (Woods, 1997).

An understanding of the complex interactions between an environmental weed and the invaded ecosystem (Walker and Smith, 1997) as well as an understanding of the weed and the area in which it has invaded is critical for successful management (Williams and West, 2000). To avoid direct exchange of one weed with another, population processes must be considered within the context of communities, as changes in one population will likely flow on to affect other populations in the community (Booth and Swanton, 2002). Environmental weeds can alter various properties of communities, including species diversity and successional pathways. Management of environmental weeds often means managing plant succession (Luken, 1990), yet targeting individual weed species through simple control measures does not help us to understand why weeds occur where they do or how they interact in communities (Booth and Swanton, 2002).

The issue of ecosystem repair after weed control should also be considered, given that many ecosystems that have been invaded, usually for a relatively long period, can not recover following weed control without additional restoration (Richardson and van Wilgen, 2004). Richardson and van Wilgen (2004) suggested that the most damaging environmental weeds are those that transform native ecosystems (see transformer species in Richardson et al., 2000) by altering ecosystem processes. Many environmental weeds are capable of altering ecosystem processes (Hobbs and Humphries, 1995; Vitousek, 1990). For example, the effects of environmental weeds on nutrient cycling have been documented in several studies (Ehrenfeld, 2003; Fogarty and Facelli, 1999; Heneghan et al., 2002; Levine et al., 2003; Lindsay and French, 2005; Matson, 1990; Standish et al., 2004; Thorpe et al., 2006; Witkowski, 1991). Changes to soil nutrient levels caused by these transformer weed species could influence which species replace a weed following control. For example in southern Australia, if a weed can increase soil phosphorus levels, control of this weed may leave a site vulnerable to invasion by other non-native species. This is because in southern Australia, soil phosphorus has been positively correlated with both the number and cover of non-native species and negatively correlated with the number and cover of native species (Morgan, 1998).

The reversibility of the impacts caused by the environmental weed should also be investigated (Hobbs and Humphries, 1995) as well as if the legacy of the invasion will persist long after the weed has been removed (Corbin and D'Antonio, 2004). Loss of native species to weed invasion may influence ecosystem function and cause a decline in the resilience of the ecosystem (Hobbs et al., 1995). Webb et al. (2001) reported that removal of exotic maples carried the risk of facilitating other invasions as well as causing additional community-level shifts away from the pre-invasion state. To help safeguard against adverse effects on native ecosystems following weed control, an integration of control strategies into a holistic process of assessment and restoration would be needed (Zavaleta et al., 2001). Vranjic et al. (2000a) suggested that given that biodiversity and long-term stability are important issues to the continued functioning of natural ecosystems, the major goals of environmental weed management should be:

- to effectively contain the spread of existing weeds,
- to manage the environment to prevent the incursion of other weeds, and
- to rehabilitate or restore the ecosystem.

The ultimate goal of any widespread environmental weed control programme, including biological control is the restoration of invaded areas (Blossey, 2004). Restoration involves the re-establishment of a native ecosystem on a site which has been previously degraded (Chapman, 1999; Headrick and Goeden, 2001; Hobbs and Mooney, 1993; McLoughlin, 1997). Restoration is often defined by actions, such as removing weeds, however such actions are not restoration in themself, given that the outcomes of restoring the native ecosystem is not always guaranteed through such actions (Chapman and Underwood, 2000). Although it has been argued that strategies are needed that will return native communities towards a pre-invasion state (Walker and Smith, 1997), a target for restoration following weed removal should not necessarily be based on this often unknown pre-invasion state. Chapman and Underwood (2000) suggested that a target based on an historic condition may not be appropriate in ecological terms, as ecological systems do not stay constant. Reference areas could be used as an alternative and could be used as the standard against which restoration following weed control is measured (Blossey, 2004; Chapman, 1999).

Bridal creeper and its biological control programme

The invasion of the widespread form (see Kleinjan and Edwards, 1999) of *Asparagus asparagoides* (L.) Druce (formerly *Myrsiphyllum asparagoides* (L.) Willd.) (Asparagaceae; common name: bridal creeper), into southern Australia will form the context for this thesis. *Asparagus asparagoides* is native to southern Africa (Morin et al., 2006a). Only one species in the Asparagaceae family is native to Australia, *A. racemosus* Willd., but this species is found in north west Australia (Clifford and Conran, 1987; Kleinjan and Edwards, 1999). Eight exotic species in the Asparagaceae family have become established in Australia and most of these have the potential to spread further (Scott and Batchelor, 2006). The other form of *A. asparagoides*, the Western Cape form (see Kleinjan and Edwards, 1999), was thought to be absent from Australia, however it was found for the first time in South Australia on 31 July 2004 by Kathryn Batchelor and myself. The distribution of this Western Cape form has now been mapped, showing that it is located in south eastern South Australia and adjacent areas in Victoria (Coles et al., 2006). The two forms of *A. asparagoides* can be distinguished on the basis of tuber morphology (Kleinjan and Edwards, 1999). All further reference to *A. asparagoides* in this thesis is to the 'widespread' form.

The biology of *A. asparagoides* is summarised by Morin et al. (2006a). It was first noted in nursery catalogues in Australia in 1857 and by the early 1900s, bridal creeper was widely used by florists in bridal bouquets (Morin et al., 2006a; Scott, 1995). Bridal creeper is now an environmental weed that has been recognised by the Australian State and Federal Governments as one of the 20 Weeds of National Significance (Thorp and Lynch, 2000) because of its threat to biodiversity and the conservation of Australia's temperate native ecosystems (ARMCANZ et al., 2000). Bridal creeper is naturalised in all states in Australia, and is most prevalent in temperate and Mediterranean climatic regions of southern Australia (Morin et al., 2006a; Scott and Kleinjan, 1991). Bridal creeper can invade a wide range of vegetation types in Australia including coastal woodland, wet and dry sclerophyll forests, heathlands and mallee scrublands (ARMCANZ et al., 2000).

Throughout its native range, bridal creeper mainly occurs as an understorey species and is usually found scrambling up other plants (Kleinjan and Edwards, 1999). Bridal

creeper prefers to grow in shade or part-shade (Meney et al., 2002; Morin et al., 2006a). A garden escapee in Australia, bridal creeper is able to invade undisturbed native ecosystems (Hobbs, 1991; Raymond, 1995; Siderov and Ainsworth, 2004), with birds being an important dispersal vector (Parsons and Cuthbertson, 2001; Stansbury, 2001). Birds eat the fleshy red fruits of bridal creeper and drop the seeds in their faeces as they perch on bushes and trees (Raymond, 1996; Thomas and Miller, 2000). Bridal creeper shoots entwine together and climb on the native understorey shrubs and small trees (Morin et al., 2006a). Once established, bridal creeper has the potential to dominate vegetation aboveground. However, its shoot biomass only represents around 13% of the total biomass, with extensive storage tubers found belowground (Raymond, 1996).

Bridal creeper is a geophyte and its roots consist of a cylindrical branching rhizome, bearing numerous tubers (Raymond, 1996). A geophyte is a plant with underground storage organs and annually renewed aerial shoots (Wheeler et al., 2002). Bridal creeper foliage is produced through-out the autumn and winter months in southern Australia (March to August and possibly into spring if the season is favourable). It flowers in later winter and early spring (August and September), with fruit produced in September and October. Willis et al. (2003) reported that bridal creeper was unlikely to develop a persistent soil seed bank. However, it is the large belowground storage reserves in the tubers which have contributed to its success as an environmental invader (Raymond, 1999). In hot, dry conditions, aboveground growth of bridal creeper ceases and its foliage begins to senesce due to lack of water. All of the aboveground parts of this plant die back over the southern Australian summer (Morin et al., 2006a; Parsons and Cuthbertson, 2001) and it is the large tuber reserves that then allows for its rapid shoot development in the following autumn.

The storage organs of bridal creeper have been identified as a major strength in the life cycle of the weed (Raymond, 1999). The root systems become intertwined, and form a thick tuberous mat, 5 to 10 cm deep in the soil (Raymond, 1999) making it difficult to distinguish between individual plants. The tuberous root mats prevent the establishment of native plants and makes chemical and mechanical control difficult (Kleinjan and Edwards, 1999). In an herbicide trial, Pritchard (1991) established that at least three consecutive years of treatment were necessary to eradicate bridal creeper infestations. Fire as a control measure has also been considered, but is unlikely to be successful on

its own because it does not kill bridal creeper plants (Willis et al., 2003). Control strategies are constrained by bridal creeper's belowground storage organs. This root system must be killed to ensure regeneration does not occur (Robertson, 1983).

The herbicide glyphosate, at a rate of 1/100 without additional wetter is effective at controlling bridal creeper (Dixon, 1996). But herbicide use can have off-target effects, especially if the spray falls on native plants, although in Dixon's (1996) study some native plant species survived spraying, probably due to the shadowing effect of bridal creeper foliage. Additionally, Dixon (1996) also reported that some native plants could tolerate this herbicide. This is supported by Pritchard (2002) who established that two annual applications in August of glyphosate at 1.8 g per litre could reduce bridal creeper's root system by 90 to 99%. The foliage of trees and shrubs on which bridal creeper scrambled over in these herbicides trials only had minimal off-target effects. However, Pritchard (2002) reported that ground vegetation of mainly sword sedges (*Lepidosperma* spp.) and introduced grasses in the trials were killed if they came in contact with the herbicide.

Raymond (1999) and Willis (2000) recommended that herbicide applications be supported with fire management. Fires in April-May could be used to remove aboveground biomass, followed by herbicide applications on the re-sprouting shoots. Willis (2000) also suggested that after controlling dense infestations of bridal creeper, little native vegetation may remain, therefore revegetation may also be needed.

Scott and Kleinjan (1991) recommended the use of biological control over other control techniques for bridal creeper invasions within conservation areas. Biological control of an environmental weed has a number of advantages over other control options, ideally being target-specific with continuous action and the agents being self-dispersing irrespective of terrain (Adair, 1995). Bridal creeper in its native Africa is an uncommon plant and is not considered a weed (ARMCANZ et al., 2000; Morin et al., 2006a). A biological control programme for bridal creeper in Australia was initiated in 1990, with a series of field surveys in South Africa, the centre of origin of the plant (Edwards, 1996). A biological control agent that directly attacked the tuber reserve of the plant would have been desirable, however surveys in South Africa failed to find such candidates (Scott and Kleinjan, 1991), although a weevil has been found in low

numbers attacking the tubers of Western Cape form of *A. asparagoides* (Kleinjan and Edwards, 2006). Investigations thus concentrated on natural enemies that affected aboveground biomass of bridal creeper.

The initial survey work for natural enemies of bridal creeper in South Africa and subsequent host-specificity studies, led to the release in Australia of an undescribed leafhopper *Zygina* sp., (Hemiptera: Cicadellidae) in 1999 and a pathogenic rust fungus, *Puccinia myrsiphylli* (Thuem.) Wint. (Basidiomycota: Uredinales) in 2000. Both these agents attack the foliage of bridal creeper, reducing its ability to photosynthesize (Batchelor and Woodburn, 2002; Morin et al., 2002). Glasshouse experiments performed with these agents showed that they could significantly reduce vegetative growth. This in turn translated into a decrease in tuber production (Batchelor and Woodburn, 2002; Kleinjan et al., 2004a; Morin et al., 2002; Turner et al., 2004). A third agent, *Crioceris* sp., (Coleoptera: Chrysomelidae) a leaf beetle was also released in 2002 (Morin et al., 2006b). Morin et al. (2006b) provides an in depth description of the initial stages of the biological control programme of bridal creeper in Australia, therefore only a brief description of the programme is given below.

All of the leafhopper's five nymphal instars and adults feed on mesophyll cells on the lower surface of the cladodes of bridal creeper (Witt and Edwards, 2000). A cladode is a modified stem that resembles a leaf. When the cladode is depleted of mesophyll, it falls from the plant (Batchelor and Woodburn, 2002). The older foliage is preferred by the leafhopper for feeding and egg laying, and eggs are laid only on bridal creeper. Populations of *Zygina* sp. have high levels of parasitism in South Africa and Witt and Edwards (2000) suggested that *Zygina* sp. was an excellent candidate for biological control in Australia as it would escape these species-specific enemies. Parasitism however, has now been recorded within eggs of *Zygina* sp. in Western Australia (Batchelor and Woodburn, 2002; Spafford Jacob et al., 2006).

Puccinia myrsiphylli (bridal creeper rust) completes its life cycle on bridal creeper, infecting cladodes and stems, and relying on wind for dispersal (Kleinjan et al., 2004b; Morin et al., 2006b). This rust fungus obtains nutrients and water from living cells of bridal creeper (Morin et al., 2002). Upon landing on a moist cladode, urediniospores of the rust germinate and the fungus penetrates plant tissue through the stoma (Kleinjan et

al., 2004b; Morin et al., 2006b). The rust fungus also destroys cladode tissue by producing fruiting bodies which reduce the photosynthetic surface of bridal creeper. Heavily infected cladodes are shed prematurely (Morin et al., 2002).

Another biological control agent, *Crioceris* sp., a leaf beetle which damages bridal creeper by stripping young stems of shoots and cladodes, was also released in Australia (Morin et al., 2006b). It is expected to be most active at the beginning of the bridal creeper annual growth cycle. The leaf beetle exclusively attacks young stems, and the three agents, now released in Australia, co-occur on *A. asparagoides* plants in their native range in South Africa (Batchelor and Woodburn, 2001). The leafhopper and the rust have demonstrated their capacity to reduce bridal creeper populations, but it is too early to determine the contribution of the leaf beetle (Morin and Edwards, 2006).

Evaluating the success of the biological control of environmental weeds

The above classical form of weed biological control relies on the knowledge that natural enemies can adversely influence the fitness of plants and suppress plant populations (Briese, 2000; McFadyen, 1998). This form of biological control consists of an introduction of a natural enemy collected from the plant's place of origin, to the area where the plant is now considered a weed (McFadyen, 1998; Morin, 2001). Crawley (1997) was critical of biological control due to the lack of before and after monitoring during the release of agents into new areas. However, once biological control agents are established in their introduced ranges, Anderson et al. (2000) details a number of approaches to evaluate the success of these biological control programmes. They include measuring a biological success where weed densities are reduced to a manageable part of the landscape, to an ecological success where the weed invasions are stopped or reversed. Anderson et al. (2000) however, chose not to deal with issues such as biodiversity and improving ecosystem health and function, suggesting they were more appropriately dealt with in the context of post-control rehabilitation. Yet, the measurement of success of any environmental weed control programme must include the response of biodiversity which the control programme is aiming to protect.

It is argued that pathogens and insects that are used in biological control can reduce the weed's ability to compete with other plants and may even kill the weed in some

instances (Anderson et al., 2000). This activity eventually brings the weed population down to reach a stable acceptable equilibrium (Morin, 2001). It is hoped that the biological control agents when released can reduce the weed population density and 'desirable vegetation' returns (Figure 1.1, Morin, 2001). This is described as the best case scenario of weed biological control by Morin (2001), where increases in 'desirable vegetation' is assumed to follow the reduction of the density of a weed following the release of a biological control agent. Unfortunately, very few studies have measured the response of this desirable vegetation following biological control (Denslow and D'Antonio, 2005).

Lesica and Hanna (2004) established that the biological control of a weed does not always lead to an associated increase in native species diversity. At one site in their study, Lesica and Hanna (2004) reported increases in invasions of other exotic plants and at another site an increase in native plants following the release of two biological control agents. After this five year study, they suggested that site conditions were important, such as history of herbicide and soil fertility, in determining the community response to weed biological control. Previous as well as future disturbances play a role in the recovery of ecosystems following weed removal and given this, biological control may need to be augmented by other restoration techniques to restore this 'desirable vegetation' (Lesica and Hanna, 2004; Tisdale, 1976).

In the classic study by Huffaker and Kennett (1959) in California, the diversity of the original perennial grassland ecosystem had been restored following release of biological control agents to control St. John's wort (*Hypericum perforatum* L.). In contrast to the Huffaker and Kennett (1959) study, St. John's wort was replaced by introduced forbs and feral grasses that had been dominant before its invasion in another part of the US, in northern Idaho (Tisdale, 1976), leading Campbell and McCaffrey (1991) to suggest that a successful biological control effort is only one part of a strategy for successful weed management.

Although there is little information on the impacts of environmental weeds, there is even less information about the effects of control efforts on the native communities that these control programmes are designed to protect (Byers et al., 2002). The impacts on native communities from the weed control efforts should also therefore be a focus of

environmental weed control programmes (Sheley and Krueger-Mangold, 2003). This has not been the focus in the past, especially in the area of environmental weed biological control and research is now needed to quantify the impacts weed control has on native communities, both plant and animal, as well as to determine if the adverse impacts environmental weeds have on native communities are actually reduced following control.

Batchelor and Woodburn (2002) indicated that the prospect of successful biological control of bridal creeper in Australia was promising. The bridal creeper rust is currently the most effective agent and has already demonstrated its ability to quickly reduce bridal creeper populations (Morin et al., 2006b). The bridal creeper rust, in conjunction with the leafhopper, is also highly likely to have an additive impact on the health of bridal creeper plants (Turner et al., 2004). If these biological control agents have a major impact on bridal creeper density, the question remains, will native plant and animal communities benefit from the control? The ability of the native plants to recolonise areas following bridal creeper control is likely to be influenced by several factors including the past impact of bridal creeper; the size and composition of the seed bank; soil quality; and plant competition, which have all been investigated within this thesis.

Objectives of this thesis

A broad range of parameters are needed to determine the impact of weeds on biodiversity, ecosystem functions and successional consequences (Adair and Groves, 1998). Raymond (1999) suggested that research on these types of impacts was needed for bridal creeper. A complete assessment of an impact of an environmental weed should include ecological processes such as seedling recruitment, nutrient cycling and plant-animal interactions (Adair and Groves, 1998). Given this, the overall aim of my project was to investigate the impacts of bridal creeper across this broad range of parameters and then to determine the barriers to restoring ecosystem health following bridal creeper control.

Invasive geophytes, such as bridal creeper, are found in most regions of the world (Raymond, 1999), including within Australia and New Zealand (Williams and West,

2000). In certain regions of Australia, including the south west, they are becoming an increasing concern in native ecosystems (Humphries et al., 1993). They can form dense underground mats of bulbs, corms, tubers and rhizomes that can crowd out native vegetation (Humphries et al., 1993). In south west Australia, many South African geophytes have spread widely, including various species of Freesia, Gladiolus, Ixia, Sparaxis, Watsonia, and Oxalis (Pate and Dixon, 1982), yet few studies have investigated the significance of geophytes as environmental weeds (Raymond, 1999).

There were four main objectives of this thesis:

1. to determine the impacts of bridal creeper on native community composition, structure and ecosystem function,
2. to determine the mechanisms behind the impacts caused by bridal creeper invasion and to determine if the residual impacts or legacies from bridal creeper invasions remained after control,
3. to assess the condition of the sites where bridal creeper was to be managed and to determine if other restoration techniques will be needed, in addition to bridal creeper control, and
4. to determine the likely successional changes on native community composition following weed suppression, via biological control.

This thesis will explore the impacts of bridal creeper on community composition through both removal experiments and with a multi-site comparison. Combining approaches of multi-site comparisons with weed removal is a powerful approach to determine weed impacts, although this combined approach has not been undertaken in the past (Adair and Groves, 1998). In moorlands in the UK, Marrs et al. (2004) undertook a removal experiment with purple moor grass (*Molinia caerulea* (L.) Moench) and concluded that a greater knowledge of initial floristic composition was needed at the site before starting restoration. Therefore as a benchmark, I will also assess the current situation of bridal creeper invaded communities and then re-assess the situation following weed suppression. Given that the speed of response of communities to weed removal may confound the results (Aarssen and Epp, 1990), ants will be used as bioindicators, as these bioindicators are able to respond quickly to changing conditions (Andersen, 1990).

As the seed supply directly affects seedling emergence (Standish et al., 2001), and the seed bank can be an indicator of future vegetation at a site (Fisher, 1999), including an insight into whether exotic plants might become abundant at a site (D'Antonio and Meyerson, 2002), the readily germinable soil seed bank in bridal creeper invaded sites will be determined. This will provide an indication of the future species that would be likely to colonise areas left vacant following the control of bridal creeper. This is important for my study sites in Western Australia, given that Bell et al. (1990) suggested that the composition of the vegetation in the first few years following restoration in Western Australia controls ecosystem function for many years that follow.

Briefly the organisation and structure of this thesis are discussed below.

In *Chapter 2*, I measure the impact of bridal creeper on perennial plant composition and abundance and also measure the plant community response to the control of bridal creeper.

In *Chapter 3*, the impacts caused by bridal creeper on native plant communities are quantified using a multi-site comparison method with nearby uninvaded areas used as a reference. The likely responses of the plant community to bridal creeper control are also investigated through an assessment of the readily germinable seed bank.

Chapter 4 details a study in which the soil nutrient levels below bridal creeper infestations are compared to reference areas again in a multi-site comparison. The differences found in soil nutrient levels are also assessed to determine if they could pose a barrier to recovery of native plant communities following the removal of bridal creeper through a glasshouse experiment.

Following the findings that soil nutrient levels below bridal creeper were higher than those in reference areas, in *Chapter 5* I investigate the differences in tissue chemistry, litter production and decomposition between bridal creeper and native species. In addition, litterfall and decomposition rates are compared between invaded areas and nearby reference areas. This led to the development of a proposed mechanism by which bridal creeper could increase soil fertility.

Chapter 6 will report on the results of a field study on the decomposition rate of the belowground biomass of bridal creeper as well as the residual impacts that this decomposing belowground biomass could have on other plants following control. The impact of the root system (both dead and alive) from mature bridal creeper plants on the growth rate and root allocation of a native plant species are measured in the glasshouse. A laboratory experiment investigating the allelopathic impacts of live and decomposing root material on germination and root development of several plant species is also presented.

In *Chapter 7*, I measure the response of native plants to bridal creeper control by herbicides coupled with the use of fire as a restoration tool.

Chapter 8 details the response of native plants following the initial stage of the biological control of bridal creeper.

In *Chapter 9*, I evaluate the suitability of using ants as bioindicators to evaluate bridal creeper impact and the effectiveness of biological control of bridal creeper.

In *Chapter 10*, I provide a synthesis of this work to demonstrate the importance of combining different approaches to determine the impacts of the environmental weed bridal creeper; explore the mechanics behind these impacts; and assess the likely responses to the widespread control of bridal creeper in southern Australia.

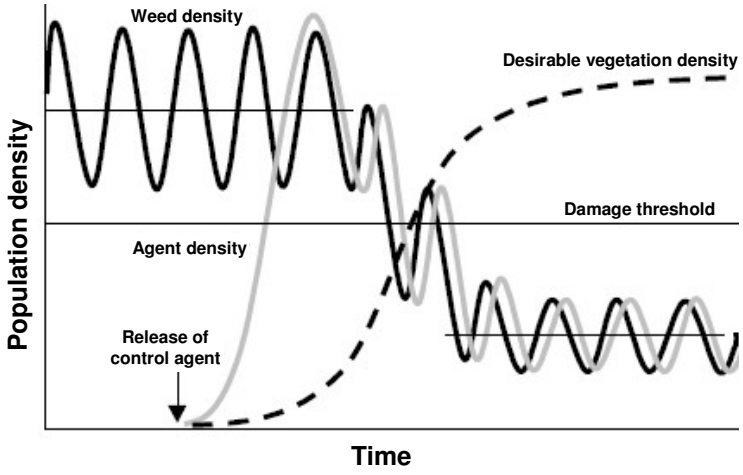

Figure 1.1. From Morin (2001), giving the best case scenario of weed biological control, where increases in desirable vegetation is assumed to follow the reduction of a weed's density following the release of a biological control agent.

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CHAPTER TWO

AN EIGHT-YEAR REMOVAL EXPERIMENT MEASURING THE IMPACT OF BRIDAL CREEPER (*ASPARAGUS ASPARAGOIDES* (L.) DRUCE) AND THE POTENTIAL BENEFIT FROM ITS CONTROL

Key words: environmental weeds, succession, weed substitution

Abstract

Bridal creeper is a weed with climbing annual shoot growth and extensive, underground storage tubers, and is capable of dominating native vegetation. Whilst its impacts appear obvious, this has been measured in few quantitative studies. In 1996, forty 3 × 3 m plots were established in a mallee remnant north of Adelaide, South Australia, to investigate this issue. Using glyphosate, bridal creeper was removed from half the plots in 1997, with follow-up treatment for the same plots in 1999.

In 2005 there was still no significant difference in the number of native plant species between plots with or without bridal creeper. There was also no significant difference in abundance of individual native species, except for the saltbush *Enchylaena tomentosa* ($p<0.01$). However, there were consistent increases in cover of the chenopod and native grass understorey in the bridal creeper removed plots, even if not significant for some species. The common chenopods *E. tomentosa* and a combined dataset for *Rhagodia parabolica* and *R. candolleana* had greater shoot biomass where bridal creeper had been controlled ($p<0.01$ and $p<0.05$ respectively). An exotic plant, *Oxalis pes-caprae* also had higher cover in plots without bridal creeper compared to untreated plots ($p<0.01$).

This study has shown that it may take many years for recovery following weed control and additional restoration work may be necessary. Dead tubers were still intact below the surface in the removal plots and their presence may be affecting seedling establishment. Recovery may also have been hindered by higher *O. pes-caprae* density.

A third possibility is a lack of suitable environmental conditions in the eight year period for germination and establishment of native species.

Introduction

Plant invasions into natural ecosystems are a threat to native biodiversity (Adair and Groves, 1998). Exotic plant species that invade and impact on natural ecosystems are commonly referred to as environmental weeds (Humphries et al., 1991; Richardson, 2001; Richardson et al., 2000). Managing environmental weeds requires knowledge of the impacts the weed has on native communities and then determining if native communities can be restored following weed control (Gratton and Denno, 2005). Predicting the influence of weed control on community dynamics is also needed when developing control strategies (Sheley and Krueger-Mangold, 2003), and thought must be given to what is likely to occur after removal has been achieved (Hobbs and Mooney, 1993). In Australia, few studies have measured the impact of environmental weeds (Adair and Groves, 1998; Grice et al., 2004), with the emphasis being more on weed control, often with little consideration even to their ecological consequences (Williams and West, 2000).

Of the studies that have investigated weed impacts, many have reported a reduction in native plant species diversity following invasion (see examples within Grice et al., 2004; and Levine et al., 2003). Yet, the majority of these have been comparisons of community structure between invaded and weed free areas or across a gradient of weed density. For example, Mullet and Simmons (1995) reported a reduction in the abundance of native species with increasing density of *Pittosporum undulatum* Vent. Sites dominated by the introduced grass, *Cenchrus ciliaris* L. (buffel grass) had fewer plant species when compared to sites without buffel grass (Jackson, 2005) and in the U.S., Kedzie-Webb et al. (2001) measured plant species along a gradient of *Centaurea maculosa* Lam. (spotted knapweed). Native perennial grass cover and species richness were inversely related to the spotted knapweed's cover. Although this method of documenting weed impacts allows rapid data collection, they are correlative studies and therefore lack the power of manipulative studies in relation to determining the cause and effect of weed invasion (Adair and Groves, 1998; Grice et al., 2004). Woods (1997) suggested that there is a clear need for a distinction between correlation and the causes

of reduced biodiversity. Although time consuming, weed removal experiments can give stronger evidence of impact, and they can also provide some indication of the long term changes that could occur after large-scale control (Adair and Groves, 1998).

Asparagus asparagoides (L) Druce (bridal creeper) mainly occurs as an understorey species in its native range in southern Africa and is usually found scrambling up other plants (Kleinjan and Edwards, 1999). Within Australia, bridal creeper has the potential to dominate native vegetation both above and belowground with its shoot biomass representing around 13% of the total biomass and extensive storage tubers found belowground (Raymond, 1996). Most populations of the small endangered shrub, *Pimelea spicata* R. Br., in south-eastern New South Wales are threatened by bridal creeper (Willis et al., 2004). A vulnerable listed ground orchid in South Australia, *Pterostylis arenicola* M.A.Clem. & J.Stewart, is also under threat from bridal creeper (Sorensen and Jusaitis, 1995) as both the weed and orchid emerge from underground organs in autumn (Vranjic et al., 2000a). In Western Australia, it has also been reported that bridal creeper can germinate faster than the native species *Clematis microphylla* DC. and therefore bridal creeper may also have an impact on this species (Fox, 1984).

Even with the above studies on bridal creeper, most Australian research on bridal creeper has focused on the chemical and biological control of this weed and it now appears that the biological control programme will go a long way towards controlling bridal creeper (Batchelor and Woodburn, 2002; Morin et al., 2006b). But, fundamental to declaring successful management of bridal creeper, is the need to investigate the impacts of bridal creeper on the whole plant community structure and determine if weed control alone is enough to enable restoration of these communities. Therefore, using the weed removal method, the aim of this study was to measure the impact of bridal creeper on perennial plant composition and abundance and hence to predict the benefit from the control of bridal creeper.

Grice et al. (2004) reviewed Australian studies that quantified weed impacts in native ecosystems. Of the 24 studies reviewed, none reported their impacts in terms of succession. When a weed has been establishment for some time, weed removal experiments do not measure the weed's impacts *per se* but the response of the native community after weed removal (Adair and Groves, 1998). Therefore experiments like

the one reported here can predict the likely successionary pathways that could occur after weed control.

Methods

The study area was in a mallee vegetation community, within a small council reserve of remnant vegetation approximately 3 km north-west of Owen, South Australia 34°14'6''S, 138°31'8''E. The reserve was adjacent to a former school site and has had minimal amenity use in the past 30 years. Native vegetation within the reserve is dominated by an overstorey of mature *Eucalyptus socialis* F.Muell. ex Miq., with mainly chenopod understorey. Soil is an alkaline clay loam. Rabbits were controlled during the period of the study by the Lower North Animal and Plant Control Board of South Australia.

Initially forty 1 × 1 m plots were chosen that had a dense coverage of bridal creeper and which contained an individual of both the most common shrub and groundcover species. The common shrub was either *Rhagodia parabolica* R.Br. or *Rhagodia candolleana* Moq. and the groundcover (which was also a shrub but with a lower habit) was *Enchylaena tomentosa* R.Br. Plots were then extended to 3 m × 3 m, giving nine 1 m^2 subplots, with the two native species within the central subplot. Bridal creeper was removed from half the plots on 1-3 October 1997 (with follow-up in spring 1999) using 33% Roundup® (360 g/L glyphosate) with 2% Pulse Penetrant® (1,020 g/L polyether modified polysiloxane), sponge applied by hand to minimise off-target contact with native plants.

Between May 1996 and March 2005, vegetation was periodically sampled within the plots. For example, bridal creeper cover was recorded in September/October 1997, 1998, 1999, 2002 and 2004. In 1999, 2002 and 2004 the number of bridal creeper shoots was also counted. The root system of bridal creeper entwines together, and forms a thick tuberous mat, 5 to 10 cm deep in the soil (Raymond, 1999). This makes it difficult to distinguish between individual plants, therefore only cover and number of shoots were measured for bridal creeper. Simple linear regression was undertaken to determine if there was a relationship between number of bridal creeper shoots and bridal creeper cover, by analysing all plots sampled in 1999, 2002 and 2004.

In May 1996 and March 2005, the number of individuals (or shoots) of other perennial plant species was recorded and in May 1998 and March 2005 the percentage areal shoot cover was also recorded. The areal cover of the native trees, being *Pittosporum phylliraeoides* DC., *Santalum acuminatum* (R.Br.) A.DC., *Senna artemisioides* (Gaudich. ex DC.) Randell and *Eucalyptus socialis*, was estimated only below the height of 0.5 m. When bridal creeper was measured in September 2004, percent areal cover was also recorded for the annual shoot growth of the exotic geophyte *Oxalis pes-caprae* L. (soursob), which was abundant within the study area. In March 2005, in addition to percentage covers, tree and shrub shoot biomass was estimated using the 'Adelaide' hand-held unit technique (Andrew et al., 1979) for all portions of foliage directly above each plot, including that of plants that were rooted outside the plots. Statistical analysis was carried out using GenStat (2003). At the end of the experiment the influence of the removal treatment on the number of native perennial species and individual species abundance, percentage cover and foliage biomass were analysed using one-way analysis of variances. A log10 or square-root transformation was applied where appropriate to meet the assumption of homogeneity of variances (Sokal and Rohlf, 1995).

In addition, from the centre of each plot, soil cores below the tuber mats were taken in March 2005. Cores 5 cm deep and 5 cm in diameter were taken 5 cm below the litter layer. Cores were bulked for each treatment and any large organic matter was removed, such as tubers and other roots. Eight sub-samples from each bulked sample were forwarded in airtight containers to CSBP laboratories for chemical analysis. Nitrogen (NO_3^- and NH_4^+), extractable phosphorus, organic carbon and pH were measured.

Results

There was a significant relationship between the number of bridal creeper shoots and cover of bridal creeper (Figure 2.1). Before treatments were applied, cover of bridal creeper within all plots in 1997 was 45.4% ± 2.9 (mean ± s.e.). Over the following years bridal creeper cover within untreated plots ranged from 35.5% to 44.9% whilst in the removal plots bridal creeper cover ranged from 0.1% to 2.4% (Figure 2.2). Before treatments were applied in 1997, mean abundance of native plant species across all plots was similar (Figure 2.3) and the year following the initial application of herbicide the

percentage cover of native species was still comparable between treatments (Figure 2.4).

In March 2005 there was no significant difference in the number of native perennial plant species between plots (Table 2.1). There was also no significant difference in abundance of native species, except for the saltbush *E. tomentosa* ($p=0.01$) (Table 2.1 and Figure 2.3). There were consistent increases in cover of the chenopod and native grass understorey, even if not significant for some species (Table 2.2 and Figure 2.4). *Enchylaena tomentosa* cover was significantly lower in untreated plots ($p<0.001$). In September 2004, the exotic plant, *O. pes-caprae* had significantly higher cover of 42.6% in plots without bridal creeper, compared to 22.5% in untreated plots ($p=0.004$).

Whilst the combined chenopod cover of *R. parabolica* and *R. candolleana* was not significantly different between treated and untreated plots (Table 2.2), there was approximately 45% less foliage biomass measured in March 2005 for combined *R. parabolica* and *R. candolleana* ($p<0.05$) (Table 2.3). *Enchylaena tomentosa* in untreated plots had on average only 15% of the foliage biomass compared to where bridal creeper had been controlled ($p<0.01$).

There was no significant difference between plots in any soil parameters that were measured in March 2005 (Table 2.4).

Discussion

Any off-target effects from the glyphosate on native plants was minimal given that the cover of these plants between treated and untreated plots was similar in 1998, one year after the initial application (Figure 2.4). Hence, differences detected between the control and herbicide treatments are largely due to differences in bridal creeper density. The experiment has shown that bridal creeper can reduce native plant biodiversity through a reduction in biomass (*E. tomentosa* and combined *R. parabolica* and *R. candolleana*) and in plant number (*E. tomentosa* and perennial grasses). However, within the eight year timeframe of this study there was no significant change detected in the number of plant species due to bridal creeper.

Adair and Groves (1998) suggested that a combination of approaches were needed when investigating weed impacts and a multi-site approach of comparing weed free areas to invaded areas, coupled with this weed removal study would increase the power of this study. This multi-site approach has been undertaken in south west Australia, where it was established that bridal creeper invaded sites contained fewer native plant species when compared to weed free areas (Chapter 3 - Turner et al., 2008c). In addition, Leah (2001) while comparing infested sites of a closely related weed species, *Asparagus declinatus* L. (bridal veil) to un-infested sites, reported that the establishment of bridal veil in South Australia resulted in a reduction of species richness and diversity.

Byers et al. (2002) posed the question that if an environmental weed is controlled, will this removal actually benefit native species. In this study, even eight years after bridal creeper control there was only a limited increase in the abundance of native plants. However, this study revealed consistent increases in the cover of perennial plant species, even if not significant for some species. In a similar study, McCarthy (1997) used the weed removal method at one site to measure the response of a forest understorey community in the U.S. After a three year period, following removal of *Alliaria petiolata* (M.Bieb.) Cavara & Grande (garlic mustard), it was shown that garlic mustard had a negative effect on the composition and structure of the understorey community. Removal resulted in the increase in annuals, vines and tree seedlings, but the effects on slow growing perennial plant species were less clear. Response of the slow growing perennials may have become evident if the study period was increased.

Weed removal experiments are labour intensive and long-term (Adair and Groves, 1998; Marrs et al., 2004), both with monitoring and the repeated removal of the weedy species. Due to this, replication across sites was missing from this study. It must be stressed then, that the results be viewed with caution when trying to extrapolate this study across regions invaded by bridal creeper. In moorlands in the U.K., Marrs et al. (2004) had replication across sites and removed *Molinia caerulea* (L.) Moench (purple moor grass) with burning, grazing and glyphosate applications, however the herbicide treatment was applied once at the start of the five year study and purple moor grass had recovered in some areas by the end of the experiment. Even so, Marrs et al. (2004) established that different sites responded differently following weed removal and that multiple outcomes following large-scale control could be possible.

In invaded heathlands in the U.K., Marrs and Lowday (1992) controlled *Pteridium aquilinum* (L.) Kuhn (bracken) by cutting or with the use of herbicide coupled with artificial seeding of native species. After ten years it was established that the final vegetation varied greatly from their goal of a heath dominated area, through to grass heaths, being mainly a mixture of two species, to other areas where two different weeds became dominant. In these areas, there was a replacement of one weed problem with another (Marrs and Lowday, 1992). In the same way, soursob, another weed from southern Africa, may have replaced bridal creeper following its control. Soursob had a higher density in the removal plots (Table 2.2) and recovery of native species may have been hindered by this higher density. Mason et al. (2004) used the correlative method of comparing native sites to weed infested sites to measure the effects of *Chrysanthemoides monilifera* (L.) Norl. ssp. *rotundata* (DC.) Norl. (bitou bush) on fore and hind-dune communities. Bitou bush adversely affected native species richness in the fore-dune while in the hind-dune species richness was not affected, however in both communities control activities increased weed species richness.

It has been reported that repeated applications of glyphosate can give good control of bridal creeper (Dixon, 1996; Pritchard, 2002) and again this herbicide worked well in this experiment. However, it was observed at the study site that dead tubers still remained in the removal plots even eight years after the weed had been killed. This may have affected seedling establishment. Bridal creeper's underground plant parts consist of a cylindrical branching rhizome, bearing numerous tubers, which become entwined together and form thick mats (Raymond, 1996). Biological control may provide better outcomes than chemical control from a conservation view point if agents were found to reduce bridal creeper's substantial root system. Intensive searches have been undertaken in South Africa to identify biological control agents that directly damage the root system, but no candidates were located (Kleinjan and Edwards, 2006). However, glasshouse experiments performed on the biological control agent *Puccinia myrsiphylli* (Thuem.) Wint., which has been released in Australia, showed that this rust could significantly reduce vegetative growth. This in turn translated into a decrease in tuber biomass (Morin et al., 2002; Turner et al., 2004), which may allow greater seedling establishment.

A third possibility for the limited increase in native species is a lack of suitable environmental conditions for germination and establishment over the previous eight year period. Marrs et al. (2004) suggested that when contemplating this kind of research a knowledge of the initial floristic composition is needed. A target for the density of native species following weed removal is also needed. A target could be an historic condition, say at a level before bridal creeper invasion, however Chapman and Underwood (2000) argued that this may not be appropriate in ecological terms, as ecological systems do not stay constant. Instead, reference sites are recommended as well as control sites. Control sites are sites similar to the site being restored, but not subjected to the weed control. Reference sites are natural areas that represent the target for restoration (Chapman, 1999). This study would have been strengthened by incorporating reference sites, areas free of bridal creeper and free of other disturbances. Comparisons between native germination and survival could then have been compared to areas where the weed was never present. However, this was not possible given the limited natural areas in the agricultural region around the study area and due to the fact that bridal creeper is widespread throughout South Australia.

Adair and Groves (1998) suggested that weed removal experiments, to determine weed impacts, were not suited to old invasions where the invader has caused irrecoverable damage. This has not been the case with this study. The chenopod and native grass understorey has started to show trends of increased cover. However, this study has also shown that it may take many years for recovery and additional restoration work may be necessary following the control of bridal creeper to speed up the recovery process and to ensure that weed substitution does not occur. An additional site in South Australia has also been established following a wild fire (see Chapter 7). This site continues to be monitored and may provide outcomes different to those reported above, given that fire can stimulate the regeneration of native plant species.

Acknowledgements

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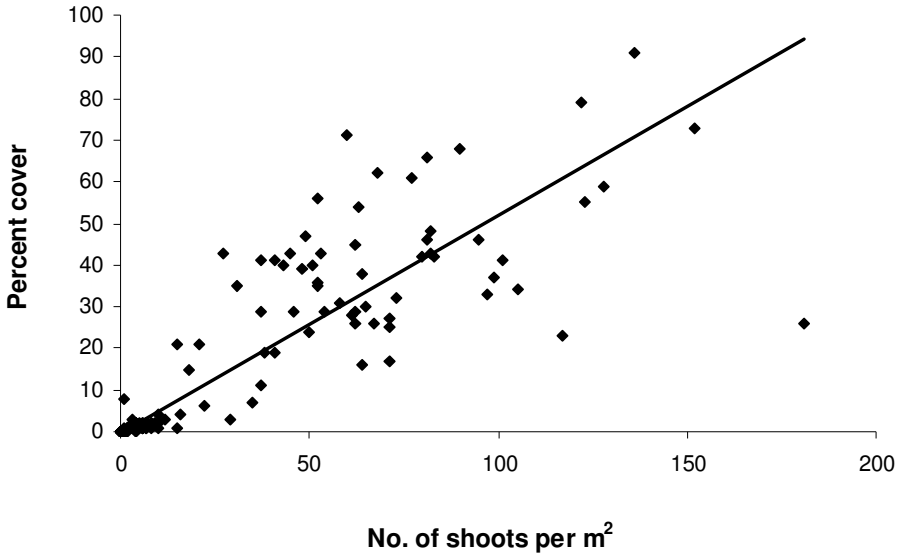

Figure 2.1. Relationship between number of bridal creeper shoots and bridal creeper cover (all plots and dates, September 1999, October 2002 and September 2004 combined).

(Square root transformation, R^2=83.3; d.f. 1,115; F=579.34; p<0.001).

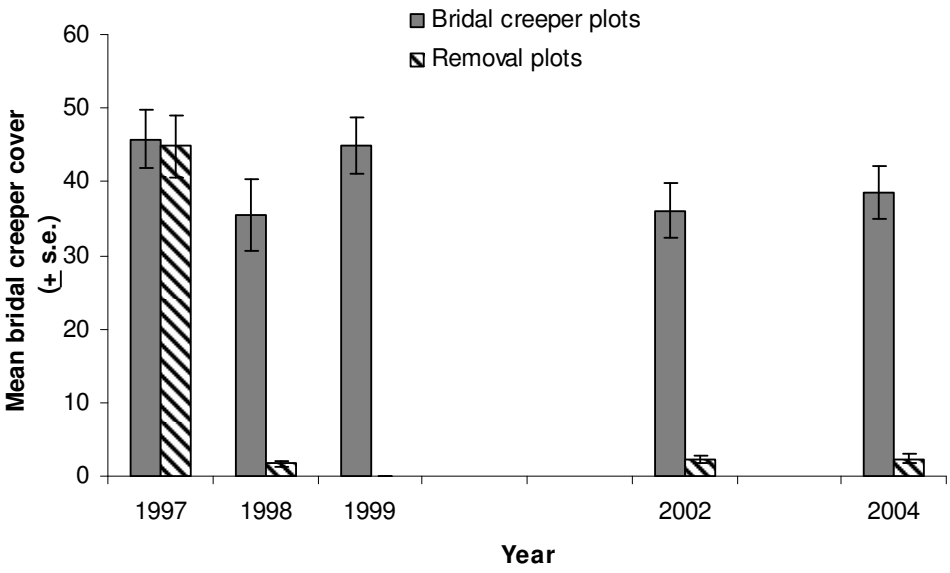

Figure 2.2. Bridal creeper cover across the period of the study.

The removal plots were treated with glyphosate in 1997 with a follow-up in 1999. Bridal creeper cover was not recorded in the years not shown.

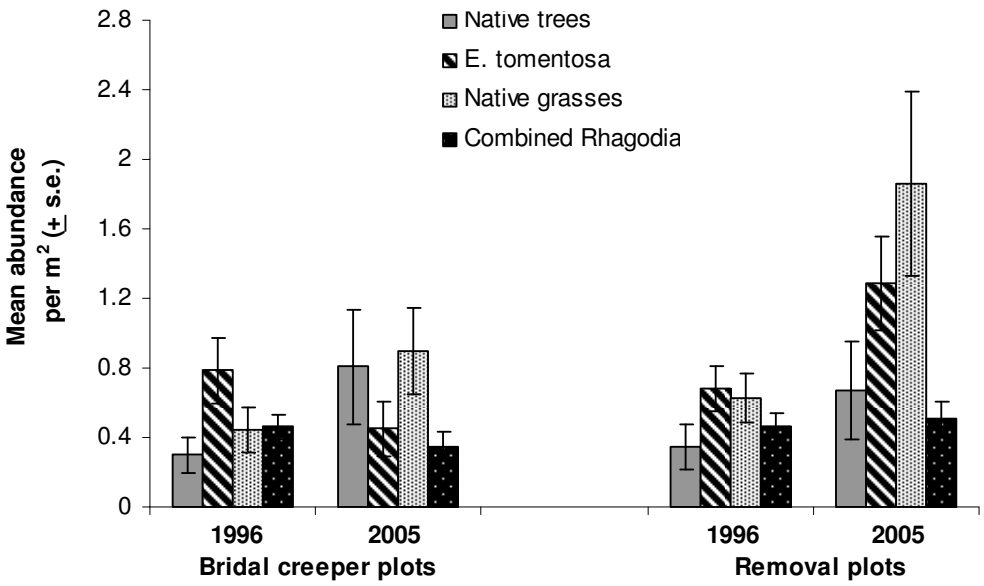

Figure 2.3. Abundance of native species in 1996, before treatments were applied, and in 2005 at the completion of the experiment.

Native trees are a combination of *Pittosporum phylliraeoides*, *Santalum acuminatum*, *Senna artemisioides* and *Eucalyptus socialis*. Native grasses are a combination of native grasses in the genera *Austrostipa* and *Austrodanthonia***.** Combined *Rhagodia* is a combined abundance for two species, *Rhagodia parabolica* and *Rhagodia candolleana*.

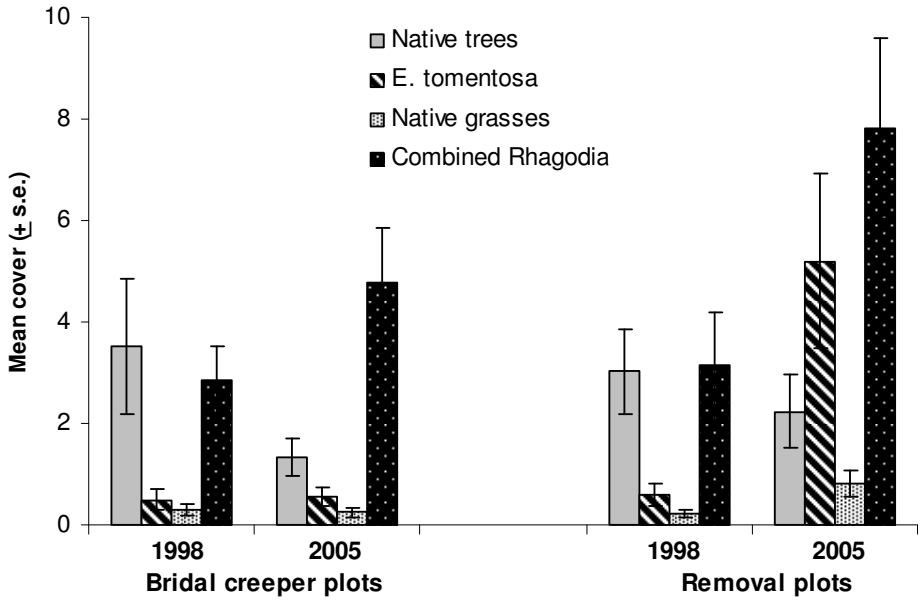

Figure 2.4. Percentage cover of native species in 1998, one year after the initial treatment was applied, and in 2005 at the completion of the experiment.
(See Figure 2.3 for details on vegetation classes monitored).

Table 2.1. Differences in mean (± s.e.) perennial plant abundance per square metre between treatments in March 2005[a].

Plant variable	Bridal creeper plots	Removal plots	F	p
No. of native species	4.10 ± 0.38	4.55 ± 0.24	1.09	0.304
Enchylaena tomentosa	0.45 ± 0.16	1.29 ± 0.27	7.25	0.011[e]
Combined *Rhagodia*[b]	0.35 ± 0.08	0.51 ± 0.10	1.50	0.228
Perennial native grasses[c]	0.90 ± 0.25	1.86 ± 0.53	2.70	0.108
Native trees[d]	0.90 ± 0.33	0.83 ± 0.30	0.02	0.890

[a] The analysis of variance models with treatment (n=20) as the only factor. A log10 transformation was applied to the variable native trees before the analysis.

[b] Combined *Rhagodia* is a combined abundance for two species, *Rhagodia parabolica* and *Rhagodia candolleana.*

[c] Perennial native grasses are a combination of native grasses in the genera *Austrostipa* and *Austrodanthonia***.**

[d] Native trees are a combination of *Pittosporum phylliraeoides*, *Santalum acuminatum*, *Senna artemisioides* and *Eucalyptus socialis*.

[e] Statistically significant ($p<0.05$).

Table 2.2. Differences in mean (± s.e.) plant cover between treatments in March 2005 except for *Oxalis pes-caprae* cover which was measured in September 2004[a].

Plant variable	Bridal creeper plots	Removal plots	F	p
Enchylaena tomentosa	0.56 ± 0.19	5.20 ± 1.72	14.32	<0.001[b]
Combined *Rhagodia*	4.77 ± 1.08	7.81 ± 1.78	1.10	0.300
Perennial native grasses	0.25 ± 0.09	0.82 ± 0.25	4.47	0.041[b]
Native trees	1.34 ± 0.38	2.24 ± 0.73	0.65	0.426
Oxalis pes-caprae	22.47 ± 3.56	42.55 ± 5.51	9.17	0.004[b]

[a] The analysis of variance models with treatment (n=20) as the only factor. A log10 transformation was applied to all variables, except Perennial native grasses and *Oxalis pes-caprae*, before the analysis.

[b] Statistically significant ($p<0.05$).

Table 2.3. Differences in mean (± s.e.) foliage biomass (dry weight g/m^2) between treatments in March 2005, as estimated using the 'Adelaide' hand held technique [a].

Plant variable	Bridal creeper plots	Removal plots	F	p
Enchylaena tomentosa	2.60 ± 0.87	17.57 ± 4.78	14.15	<0.001[b]
Combined *Rhagodia*	23.76 ± 4.33	43.01 ± 8.30	4.23	0.047[b]
Native trees	26.07 ± 7.87	45.42 ± 11.70	0.90	0.350

[a] The analysis of variance models with treatment (n=20) as the only factor. A log10 transformation was applied to all variables, except Combined *Rhagodia*, before the analysis.

[b] Statistically significant ($p<0.05$).

Table 2.4. Differences in mean (± s.e.) soil variables between treatments in March 2005[a].

Soil variable	Bridal creeper plots	Removal plots	F	p
Nitrate (mg/Kg)	7.50 ± 1.45	9.75 ± 1.73	0.99	0.336
Ammonium (mg/Kg)	2.75 ± 0.65	2.00 ± 0.33	0.84	0.374
Phosphorus (mg/Kg)	10.75 ± 1.44	13.75 ± 1.56	2.25	0.156
Organic carbon (%)	2.84 ± 0.23	2.57 ± 0.16	0.96	0.344
pH	8.45 ± 0.03	8.45 ± 0.04	0.00	0.997

[a] The analysis of variance models with treatment (n=8) as the only factor. A square root transformation was applied to the variables ammonium, phosphorus and pH before the analysis.

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CHAPTER THREE

THE ECOLOGICAL BARRIERS TO THE RECOVERY OF BRIDAL CREEPER (*ASPARAGUS ASPARAGOIDES* (L.) DRUCE) INFESTED SITES: IMPACTS ON VEGETATION AND THE POTENTIAL INCREASE IN OTHER EXOTIC SPECIES

Key words: biological control, geophyte, native plant communities, restoration, seed bank, weed substitution

Abstract

To protect native biodiversity from environmental weeds, the impacts that these weeds cause need to be known before weed control commences. *Asparagus asparagoides* (L.) Druce (bridal creeper) (Asparagaceae) is a serious environmental weed and has been selected for biological control in Australia. To predict the responses of plant communities to the control of bridal creeper, a pre-release baseline of the impacts of bridal creeper on native plant communities was undertaken. Plant assemblages in areas invaded by bridal creeper were compared to reference areas that contained little or no bridal creeper within southern Western Australia. Areas invaded by bridal creeper contained 52% fewer native plant species when compared to nearby reference areas. However, there was no difference in the number of other exotic plant species between areas. Similar trends were found for the germinable seed bank. Although a greater number of exotic species were present in the seed bank compared to the vegetation surveys, there was still no difference between areas with and without bridal creeper. In a glasshouse trial, exotic species germinated more frequently compared to native species. This could indicate that as bridal creeper density decreases following control, exotic species have an advantage over native species when colonising areas left vacant by bridal creeper. Secondly, as bridal creeper areas contained reduced native species richness and cover, they may be susceptible to further weed invasion after bridal creeper

is removed. Therefore, simply reducing the presence of bridal creeper may not guarantee successful restoration of invaded areas, and additional restoration efforts will be needed to ensure the ultimate goal of protecting native biodiversity is reached.

Introduction

To improve the role of environmental weed management, especially when undertaking biological control, a better understanding of the impacts of weeds is needed (Thomas and Reid, 2007). The knowledge of the impacts that these exotic plants have on native communities and ecosystem processes is required if we are to properly restore native communities following weed control (Gratton and Denno, 2005; Walker and Smith, 1997). But in Australia, few studies have measured the impact of environmental weeds (Adair and Groves, 1998; Grice et al., 2004; Williams and West, 2000) and more generally the impacts of exotic species are not well known globally (Byers et al., 2002).

Although environmental weed impact studies are rare, there is even less information about the impacts caused by weed control programmes on the native biodiversity that they are hoping to protect (Byers et al., 2002). In particular, indirect effects of biological control on native plant communities are poorly understood (Denslow and D'Antonio, 2005). Responses of invaded communities to a reduction in weed density following biological control are scarce, yet of the studies that have investigated this issue, many have reported the target weed being replaced by other exotic species (Thomas and Reid, 2007). For example, Denslow and D'Antonio (2005) suggested that the biological control of a weed may increase native species diversity, however it could also lead to replacement by other exotic plants. This process has been described as the 'invasive species treadmill' (Thomas and Reid, 2007).

The assessment of sites is needed before control of an invasive weed is undertaken. This gives an opportunity to determine the impacts of the weed, with the added benefit of increasing our ability to predict the responses of native communities to the control (Denslow and D'Antonio, 2005). This will highlight additional restoration activities that will be needed to properly restore sites following the reduction in weed status.

Bridal creeper (*Asparagus asparagoides* (L.) Druce) is an environmental weed in southern Australia (Morin et al., 2006a) and provides an opportunity firstly to study its impact on native plant communities, but also to predict the likely response of these native communities to biological control. For a well established environmental weed such as bridal creeper, the only economically viable option for its widespread control is the use of biological control. In Australia, three biological control agents have been released to control bridal creeper; a leafhopper *Zygina* sp., the bridal creeper rust fungus *Puccinia myrsiphylli* (Thuem.) Wint. and the bridal creeper leaf beetle *Crioceris* sp. (Morin et al., 2006b). An initial study indicated that the rust is currently the most active agent (Morin et al., 2006b) and it appears that this biological control programme will have a significant effect on bridal creeper density (see Batchelor and Woodburn, 2002; Morin et al., 2002; Turner et al., 2004).

In Australia, bridal creeper is able to invade undisturbed native ecosystems (Hobbs, 1991; Raymond, 1995). The impacts and threats of bridal creeper on individual native plant species have already been documented (see Fox, 1984; Sorensen and Jusaitis, 1995; Willis et al., 2003; Willis et al., 2004). For example, bridal creeper is the primary threat to the largest remaining population of the endangered shrub, *Pimelea spicata* R. Br., which is found in the Cumberland Plain Woodland community south-west of Sydney (Willis et al., 2003). Another study in South Australia also monitored the impact of bridal creeper removal on a perennial plant community (Chapter 2 - Turner and Virtue, 2006).

To quantify the impacts caused by bridal creeper to native plants and to estimate the likely benefits of its control, this study used a multi-site comparison (see Adair and Groves, 1998). This is a common method to determine weed impacts but has not been used with bridal creeper in any of the above studies. All published studies thus far have been single site evaluations of impact. An assessment of the readily germinable seed bank was also undertaken, as a seed bank provides an indication of future species that could colonise areas left vacant following the decline of bridal creeper.

Methods

A multi-site comparison was undertaken in Western Australia to determine the impacts of bridal creeper on plant communities. Sample units were located within areas where bridal creeper was present and in comparable reference areas where the weed was absent or at low numbers.

STUDY AREA

The study was undertaken at four sites in southern Western Australia (Figure. 3.1). One site was located in Glenlynn Conservation Reserve (GC) (34.002S, 116.155E) near Bridgetown. This reserve has a high disturbance history, being surrounded by grazing land. The three other sites were all located in or adjacent to a relatively remote national park, Fitzgerald River National Park (FRNP) on the central southern coast of Western Australia. The Quell Creek site (QC) (34.254S, 119.414E) is in an isolated area within FRNP. The Quaalup Homestead site (QH) (34.263S, 119.410E) is within a private property surrounded by the national park, following the park's establishment in 1954 (Anonymous, 1991). This site had some grazing disturbances in the past, but the native areas within this property are now managed as part of a wilderness retreat. The third site associated with FRNP is located next to the Gairdner River (GR) (34.373S, 119.427E). This land is owned by the local government but managed as part of the national park and is visited very infrequently for fishing and camping.

PLANT BIODIVERSITY WITH AND WITHOUT BRIDAL CREEPER

Each of the four sites contained relatively homogeneous stands of bridal creeper of a sufficient size to accommodate at least two 10 x 1 m plots, separated by at least 10 m. GC and QC had larger infestations and three plots were established within each stand, while at GR and QH two plots were established within their bridal creeper infestations, representing a total of ten bridal creeper plots.

Each plot commenced in a zone of high bridal creeper density at the base of a tree with the long axis of the rectangular plot running towards the edge of the stand. The plots crossed the boundary of the infestation approximately seven or eight metres from the beginning of the plot. Plots commenced below a tree, given the clumped nature of bridal creeper below these structures. A rectangular plot was chosen as it has been suggested

that this increases the variation within plots, while decreasing the variation among plots (Mueller-Dombois and Ellenberg, 1974). Rectangular plots can increase the accuracy of counts given the tendency of the vegetation, such as bridal creeper, to be clumped. Further to this, if the long axis of the plot cuts across any banding of vegetation (as is the case within this study) it increases the sampling intensity per sample (see Mueller-Dombois and Ellenberg, 1974). In addition, as up to 87% of the biomass of bridal creeper is belowground and found only in the top 10 to 20 cm of the soil (Raymond, 1996), plots with bridal creeper were established beyond the aboveground infestation to capture both edge effects as well as any impacts from the root biomass belowground.

Each of the ten bridal creeper plots were paired to native vegetation reference plots (also 10 x 1 m) located directly adjacent to the bridal creeper areas and at least 10 m away from other plots. The reference plots had a similar aspect, slope and elevation and also commenced from below the same tree species as its adjacent paired bridal creeper plot. The reference plots were located within the native vegetation with little or no bridal creeper present. Soil pH ranged from 5.9 to 6.6 in the bridal creeper invaded areas and from 5.7 to 6.7 in the reference areas. Stansbury (1999) established that bridal creeper was most productive in Western Australia where soils were slightly acidic between a pH of 6 and 7. The management plan for FRNP (Anonymous, 1991) has also suggested that bridal creeper is still spreading along the river flats within FRNP, indicating that the reference areas are useful for comparisons to areas already invaded by bridal creeper. Plots within these areas were established in October 2004 at the commencement of the dry season. At this time, all vascular plant species were identified and percentage areal shoot cover of the understorey, which reached a maximum height of 1.5 m, was estimated visually for each species. Bridal creeper is an understorey species and in Australia it is the understorey species that are predicted to be most impacted (Stansbury and Scott, 1999; Chapter 2 - Turner and Virtue, 2006).

The influence of site (GC, QC, QH and GR) and area (invaded or reference) on percentage cover and species number, of both exotic and native species, were analysed using two-way analysis of variances (ANOVAs) (GenStat, 2003). Exotic plant species are defined here as plant taxa whose presence in an area was due to introduction by human activity (Richardson et al., 2000). Additional analysis on the percentage cover of a subset of data, being the woody understorey of native trees and shrubs, was

undertaken. Square-root transformations were applied where appropriate to meet the assumption of homogeneity of variances (Sokal and Rolf 1995).

ESTIMATION OF THE READILY GERMINABLE SOIL STORED SEED BANK

The soil seed bank was estimated through the seedling emergence method (for example see King and Buckney, 2001; Navie et al., 2004). Soil and leaf litter was collected from three of the four plant survey sites in March 2005. This was just prior to the main germination event in south west Australia, following the break of the dry season. Quell Creek was not sampled as it was inaccessible at the time. In southern Western Australia, Fisher (1999) established that the majority of seeds are located in the litter and top 5 cm of the soil. At each of the three sites, 40 soil cores (9.5 cm in diameter to a depth of 8 cm) were collected randomly to determine the germinable seed bank density. Twenty of the 40 cores were taken within each bridal creeper stand and 20 were taken from each reference area. Soil cores were collected adjacent to but not in each 10 x 1 m vegetation survey plot (to minimise disturbance). Soil cores were stored at 4^{o}C in the dark until being placed in a glasshouse on 5 April 2005.

The 20 cores from each area were bulked to form a single sample creating a total of six samples. Soil from each sample was sieved through 1 cm mesh and litter and roots including bridal creeper tubers were removed. Soil was then spread evenly in plastic germination trays (34 cm long and 28 cm wide) to a depth of 2 cm on top of river sand, also 2 cm thick. An additional three trays containing 4 cm deep river sand were also placed in the glasshouse to determine if the sand which was used as a base in the seedling trays contained any seed. These trays were placed in a glasshouse under natural light conditions and watered as required. The temperature of the glasshouse ranged from 10 to 30^{o}C. Trays were randomly moved around benches within the glasshouse every fortnight.

This part of the study determined which seeds would readily germinate in the field without any other management. Seedlings were monitored regularly with seedlings removed from the trays as they appeared and allowed to grow until they could be identified. After two months the rate of germination slowed, so on 25 July 2005 soil in the trays was remixed and smoke water was applied to stimulate further germination. Regen 2000® Smokemaster was applied as a spray at manufacturers recommendation of

100 mL per m^2 (Anonymous, 2005). This product and concentration were selected as they have been effectively used to increase germination levels of a number of local Western Australian plant species (see Lloyd et al., 2000; Rokich et al., 2002). The experiment ceased as seedling emergence slowed again, six months after trays were placed in the glasshouse and 2.5 months after the application of smoke water.

Plants were grown on until 5 February 2006 for identification. Some plants died during this process and some plants could not be identified to species level. Therefore for analysis, plants were placed into two groups. All exotic species that could be identified were placed into an 'exotic' category and all plants identified as native were grouped with dead and unidentified species into a category labelled 'other' species. This was done to be conservative in the estimation of the exotic seed bank.

After six months and excluding bridal creeper, the influence of area (invaded or reference) on: (i) the exotic abundance; (ii) abundance of 'other' species; and species number, of both (iii) exotic; and (iv) 'other' species, were analysed using a series of one-way ANOVAs (GenStat, 2003). In addition, to determine if there was an overall difference in the abundance of exotics and 'other' species emerging from the seed bank at a site level as well as a difference in the number of exotic and 'other' species, the two areas at each site were combined and two one-way ANOVAs were undertaken. This was to determine what would most likely replace bridal creeper after control. The whole site was analysed together as potential colonisers could be from across the site. This gave an overall picture of seed bank density at the sites. Transformations were applied when appropriate, via a log10 transformation, to meet the assumption of homogeneity of variances (Sokal and Rohlf, 1995).

Results

PLANT BIODIVERSITY WITH AND WITHOUT BRIDAL CREEPER

Bridal creeper cover ranged from 40.3 to 61.7% in the bridal creeper invaded areas across the four sites, while in the reference areas the cover was 0.2 to 5.1% (Figure 3.2a).

There were on average 3.6 ± 0.8 (mean ± s.e.) exotic species in bridal creeper plots and 4.0 ± 0.6 in reference plots, which was not significantly different (F=0.34; d.f. 1,12; p=0.572 and Figure 3.2b). The cover of all exotic species excluding bridal creeper, was not statistically different, with exotic cover in reference areas being 10.1% ± 3.4, compared to 4.4% ± 1.6 in the bridal creeper areas (after square root transformation F=4.11; d.f. 1,12; p=0.065 and Figure 3.2c).

Both the mean number of native plant species and the percentage cover of all native understorey plants were significantly lower in bridal creeper areas compared to reference areas (F=82.66; d.f. 1,12; p<0.001 and Figure 3.3a, F=30.31; d.f. 1,12; p<0.001 and Figure 3.3b respectively). Bridal creeper plots averaged 4.9 ± 0.7 native species while reference plots averaged 10.3 ± 0.9, while the cover of native understorey was 22.0% ± 4.0 in the invaded plots and 48.1% ± 4.5 in the reference plots.

Across all sites, 31 native species were only found in reference areas. Of these, two were climbers, nine were herbs and 20 species or 65% were woody trees or shrubs. The cover of the understorey woody plants was also significantly lower in bridal creeper areas (after square root transformation F=9.86; d.f. 1,12; p=0.009 and Figure 3.3c), with 6.1% ± 1.7 cover found in bridal creeper plots compared to 27.0% ± 6.5 cover in reference plots. In contrast, six native species were found only in bridal creeper plots, one climber, two herbs and three species being shrubs or trees.

ESTIMATION OF THE READILY GERMINABLE SOIL STORED SEED BANK

No seedlings were observed in the three trays containing only sand. There was no difference in the number of exotic or 'other' seedlings that emerged between areas after six months. Excluding bridal creeper, exotics averaged 3,919 ± 1,874 (mean ± s.e.) seedlings/m^2 emerging from bridal creeper areas and an average of 3,834 ± 1,681 seedlings/m^2 emerging from reference areas (F=0.00; d.f. 1,4; p=0.975). 'Other' species averaged 54 ± 2 seedlings/m^2 emerging from bridal creeper areas and an average of 367 ± 245 seedlings/m^2 emerging from reference areas (after a log10 transformation, F=4.01; d.f. 1,4; p=0.116). Within the areas containing bridal creeper there was an average of 105 ± 49 bridal creeper seedlings/m^2 across the three sites, however only one bridal creeper seedling emerged from the soil collected from the reference areas.

Excluding bridal creeper and again after six months, on average 16.0 $\pm$ 2.9 exotic species were found in the bridal creeper areas while 18.7 $\pm$ 2.2 species where found in the reference areas but this difference was not significant ($F=0.52$; d.f. 1,4; $p=0.502$). However, a greater number of 'other' species were detected in the reference areas ($F=10.0$; d.f. 1,4; $p=0.034$), with an average of 7.3 $\pm$ 0.3 species compared to 4.0 $\pm$ 1.0 in the bridal creeper areas.

Even with bridal creeper seedlings removed from the analysis, at the end of the experiment a greater number of exotic seedlings had germinated from the seed bank compared to 'other' species (after a log10 transformation $F=11.10$; d.f. 1,4; $p=0.029$, Figure 3.4a). Exotic species dominated the seed bank with an average of 3,876 $\pm$ 1,765 exotic seedlings/m^2 emerged per site compared to 210 $\pm$ 121 seedlings/m^2 classified as 'other'. Across the three sites, a greater number of exotic species 22.0 $\pm$ 1.2 (excluding bridal creeper) emerged from the seed bank compared to 'other' species 8.3 $\pm$ 0.9 ($F=88.47$; d.f. 1,4; $p<0.001$ and Figure 3.4b). This result was after the application of smoke water, which appeared to benefit both exotic and 'other' species.

After the smoke water application, seven new 'other' species were detected across the three sites, but an additional five exotic species were also recorded. From these 12 species, the species that germinated the most was the native cowslip orchid, *Caladenia flava* R.Br. ssp. *flava*. However, only 12 individuals germinated from the GR reference area, seven from the QH reference area and one from the QH bridal creeper area.

A total of 34 exotic species were recorded across all sites, of this 22 species (65%) were represented by less than 10 seedlings per site. Eighteen exotic species, being autumn and winter germinating annual herbs or grasses, were absent in the vegetation survey but were found in the seed bank. Native tree and shrub species were poorly represented in the seed bank study when compared to the vegetation survey.

Discussion

PLANT BIODIVERSITY WITH AND WITHOUT BRIDAL CREEPER

The ultimate success of environmental weed control must be measured on the level of replacement of the targeted weed with other vegetation (Adair, 1995) and not just a

reduction in the density of the weed. In an attempt to control weeds in native ecosystems, there is an assumption that weed control alone will allow the re-establishment of native species. There is an additional assumption that the gradual decline in a weed species following biological control will also provide sufficient time for the native community to re-establish. Based on my study, these assumptions are unlikely to be met.

In my study, bridal creeper invaded areas contained fewer native species compared to reference areas. Bridal creeper areas are at risk of further weed invasions following the control of bridal creeper, as communities with low species richness are thought to be less resistant to invasions (see Elton, 1958; Prieur-Richard and Lavorel, 2000; Shea and Chesson, 2002). This is supported by Turner and Virtue (Chapter 2 - 2006) who reported an increase in cover of an exotic plant following the removal of bridal creeper in South Australia. In a study in the US, Alvarez and Cushman (2002) also reported lower native species number in *Delairea odorata* Lem. (Cape ivy) invaded areas. Weed removal there resulted in increased abundances of both native and exotic seedlings.

Given that the impacts of bridal creeper on native plant communities reported here are based on a comparison of areas, they do not indicate causation. For example, the plant species composition of the invaded areas may have been different prior to the invasion of bridal creeper (Adair and Groves, 1998). The presence of bridal creeper at a site may in fact relate to a previous disturbance and therefore the impacts reported here may not be as a result of the invasion. Therefore, as the initial cause of the species decline is not known, weeds need to be treated as a symptom of the problem, not just the cause (Williams and West, 2000). If the low native species numbers are a result of a disturbance that then facilitated bridal creeper invasion, weed control will do little to increase native biodiversity unless the impacts of the original disturbance are addressed (Woods, 1997).

The histories of my sites are not fully known and therefore impacts of bridal creeper remain speculative. Unfortunately all methods that determine weed impacts have disadvantages (see Adair and Groves, 1998). However given that this paper reports on a multi-site comparison that established similar findings to an eight-year removal experiment (Chapter 2 - Turner and Virtue, 2006), it adds support to the view that bridal

creeper is the cause of some of the decline in both native species number and abundance. Turner and Virtue (2006) found that the biomass of native trees was 43% higher in plots where bridal creeper had been removed eight years earlier, compared to plots where bridal creeper remained. Although this was not significant, Turner and Virtue (2006) established that it was the native shrubs that were significantly impacted, with the shrub *Enchylaena tomentosa* having significantly more biomass, being 85% higher in the removal plots. Shrubs in the genus *Rhagodia* were also 45% higher in biomass in the removal plots and this was also statistically significant (see Table 2.3). These results support this study, with bridal creeper invasion associated with reduced cover of the understorey native trees and shrubs.

Bridal creeper grows best in shady areas (Morin et al., 2006a). Bridal creeper mainly occurs as an understorey species in its native range in southern Africa and is usually found scrambling up other plants (Kleinjan and Edwards, 1999). But in Australia bridal creeper utilises and often smothers the understorey trees and shrubs. When these woody structures are present, the growth, competitive ability and fruiting potential of bridal creeper increases (Stansbury, 1999). When supports are available for bridal creeper, bridal creeper's aboveground biomass is significantly higher than if no support was available (Stansbury et al., 2007). Birds, an important dispersal vector, eat berries produced by bridal creeper and drop the seeds in their faeces as they perch on shrubs and trees (Thomas and Miller, 2000). Bridal creeper is then found scrambling up and forming clumps around these shrubs and trees (Morin et al., 2006a; Siderov and Ainsworth, 2004).

ESTIMATION OF THE READILY GERMINABLE SOIL STORED SEED BANK

The mix of seedlings emerging in the seed bank, being composed primarily of annual herbs, is not unusual when using the technique described in this study. Similar patterns have been described in other studies (Holmes and Cowling, 1997; Navie et al., 2004). However, given the pressure from the number of germinating exotics, exotic plants may become established at the expense of native plants (see Figure 3.4, and supported by Perez-Fernandez et al., 2000).

Although the estimation of native seed bank from my study is not an indication of the total native seed bank with shrubs and trees poorly represented, my study reveals which

species will readily germinate at the sites if no additional efforts towards restoration beyond the removal of bridal creeper are undertaken. Coupled with the knowledge that the vegetation aboveground within the bridal creeper areas had low native species richness, it seems plausible that these invaded areas may become vulnerable to further weed invasion. This is supported by the Davis et al. (2000) suggestion that as resource utilisation and competition decreases at a site, it becomes more susceptible to plant invasions. Following the biological control of bridal creeper, it is hoped that the competition intensity of bridal creeper will decrease, however this may also leave a site more prone to invasion. Therefore, weed control needs to be accompanied by additional restoration efforts to prevent weed substitution.

In Western Australia, a large number of leguminous shrubs, such as acacias, require heat pre-treatment before germination occurs (Shea et al., 1979) and therefore my technique would underestimate the number of these species in the seed bank. Smoke water used in my study assisted in the germination of both native and exotic species, but not the germination of those native species which require heat. It would be useful therefore, for studies to investigate the role of fire as a restoration tool following weed control. This may help tip the balance back towards native species, by increasing the number of native germinations and reducing the pressure from the large number of germinating exotic seedlings. Another study in South Australia investigated the impact of bridal creeper after a wildfire (see Chapter 7 - Turner and Virtue, in press). All exotic species, including bridal creeper, remained at low densities after the fire, with bridal creeper having no impact on native plant assemblages. Acacias and other native trees now dominate the site ten years following the fire (Turner and Virtue, in press).

IMPLICATIONS FOR OTHER WEED CONTROL PROGRAMMES

Both Luken (1997) and Downey (2008) have suggested that the actions of weed management need to be revisited as weed control alone will not be enough to restore invaded areas. To overcome this, weed management should be attempting to change the successional trajectory of invaded sites by both encouraging desirable species as well as discouraging undesirable species such as weeds (Hobbs and Mooney, 1993; Luken, 1997). Environmental weeds can alter biodiversity as seen in this study, but removal of these weeds in isolation can also result in unexpected changes to biodiversity, such as the replacement of one exotic species with another (Zavaleta et al., 2001).

The bridal creeper rust is now widespread across southern Australia (Morin et al., 2006b) and it has since been released at all of the above four study sites. Even within one year, bridal creeper cover has decreased by 19% across my four sites (P. Turner, unpublished data, 2005). Monitoring of these sites will continue to record changes in plant community composition (which are reported in Chapter 8), however based on the above study it appears that further restoration work would be needed at these sites.

Acknowledgements

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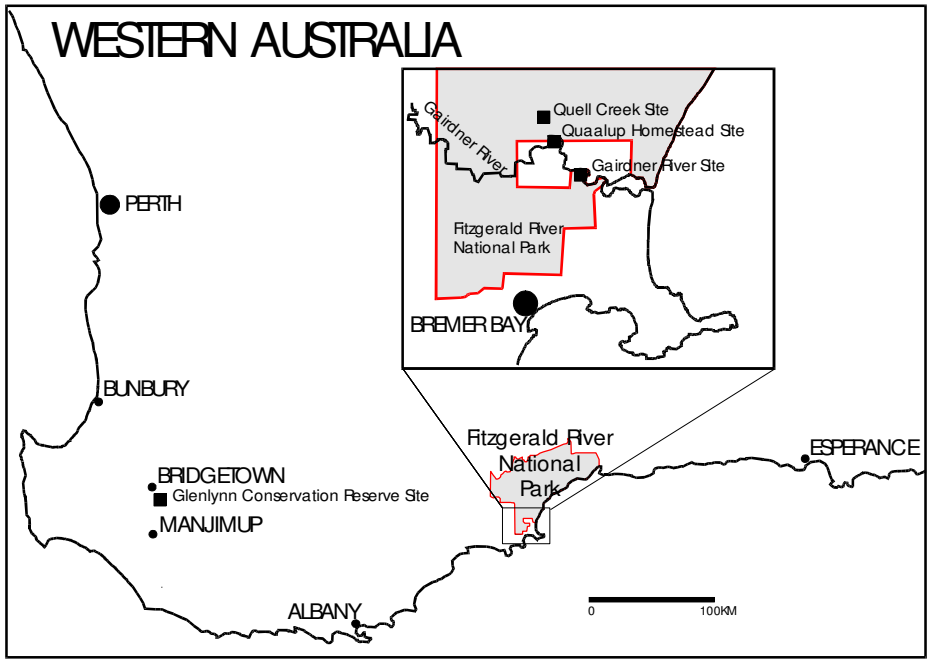
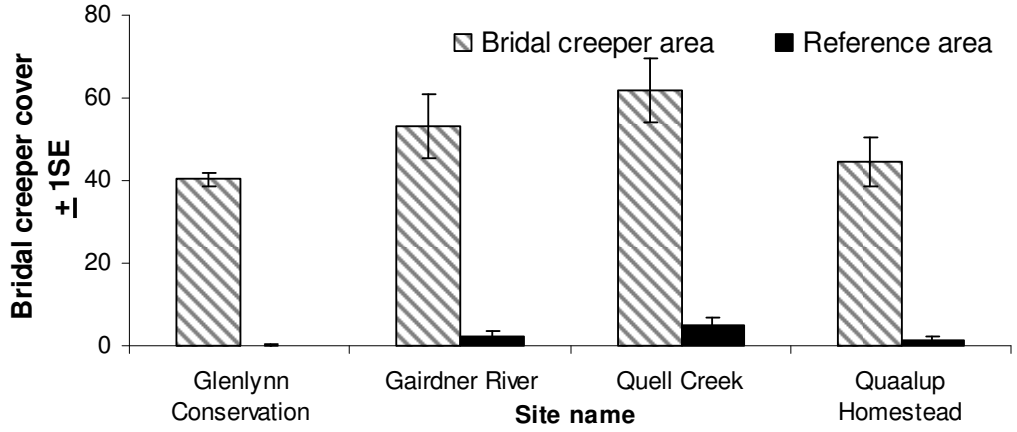


Figure. 3.1. South west Australia and the locations of study sites.

a)



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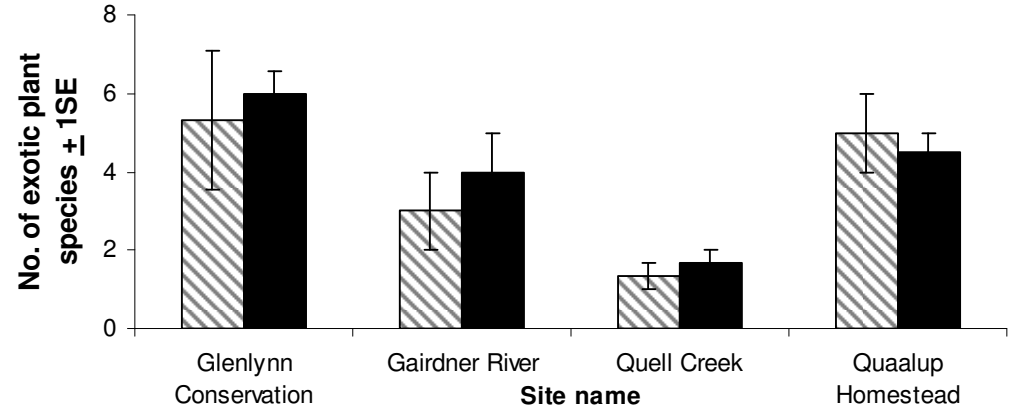

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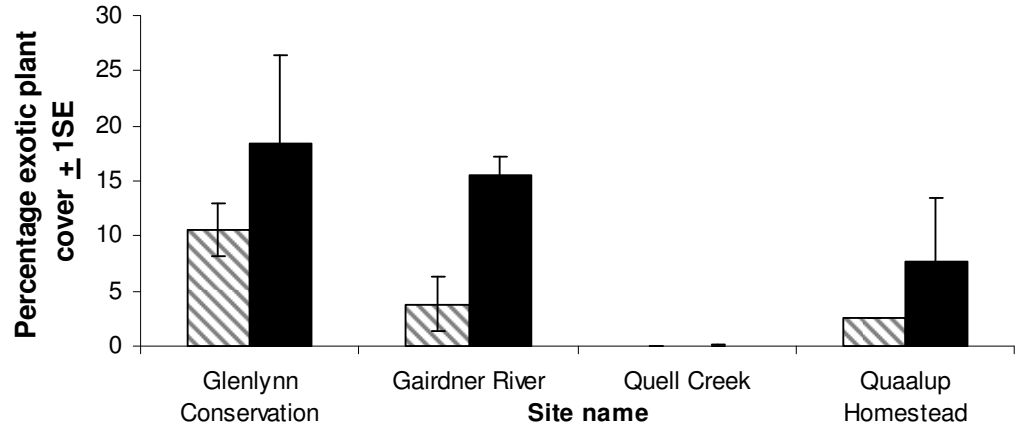
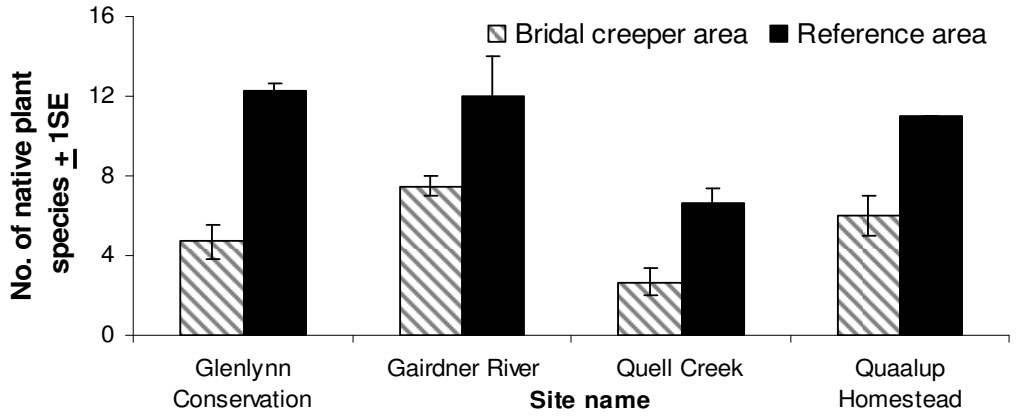


Figure 3.2. a) Mean (± s.e.) percentage cover of bridal creeper across the four sites. b) Mean number of exotic plant species (including bridal creeper) per 10 m^2. c) Mean percentage cover of the other exotic species (excluding bridal creeper).

a)



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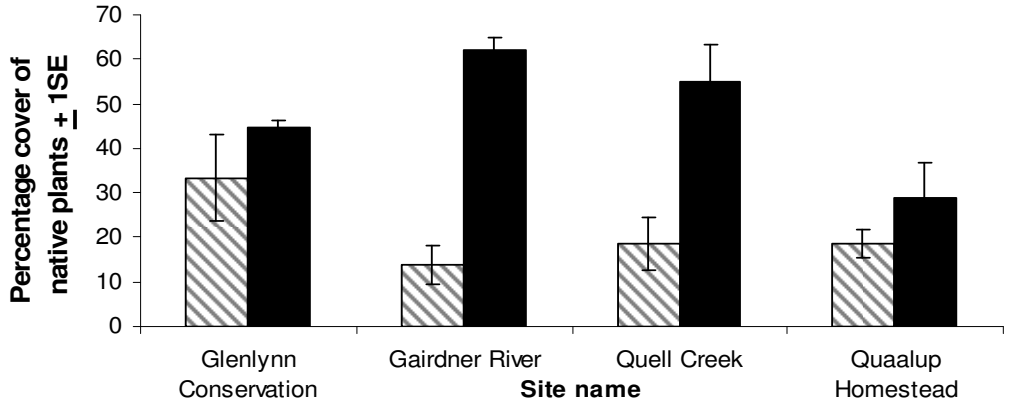

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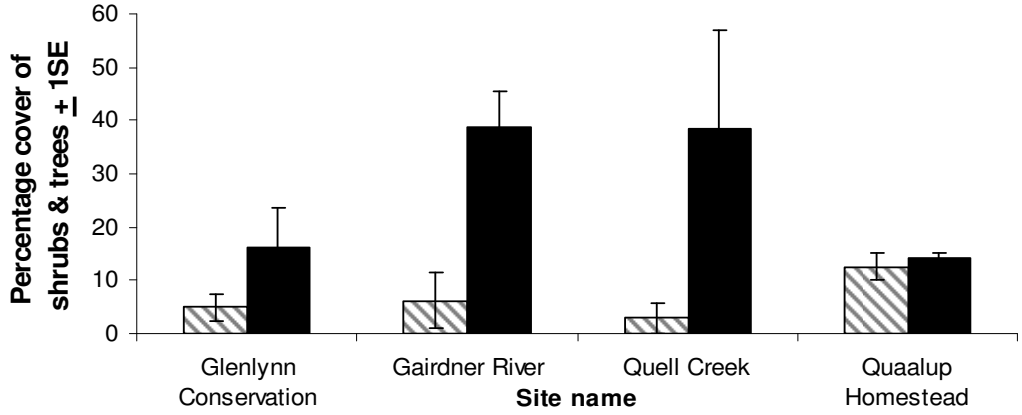
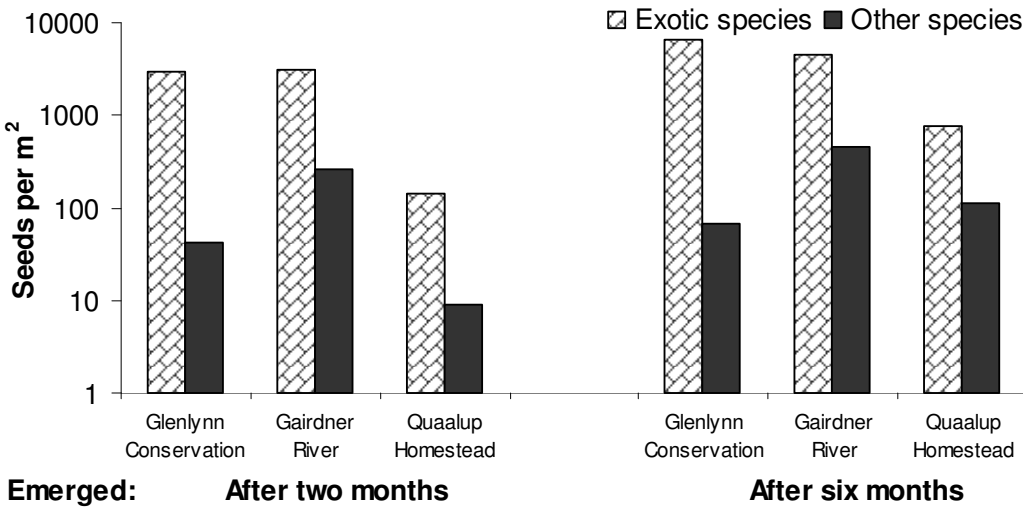


Figure 3.3. a) Mean number of native species per 10 m^2 across the sites. b) Mean percentage cover of all native plants. c) Mean percentage cover of the native understorey trees and shrubs.

There was no variation between plots in areas where error bars are not shown.

a)



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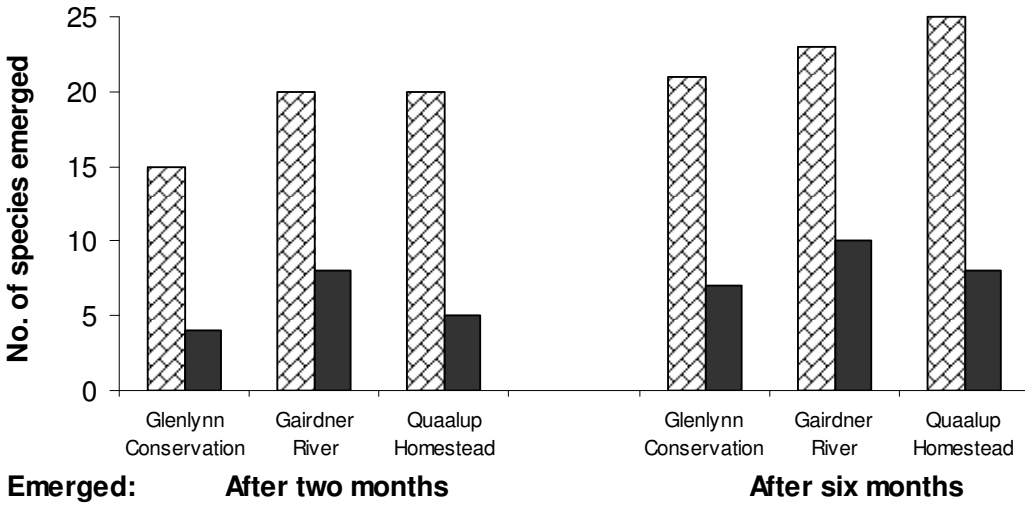

Figure 3.4. a) Total densities of exotic and 'other' plant species which emerged from the seed bank study from the three sites, with the bridal creeper and reference areas combined. b) The number of species that emerged from the seed bank.

'Other' species are a combination of native species and species that were not identified. Results are shown after two months before the smoke water was applied and after six months at the end of the study. (As soil cores were bulked at each site, no variation within sites is reported.)

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CHAPTER FOUR

THE ECOLOGICAL BARRIERS TO THE RECOVERY OF BRIDAL CREEPER (*ASPARAGUS ASPARAGOIDES* (L.) DRUCE) INFESTED SITES: ELEVATED LEVELS OF AVAILABLE PHOSPHORUS

Key words: environmental weeds, invasive plants, relative growth rate, soil nutrients, weed substitution

Abstract

In Australia, soil nutrient enrichment has been shown to favour invasions by exotic species. In this study, it was established that the soil in areas invaded by the environmental weed bridal creeper, *Asparagus asparagoides* (L.) Druce, in south west Australia have higher levels of available nutrients than nearby weed free areas, regardless of the proximity to agriculture or other disturbances. These study areas historically had naturally very low levels of nutrients such as phosphorus, and the native flora is locally adapted to these low nutrient levels. Glasshouse experiments were used to determine the influence of these increased soil nutrients on both exotic and native plants that co-occur with bridal creeper in south west Australia, in order to assess the impact of changes in soil conditions. The growth rate of bridal creeper, two native shrubs (*Thomasia angustifolia* Steud. and *Billardiera heterophylla* (Labill.) L.Cayzer & Crisp) and an exotic grass (*Ehrharta longiflora* Sm.) were determined in three types of soil; collected from within a stand of bridal creeper, collected from a nearby native reference area, and a potting mix with high levels of phosphorus and potassium.

There was no difference between the relative growth rate (RGR) of bridal creeper when grown in nutrient poor reference soil or bridal creeper soil, indicating that bridal creeper can grow and survive in a nutrient poor environment. The RGR of bridal creeper was

significantly higher in the soil with the highest nutrients, the potting mix, compared to the RGR of bridal creeper when grown in nutrient poor reference soil or bridal creeper soil, suggesting that bridal creeper responds to a greater extent to increases in phosphorus and potassium. *Thomasia angustifolia* showed no significant change in growth rate across the three soil types. *Billardiera heterophylla*, a native species but an environmental weed in eastern Australia and the exotic *E. longiflora* showed increased growth rates when grown in bridal creeper soil and potting mix when compared to reference soil. This implies that although bridal creeper has been targeted for biological control, without additional restoration, controlling this exotic species may leave these areas vulnerable to increases in abundance of other plants, including exotics, which respond positively to higher nutrient conditions such as *B. heterophylla* and *E. longiflora*.

Introduction

Many Australian plants have adapted to soils low in nutrients, especially phosphate (Adam et al., 1989; Beadle, 1953; Beadle, 1966). Because of this low soil fertility, many Australian plant communities are thought to be protected against invasion from plants with higher nutrient requirements (Beadle, 1953; Beadle, 1966). Similarly, Lake and Leishman (2004) suggested that nutrient enrichment of low fertility soils within Australia was a prerequisite for exotic species invasion. Increases in nutrient availability, phosphorus in particular, has been strongly associated with the decline of native species and the presence of exotic species across a variety of plant communities within Australia (Adam et al., 1989; Allcock, 2002; Clements, 1983; Fogarty and Facelli, 1999; Hester and Hobbs, 1992; King and Buckney, 2002; Lake and Leishman, 2004; Leishman et al., 2004; Leishman and Thomson, 2005; Milberg et al., 1999; Morgan, 1998; Prober et al., 2002; Thomson and Leishman, 2004; Thomson and Leishman, 2005). However, the widespread form of *Asparagus asparagoides* (L.) Druce (Asparagaceae) (bridal creeper) has become a serious environmental weed in southern Australia (Morin et al., 2006a) as it is able to invade undisturbed native ecosystems (Hobbs, 1991; Raymond, 1995; Siderov and Ainsworth, 2004) and therefore may not require nutrient enrichment of the habitat as a precursor to invasion.

My first objective of this study was to investigate the soil nutrient conditions in the field where bridal creeper had invaded and compare them to nearby, reference areas. Soil nutrient data collected from the field were also compared to data on plant assemblages to investigate the degree to which soil nutrients were associated with the plant community at these sites.

Being a climber, the smothering habit of bridal creeper has been shown to increase its competitive ability, growth rate and fruiting potential when provided with native species as supports (Stansbury, 1999; Stansbury et al. 2007). Additionally, bridal creeper invasion in south west Australia has been shown to decrease native plant species (Chapter 3 - Turner et al., 2008c). Although competition can explain some portion of bridal creeper's success, the relative importance of competition would be expected to change as nutrient levels vary (Daehler, 2003; Grime, 1979). Therefore, my second objective was to test the effect of competition under various nutrient regimes on the growth of bridal creeper. The growth of this environmental weed was evaluated against the influence of both nutrient levels and the interaction with other plant species.

My third objective was to assess the impact of the soil that bridal creeper grows in on other plants. I hypothesised that if the soil nutrient levels in bridal creeper infested areas are greater than that of the reference areas, and this affects the growth of native and other plants in the absence of bridal creeper, then the soil itself may pose a barrier to recovery of native plant communities following the removal of bridal creeper from an area. Several biological control agents have been released against bridal creeper in Australia and already the bridal creeper populations are in decline (Morin et al., 2006b; Chapter 8 - Turner et al., 2008b). This study will therefore provide information necessary for the restoration of these areas and for protection from further weed encroachment.

Methods

COMPARISON OF INVADED AND REFERENCE SOILS

Soil nutrient status from within areas where bridal creeper was abundant and in comparable reference areas where the weed was at low abundance was determined across four sites in south Western Australia. Although the exact history of each site was

not known, there was no evidence of differences in land-use in the past between the bridal creeper area and reference area at each site (see Chapter 3 - Turner et al., 2008c for further description of areas and sites). Bridal creeper cover in October 2004, across these study sites, ranged from 40.3 to 61.7% in the bridal creeper areas and 0.2 to 5.1% in the reference areas (Chapter 3 - Turner et al., 2008c). No study sites were located close to urban development as those areas have been shown to have elevated soil nutrients, such as phosphorus (Clements, 1983; King and Buckney, 2002; Leishman et al., 2004). However, one site at Glenlynn Conservation Reserve (GC) was located next to farming land. The three other sites were all located in or adjacent to Fitzgerald River National Park (FRNP) on the southern coast of Western Australia. FRNP has been a reserve since 1954 (Aplin and Newbey, 1990). The Quell Creek site (QC) was in an isolated area within FRNP. The Quaalup Homestead site (QH) was adjacent to the park and managed as a wilderness retreat and the third site was next to the Gairdner River (GR) at the edge of FRNP.

SOIL SAMPLING

Between October 2004 and January 2005, 30 soil cores (5 cm deep and 5 cm in diameter) were collected haphazardly (but at least 1 m apart) within each invaded and reference area at each of the four sites. Bridal creeper produces a mat of rhizomes, tubers and conventional roots just below the soil surface (Chapter 6 - Turner et al., 2006). Therefore, in each bridal creeper area, soil cores were taken below the major part of tuber mats, 5 cm below the soil surface. For consistency, soil cores were taken 5 cm below the surface in the reference areas as well. Although sites were sampled on different days, samples were collected from the paired reference and bridal creeper area within the same site on the same day. The soil was placed in coolers during transport back to the laboratory then stored at 4^{o}C in the dark. In the laboratory, samples were passed through a 2 mm sieve. Five cores from each area within each site were bulked to form one sample, mixed thoroughly and any large organic matter, such as tubers and other roots, was removed. The resulting 12 samples per site (six from each area) were analysed by CSBP Laboratories (W.A.) for nitrate, ammonium, extractable phosphorus (P), potassium (K), organic carbon, reactive iron (Fe) and pH.

The ammonium and nitrate were measured simultaneously using a Lachat Flow Injection Analyser. Soils were tumbled with 1M KCl solution for 1 h at 25^{o}C using a

soil to solution ratio of 1:5. Extractable P and K were determined through bicarbonate extractions using a modified Colwell (1963) method (Rayment and Higginson, 1992 p. 64). Organic carbon was determined as described by Walkley and Black (1934). Reactive Fe was extracted with oxalic acid/ammonium oxalate. This method does not measure the amount of Fe available to the plant, but measures the amount of Fe that will react with phosphate in the soil (Foulds, 1993). Soil pH was determined by using 1:5 soil to water extract (Rayment and Higginson, 1992 p. 15).

There has been a diverse range of soil tests developed to investigate inorganic P and its availability in soil because the tests need to respond to the soil characteristics in a similar manner to plants (Kuo, 1996). Different tests of inorganic P are needed as its availability in soil is different between plant species. The Colwell method described above was used in this study as this is a common approach used in Australia (for example see McArthur, 1991) and this would allow for comparison with other studies. However, this approach was developed for wheat (Colwell, 1963), and therefore, a second collection of soil was taken from both areas within the four study sites in September 2005 to determine available inorganic P using a second method, Bray and Kurtz No. 2 acid fluoride extraction (Kou 1996). Surface soils, excluding litter, were sampled to a depth of 10 cm, by a core 5 cm in diameter. At each site, within each bridal creeper area, two sub-samples within 5 m of the dominant tree species where taken and bulked. This was then repeated in the reference area, again within 5 m of the same species of tree. This was repeated three times in each area, giving six samples per site. Available inorganic P was then determined for these samples through Bray and Kurtz No. 2 acid fluoride extraction (Kou 1996).

STATISTICAL ANALYSES

The soil nutrient concentrations for invaded and reference areas were compared using multivariate analysis techniques (Primer 6, Clarke and Warwick, 2001). For each area sampled across all sites, a rank-similarity matrix was constructed using the Euclidean distance measure of dissimilarity, on log transformed and normalised measurements of all soil nutrients (see Clarke, 1993; Clarke and Warwick, 2001). Following this, nonmetric multidimensional scaling (nMDS) was used to create an ordination plot. An analysis of similarity (ANOSIM) then determined differences between invaded and reference areas. The influence of site and area for each nutrient and soil measurement,

were also analysed using a two-way analysis of variances (ANOVAs) (GenStat, 2003). Transformations were applied when appropriate, via a log10 transformation, to meet the assumption of homogeneity of variances.

In addition to this, in October 2004 plant assemblages were sampled within each area at each site. The differences in percentage cover and number of plant species from each of these sites have been analysed and included in Turner et al. (Chapter 3 - 2008c). Soil nutrient data collected from this study were compared to plant assemblage data collected by Turner et al. (Chapter 3 - 2008c), to determine if soil nutrient data were correlated with plant assemblage patterns. A Bray-Curtis similarity index on log transformed percentage cover of each plant species was calculated to construct a rank-similarity matrix (see Clarke, 1993; Clarke and Warwick, 2001). The BEST procedure with the Spearman rank correlation method (see Clarke and Gorley, 2006 p. 121) was then followed to determine the degree to which the soil nutrient concentrations could explain the plant assemblage patterns recorded at these same sites. The BEST procedure gives a measure of the agreement between plant and soil resemblance matrices. The null hypothesis that there was no agreement in the multivariate patterns of soil nutrients and plant assemblages (see Clarke and Gorley, 2006 p. 121) was tested through the use of 999 permutations.

PLANT GROWTH ACROSS THREE SOIL NUTRIENT LEVELS

A glasshouse experiment was undertaken using three types of soil: i) soil collected from below a stand of bridal creeper that had elevated nutrient levels compared to; ii) soil collected from a nearby native reference area; and iii) a potting mix with the highest levels of phosphorus and potassium. In these soils, the growth rate of bridal creeper was determined. In addition, the growth rates of two native species (*Thomasia angustifolia* Steud. Sterculiaceae and *Billardiera heterophylla* (Labill.) L.Cayzer & Crisp - formerly *Sollya heterophylla* Lindl. (Cayzer et al., 2004) and referred to as *B. fusiformis* by Williams et al., 2006 - Pittosporaceae) and an exotic species (*Ehrharta longiflora* Sm. Poaceae) were determined with or without the presence of bridal creeper.

The response to changes in soil nutrients was measured for bridal creeper and these three other species which co-occur with bridal creeper in Western Australia. In a plant survey described in Chapter 3, *Thomasia angustifolia* was identified as the most

abundant native shrub at the Quell Creek site. Two other species were identified from the seed bank trial in Chapter 3 as being abundant and would readily germinate in bridal creeper areas: annual veldt grass (*Ehrharta longiflora*), and bluebell creeper (*Billardiera heterophylla*). Annual veldt grass is native to South Africa, but a weed across south Western Australia (Wheeler et al., 2002). Bluebell creeper is native to Western Australia but it has been demonstrated that it can be very competitive and is considered an environmental weed in south eastern Australia (Traeger et al., 2004; Williams et al., 2006).

Fruits of bridal creeper were collected on 13 October 2005 from Quell Creek and stored in a paper bag in the laboratory before being planted out into seedling trays in a glasshouse on 23 January 2006. Seeds of veldt grass were collected along the roadside near the western entrance of FRNP on 14 October 2005, stored also in the laboratory before being planted into seedling trays on 7 February 2006. Seeds of the *Thomasia* species were collected from Quell Creek on 1 December 2005, stored in the laboratory before being placed in boiling water on 23 January 2006 and left to cool overnight (method to germinate *Thomasia* advised by C. Wilkins, UWA, personal communication). The next day, seeds were placed on moistened filter paper in Petri dishes and placed in a growth chamber (15^{o}C, 12 hour light/dark cycle). Germinating seeds were then placed in seedling trays in the glasshouse on 27 February 2006. Bluebell creeper fruits were collected in September 2004 from Meelup Regional Park (33.563S, 115.071E). Seeds were removed from the fruits and stored in the laboratory until 30 December 2005. Seeds were germinated using a method developed by Williams et al. (unpublished data). On 7 February 2006, germinated bluebell creeper seeds were placed in seedlings trays in the glasshouse.

On 13 October 2005, soil was collected from the Quell Creek site, both in the bridal creeper area and reference area. At the site, ten soil samples (50 cm x 50 cm) were collected haphazardly from the invaded and reference areas to a depth of 10 cm. All ten samples from each area were combined and sieved (1 cm mesh) to remove stones and any large organic matter. Soil was then stored in a cool room (4^{o}C) in the dark before being placed into pots in a glasshouse on 20 January 2006. Soil was placed into pots 11 cm tall, 10 cm in diameter at the top and 8.5 cm in diameter at the base. Pots were watered and any plants that emerged were removed. Additional pots were also prepared

with potting mix high in phosphorus and potassium. Three sub-samples of the soil from each treatment were analysed for nutrients using the methods described above. The reference soil was lowest in nutrients, with invaded soil having elevated levels compared to the reference soil. The potting mix had high levels of P and K but was low in nitrogen (Table 4.1).

Soil was washed from the roots of the seedlings and seedlings transplanted into the pots described above to commence the experiment on 21 March 2006. In each soil type, there were seven treatments: four treatments consisted of each species grown individually. The other three treatments comprised a bridal creeper seedling grown with one of the other three species described above. Eight replicates per treatment were prepared, giving a total of 168 pots. An additional eight plants of each species were washed of soil and dried at 70^{o}C for four days to determine initial dry weights. Any seedlings that did not survive being transplanted within the first two weeks were replaced.

The relative growth rate (RGR) of each species was used (Hoffmann and Poorter, 2002) as this has been a common measure when comparing invasive and native plants (Daehler, 2003). RGR is the increase in plant material per unit of material per unit of time and it allows comparisons because it is independent of the scale or size of the plant (Hunt, 1978). RGRs were calculated by pairing plants from the first harvest period to the second harvest period based on weight (Evans, 1972; Hunt et al., 2002). For each species, the largest plant at the initial harvest was paired with the largest plant at the end of the experiment. RGR was calculated for each pair with the estimator:

$$\text{RGR} = (\ln(W_2) - \ln(W_1))/t_2 - t_1$$

where W_1 is dry weight of a plant at time 1 and W_2 is the dry weight of another plant at time 2 and t is time (day). RGR was then calculated for each pair, and the values averaged over all pairs.

The experiment ran for 94 days during which the temperature in the glasshouse ranged from 5 to 25^{o}C. At completion, the number of tubers per bridal creeper plant were counted and all plants were dried at 70^{o}C for six days, before total dry weights were

determined. Root to shoot ratios were determined by weighing separately the total belowground growth and the total aboveground growth. After dry weights were determined the total aboveground foliage from plants grown individually were collected. The foliage for each species was grouped then separated into two sub-samples per species and analysed by CSBP Laboratories to determine P concentrations (McQuaker et al., 1979).

STATISTICAL ANALYSES

A two-way ANOVA compared the RGR of species when grown individually across three soil types (four species by three soil types), however due to a significant interaction between species and soil type, additional analysis was required using a series of one-way ANOVAs (an approach discussed by Quinn and Keough, 2002). The RGR of each species between soil types was analysed with four separate one-way ANOVAs (one for each species: bridal creeper, *Thomasia*, bluebell creeper and veldt grass). The differences in the RGR between species within each soil type was also analysed with another three one-way ANOVAs. Due to these multiple comparisons, an adjustment to the significance level was made under the Bonferroni Method, $\alpha = 0.004$ (12 possible comparisons therefore 0.05/12). With each one-way ANOVA, a pair wise comparison was conducted using Tukey's test (GenStat, 2003).

Phosphorus (P) concentrations in the foliage of plants grown individually (four species) across the three soil types were compared by two-way ANOVA. To determine the ability of these species to access P when growing in a nutrient poor environment, a one-way ANOVA tested for differences in P concentrations across species grown solely in reference soil. With each ANOVA, pair wise comparisons were conducted using Tukey's test (GenStat, 2003). The soil from the reference area was specifically singled out as my study areas had historically naturally very low levels of P, with a native flora locally adapted to these low P levels, but not normally the exotic species (see Chapter 5 for further details).

The RGR, the number of tubers and the root to shoot ratio of bridal creeper were also analysed using two-way ANOVAs (GenStat, 2003) to compare the influence of soil type (three soil types) and the presence of a competitor (bridal creeper grown individually, or bridal creeper grown with either *Thomasia*, bluebell creeper or veldt

grass). The two-way ANOVA for root to shoot ratios of bridal creeper revealed a significant interaction between the factors; soil type and the presence of a competitor. Therefore a separate sub-analysis of the effect of soil type on the root to shoot ratio of bridal creeper within each group (bridal creeper grown alone, bridal creeper grown with either *Thomasia*, bluebell creeper or veldt grass) was undertaken using four separate one-way ANOVAs. Due to these multiple comparisons, an adjustment to the significance level was made under the Bonferroni Method, $\alpha = 0.0125$ (4 comparisons therefore 0.05/4).

The RGR and root to shoot ratios of each of the three other species were analysed separately, with the influence of bridal creeper (present or absent) and soil type of each species analysed using two-way ANOVAs. For each of the above analyses, transformations, via a log10 or square root, were applied when appropriate to meet the assumption of homogeneity of variances. If significant differences were found in any of the above analyses, it was followed by a pair wise Tukey comparison test (GenStat, 2003).

Results

COMPARISON OF INVADED AND REFERENCE SOILS

Areas invaded by bridal creeper had very different soil nutrient levels compared to native reference areas where bridal creeper was absent or in low numbers (Figure 4.1). Multivariate analysis indicated there was a significant difference between invaded areas and reference areas, when comparing all eight soil variables simultaneously ($R=0.302$; $p=0.029$).

Between areas, pH was not significantly different (Table 4.2). There were significant interactions between site and area for all other soil variables except P (Bray #2 method) (Table 4.2). This was due to the small differences in nutrient levels between areas at the Gairdner River site (Figure 4.1). However, both P measurements (Bray # 2 and Colwell) and Fe concentrations were consistently higher in bridal creeper areas across the four sites. Across the four sites, P averaged 10.7 ± 2.1 (mean $\pm$ s.e.) mg/Kg (Colwell) in bridal creeper areas and 6.9 ± 1.4 in reference areas. The Bray #2 extractions showed higher P levels at 9.3 ± 3.1 mg/Kg in invaded areas and 2.4 ± 0.7 in reference areas.

Iron (Fe) levels were lower in reference areas, being only 36% of that found in invaded areas (998 $\pm$ 470 mg/Kg in reference areas and 2775 $\pm$ 1570 in bridal creeper areas).

Potassium (K) was 34% higher in invaded areas (293 $\pm$ 45 mg/Kg in bridal creeper invaded areas and 219 $\pm$ 89 in reference areas). Nitrogen levels were also higher in bridal creeper invaded areas, being 3.0 $\pm$ 0.8 and 5.8 $\pm$ 1.8 mg/Kg of nitrate and ammonium compared to levels in reference areas of 1.7 $\pm$ 0.3 and 2.5 $\pm$ 0.6 respectively, with organic carbon 38% lower in reference areas (4.5% $\pm$ 0.6 in invaded areas and 2.8% $\pm$ 0.5 in reference areas).

A correlation between soil nutrients and plant assemblages was evident, but this was not significant at the 0.05 level (rank correlation p =0.61, p=0.096). Nevertheless, the BEST procedure revealed that Fe, K and P (Colwell method) were the best combination of variables describing the plant assemblages.

PLANT GROWTH ACROSS THREE SOIL NUTRIENT LEVELS

When grown individually, soil type affected RGR of each species differently (F=4.82; d.f. 6,84; p<0.001, Figure 4.2). Because of the significant interaction, the RGR of each species in the different soils was analysed separately. When grown individually, veldt grass (F=151.37; d.f. 2,21; p<0.001) and bluebell creeper (F=63.76; d.f. 6,84; p<0.001) had significant increases in RGRs, with plants in reference soil having the lowest, the plants in bridal creeper soil having intermediate and plants in the potting mix having the highest RGRs (Figure 4.2). There was no significant difference in RGRs of *Thomasia* when grown individually across the three soil types (F=4.09; d.f. 2,21; p<0.032, Figure 4.2). There was no significant difference in bridal creeper's RGRs when grown in reference or bridal creeper soil, however it was higher when grown in potting mix (after a square root transformation F=8.13; d.f. 2,21; p=0.002, Figure 4.2).

When growing in bridal creeper soil or reference soil there was no significant difference in RGRs between individually grown bridal creeper and blue-bell creeper plants, however these two species had significantly lower RGRs than individually grown *Thomasia* and veldt grass (bridal creeper soil F=26.67; d.f. 3,28; p<0.001, and reference soil F=51.34; d.f. 3,28; p<0.001). In potting mix, only veldt grass had a significantly higher RGR (F=11.63; d.f. 3,28; p<0.001).

The increase in concentration of P across the three soil types is reflected in the concentration of P in the foliage for all four species (after a log10 transformation $F=633.71$; d.f. 2,12; $p<0.001$, Table 4.3). Across all soils, concentration of P in foliage of veldt grass was significantly lower than the other three species, while *Thomasia* had the highest concentration (log10 transformation $F=85.53$; d.f. 3,12; $p<0.001$). There was no difference in P foliage concentrations between bridal creeper and bluebell creeper. There were significant differences in P foliage concentrations between species when grown in the nutrient poor, reference soil ($F=57.98$; d.f. 3,4; $p<0.001$, Table 4.3). When grown in reference soil, bridal creeper and *Thomasia* had significantly higher foliage P concentrations than bluebell creeper. Veldt grass had the lowest P phosphorus concentrations of all four species.

Even when bridal creeper was grown in the presence of other species, the RGR of bridal creeper was still higher in potting mix than in the other two soil types ($F=27.28$; d.f. 2,84; $p<0.001$, Figure 4.3a). The RGR of bridal creeper was affected by the presence of other species ($F=5.82$; d.f. 3,84; $p=0.001$, Figure 4.3b). The average RGR of bridal creeper when grown with veldt grass was lower than the average RGR of bridal creeper when grown with either bluebell creeper or *Thomasia.* For the RGR of bridal creeper, the outcome of competition did not depend on soil type ($F=1.13$; d.f. 6,84; $p=0.350$).

A two-way ANOVA on the root to shoot ratio of bridal creeper revealed a significant interaction between soil type and the specific competitor ($F=4.93$; d.f. 6,84; $p<0.001$, Figure 4.3c). There was no difference in the root to shoot ratio of bridal creeper when grown alone ($F=2.74$; d.f. 2,20; $p=0.089$) or with *Thomasia* ($F=3.79$; d.f. 2,20; $p=0.040$) across the three soil types, however the root to shoot ratio was significantly higher in reference and bridal creeper soil compared to potting mix when bridal creeper was grown with either bluebell creeper (after a log10 transformation $F=9.42$; d.f. 2,21; $p=0.001$) or veldt grass ($F=10.45$; d.f. 2,21; $p<0.001$).

A two-way ANOVA on the number of tubers of bridal creeper revealed a significant interaction between soil type and the specific competitor ($F=3.32$; d.f. 6,84; $p=0.006$). When grown in reference soil, there was no difference in the number of tubers bridal creeper produced with or without competition ($F=1.68$; d.f. 3,28; $p=0.193$). Individually

grown bridal creeper plants also produced the same number of tubers, regardless of the soil type it was grown in (after a log10 transformation $F=1.42$; d.f. 2,21; $p=0.264$).

There was no significant difference in RGR or root to shoot ratio of veldt grass ($F=0.47$; d.f. 1,42; $p=0.50$ and $F=0.75$; d.f. 1,42; $p=0.40$ respectively), bluebell creeper ($F=2.47$; d.f. 1,42; $p=0.12$ and $F=0.74$; d.f. 1,42; $p=0.40$ respectively) or *Thomasia* ($F=2.91$; d.f. 1,42; $p=0.10$ and $F=0.67$; d.f. 1,42; $p=0.42$, after a log10 transformation, respectively) when grown individually or with bridal creeper. Again when grown individually or with bridal creeper, the RGR of veldt grass increased significantly with increases in soil fertility ($F=183.91$; d.f. 2,42; $p<0.001$) and the root to shoot ratio was significantly higher when grown in the reference soil but was not different between the bridal creeper soil and the potting mix ($F=9.78$; d.f. 2,42; $p<0.001$). The RGR of bluebell creeper was significantly lower when grown in reference soil, yet there was no difference when grown in either bridal creeper soil or potting mix ($F=21.61$; d.f. 2,42; $p<0.001$). The root to shoot ratio of bluebell creeper was higher in the potting mix, but there was no difference between reference and bridal creeper soil ($F=6.38$; d.f. 2,42; $p=0.004$). The RGR of *Thomasia* was significantly higher in the bridal creeper soil and not different between reference soil or potting mix ($F=6.39$; d.f. 2,42; $p=0.004$), but there was no difference in the root to shoot ratio across the three soil types (after a log10 transformation $F=0.33$; d.f. 2,42; $p=0.72$).

Discussion

COMPARISON OF INVADED AND REFERENCE SOILS

Bridal creeper invaded areas in this study are associated with modified soil characteristics. Areas invaded by bridal creeper had higher levels of nutrients, particularly phosphorus and iron, when compared to nearby weed free areas. There is some evidence to suggest that these two nutrients, in addition to potassium, are correlated with the plant assemblages at each site. Higher nutrient availability following weed invasions has been reported around the world. For example in South Australia, higher nitrogen and phosphorus levels were found in areas invaded by the leguminous shrub *Cytisus scoparius* (L.) Link. (Fogarty and Facelli, 1999). In the US, Heneghan et al. (2006) found that soils in areas invaded by *Rhamnus cathartica* L. had higher nitrogen, carbon and pH when compared to areas where this weed was absent. Boswell

and Espie (1998) reported increased phosphorus concentrations below *Hieracium pilosella* L. when compared to nearby grasslands, free of this weed, in New Zealand. In heathlands in the U.K., Mitchell et al. (1997) established that invasion by *Betula* spp. increased pH, calcium and phosphorus and suggested that due to this, restoration of these invaded sites may be more difficult than other parts of the heathland that had been invaded by other weeds.

It is unknown if bridal creeper originally invaded the nutrient rich areas sampled or if it has modified its environment. Many weeds invade areas following nutrient enrichment (Morgan, 1998). However, changes to ecosystem processes caused by environmental weeds may be relatively common (Gordon, 1998). For example, changes in plant community composition as a result of a weed invasion can also alter soil properties, especially when the weed has a different growth form or litter chemistry (Ehrenfeld, 2001). Furthermore invasive plants frequently change the soil nutrient cycling process through increases in net primary production, increases in nutrient availability and production of litter with faster decomposition rates when compared to co-occurring native plants (Ehrenfeld, 2003). Given the comparison of soil nutrients in bridal creeper invaded areas to nearby reference areas, it seems likely that bridal creeper is modifying its environment. This is supported by a removal experiment (Chapter 7) where soil nutrient levels were higher where bridal creeper was not controlled compared to areas where bridal creeper had been controlled ten years earlier (Table 7.2). The modification of soil nutrient levels may be through changes in the type and timing of litterfall, nutrient interception by bridal creeper's tuberous root mats or root exudates making more P available. These are explored and discussed further in Chapter 5.

PLANT GROWTH ACROSS THREE SOIL NUTRIENT LEVELS

Comparing exotic and native plant interactions, Daehler (2003) reviewed 79 studies and found no statistical difference between growth rates of native versus exotic plants. In addition, from 55 studies that had a variety of growing conditions, 94% had native performance equal to or greater than the exotic species (Daehler, 2003). In my study, bridal creeper seedlings did not have a superior RGR when compared to the two native species. Also, bridal creeper's growth rate did not significantly change when in competition except in the presence of another weed, veldt grass. However, when faced with competition from the invasive veldt grass or bluebell creeper, bridal creeper's root

to shoot ratio was significantly higher in the nutrient poorer soils, ensuring that root biomass was maintained. This is important given that bridal creeper is a geophyte and relies on its belowground biomass for growth in the following year (Morin et al., 2006a).

When grown individually, the native *Thomasia* showed no significant change in growth rate across the three soil types. Very high levels of phosphorus were found in *Thomasia* foliage when grown in potting mix (Table 4.3). Although foliage concentrations for *Thomasia* could not be located in other studies outside of this thesis, Foulds (1993) measured the foliage concentrations of four species in the same family, Sterculiaceae, and reported a phosphorus range of 0.6 to 1.5 mg/g. In Chapter 5, *Thomasia* phosphorus foliage concentrations from field collections range from 0.69 to 0.74 mg/g (Table 5.2). In this study, when grown in potting mix, the concentration was 9.04 mg/g and it was also relatively high when grown in bridal creeper soil (2.29 mg/g - Table 4.3).

When grown individually the other native plant, bluebell creeper, showed an increased growth rate in bridal creeper soil compared to reference soil. Bluebell creeper's growth rate was even higher in the potting mix. Thus the different responses to available phosphorus may relate to the weediness of certain native species, as bluebell creeper is now becoming an environmental weed in eastern Australia (Traeger et al., 2004). Alternatively, higher nutrients may affect plants in other ways. For example, fertiliser applications to native heath have been shown to increase the growth of native plants, however this was at the expense of longevity (Specht, 1963; Specht et al., 1977).

The two native species used in my experiment, however, should be able to respond positively to an increase in nutrients, especially in the short term as both these species appear to be fire adapted. In south west Australia the main germination event for bluebell creeper occurs after a fire (A. Williams personal communication), and given that *Thomasia* in my study germinated after heat shock, this could indicate that this species may be fire adapted. Nutrient availability in the soil is increased for a short time following fire (Handreck, 1997; Hobbs and Huenneke, 1992). Therefore, the two native species in this experiment should be able to persist in elevated soil nutrients at least at the seedling stage and have a rapid nutrient uptake directly following a fire before nutrients are leached away. Later successional plant species may not be able to persist

within higher nutrients or their competitive abilities may be reduced compared to other species that respond to higher nutrients. Bridal creeper invasion has been associated with decreases in native plant abundance and composition (Chapter 3 - Turner et al., 2008c; Chapter 2 - Turner and Virtue, 2006), however these changes could be as a result of changes in soil nutrient levels.

The flora of south west Australia is species rich and one of the world's 25 biodiversity hotspots (Myers et al., 2000), despite growing in low fertility soils. For example, 84% of 134 sites sampled by McArthur (1991) in south west Australia have phosphorus levels of 5 mg/Kg or less (Colwell method). The similar RGR of bridal creeper in reference soil and bridal creeper soil indicates bridal creeper has the potential to persist in the low fertility native ecosystems examined. This is supported in Chapter 7, where bridal creeper was able to achieve a high abundance even at phosphorus levels of 3.6 mg/Kg (Table 7.2).

As mentioned above, it is unknown if bridal creeper originally invaded the nutrient rich areas sampled or if it has modified its environment, however it could be the case that bridal creeper can invade both phosphorus rich and phosphorus poor environments. Bridal creeper plants that survive in the poorer soils over time could slowly change the soil conditions (see Chapter 5). Although veldt grass had a higher RGR in the higher nutrient soils, this does not necessarily translate that the high soil nutrients below bridal creeper would facilitate the invasion or expansion of other exotics such as veldt grass. Bridal creeper is able to form monocultures and in Chapter 3 at these study sites, there were on average 3.6 $\pm$ 0.8 other exotic species in the bridal creeper plots and 4.0 $\pm$ 0.6 in the reference plots (Figure 3.2b). The cover of all exotic species excluding bridal creeper, was also not statistically different, with exotic cover in reference areas being 10.1% $\pm$ 3.4, compared to 4.4% $\pm$ 1.6 in the bridal creeper areas (Figure 3.2c). However, higher nutrients in the soil could facilitate the expansion of other exotics such as veldt grass, if bridal creeper was controlled.

IMPLICATIONS FOR RESTORING BRIDAL CREEPER INVADED AREAS

Changes to ecosystem processes can potentially influence many species within the invaded community (Vranjic et al., 2000b) and have important implications for the management of invasions and restoration of native communities (Ehrenfeld and Scott,

2001; Thorpe et al., 2006). Many studies from outside Australia have investigated the effects of invasive plants on nutrient cycling, but primarily concentrating on the effects of increased nitrogen (eg Corbin and D'Antonio, 2004; Evans et al., 2001; Haubensak and Parker, 2004; Hawkes et al., 2005; Mack et al., 2001). Phosphorus may be more important in many regions of Australia given that in south east Australia native species richness has been found to be inversely related to total phosphate (Adam et al., 1989), while non-native species richness and cover was reported to be positively correlated to soil phosphorus (Morgan, 1998). However, long-term experiments of the impacts of the changes in soil status on the native plant communities which have been invaded by bridal creeper are required.

Given that low soil nutrient levels, mainly phosphorus, have shaped the composition and structure of Australia's vegetation (Adam et al., 1989; Specht, 1963; Specht et al., 1977), elevated soil nutrients associated with bridal creeper could form a barrier to restoration. Biological control is currently being used as a way to control bridal creeper across Australia (Morin et al., 2006b). Increases in nutrient levels reported here could increase the chances of further weed invasion in south west Australia following the control of bridal creeper. This is supported by my glasshouse study which established that veldt grass' RGR was higher when grown in soil collected from below bridal creeper compared to reference soil. Davis et al. (2000) suggested that a community becomes more susceptible to invasion as resource availability increases with either an increase in the supply of resources or a reduction in the uptake of resources by resident vegetation. Even if bridal creeper is not responsible for the increased nutrient levels, restoration activities will still need to take into account these levels.

In Australia, nutrient enrichment has been shown to favour exotic species and therefore without additional restoration work, controlling bridal creeper may leave invaded areas vulnerable to further invasions and/or expansion by other exotic species. At these study sites, Turner et al. (Chapter 3 - 2008c) suggested that the biological control of bridal creeper may result in bridal creeper being replaced by other exotic species. This was due to the large number of exotic seedlings compared to native seedlings that would readily germinate from seed bank. Therefore, with the pressure from a high number of exotic seedlings coupled with relatively high soil nutrients, this could become a barrier to the restoration of these invaded areas following the biological control of bridal

creeper. Additional restoration efforts will be needed to ensure the ultimate goal is reached of protecting native biodiversity.

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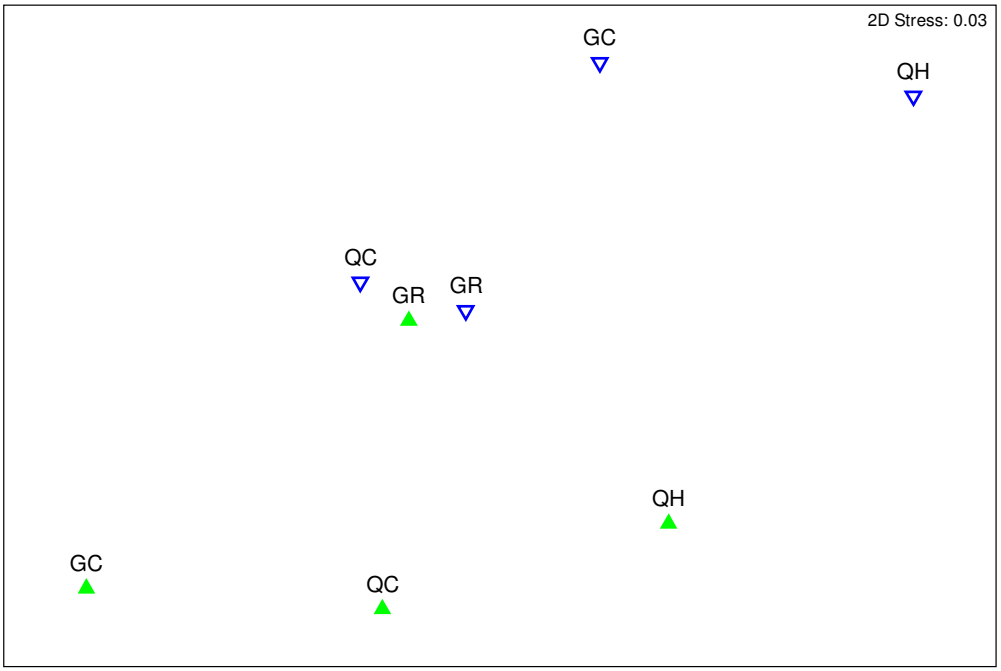

Figure 4.1. Ordination plot of eight soil variables (nitrate, ammonium, phosphorus (Colwell & Bray #2 method), potassium, pH, organic carbon and reactive iron) from soil samples collected from QC = Quell Creek, QH = Quaalup Homestead, GR = Gairdner River and GC = Glenlynn Conservation Reserve.

Open triangles represent reference areas, closed triangles represent bridal creeper areas. The relative distances between triangles represent the degree of dissimilarity of soil nutrients between areas and sites. (Multivariate analysis indicated there was a significant difference between bridal creeper areas and reference areas - ANOSIM R=0.302, p=0.029. MDS plot constructed from log transformed and normalised data and a Euclidean distance measure of dissimilarity, Stress = 0.03.)

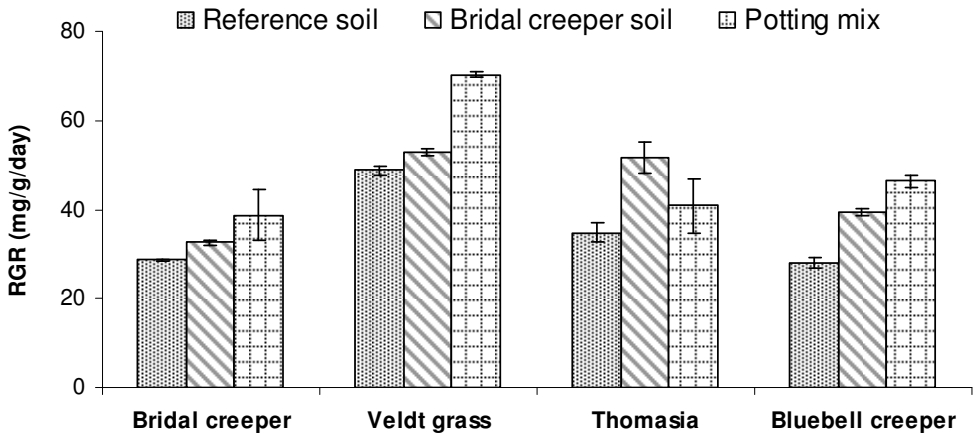

Figure 4.2. Relative growth rates (mean ± s.e.) of four species grown individually in three soil types.

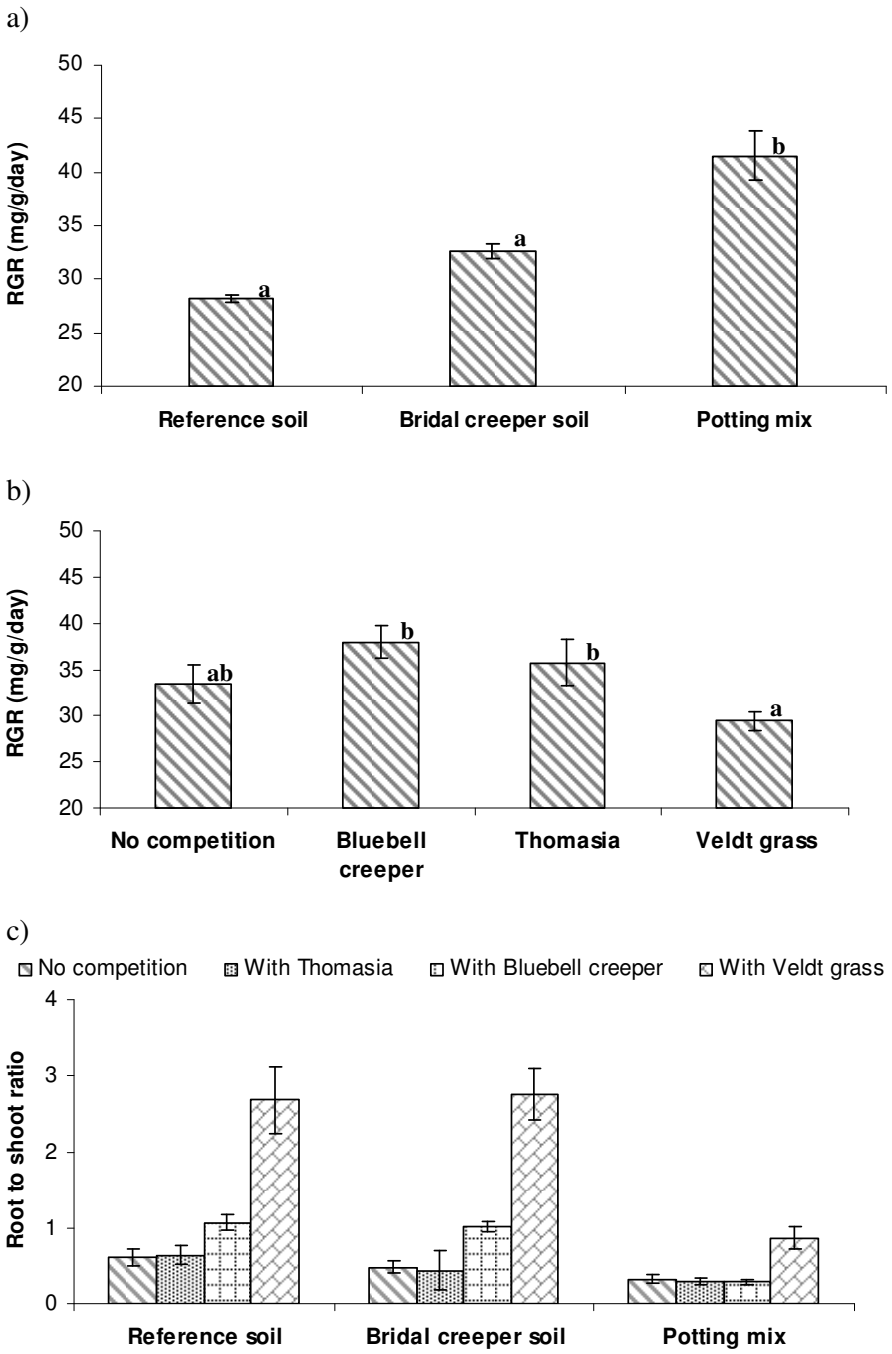

Figure 4.3. a) Mean relative growth rates (± s.e) of bridal creeper (with and without the presence of other species) when grown across three soil types. b) Mean relative growth rates of bridal creeper (pooled across all soil types) when grown individually or with the other three species. c) Root to shoot ratio (mean ± s.e.) of bridal creeper grown individually or in presence of other species across three soil types.

Letters above bars indicate RGRs that were not significantly different in *post hoc* Tukey tests

Table 4.1. Mean (± s.e.) nutrient concentration of soils used in the glasshouse experiment.

	Reference soil	**Bridal creeper soil**	**Potting mix**
pH	6.2 ± 0.0	6.7 ± 0.1	6.3 ± 0.1
P (Colwell) (mg/Kg)	3.7 ± 0.3	7.0 ± 1.2	116 ± 4
Nitrate (mg/Kg)	3.7 ± 0.3	12.3 ± 1.8	1.0 ± 0.0
Ammonium (mg/Kg)	1.0 ± 0.0	5.7 ± 2.3	1.0 ± 0.0
K (mg/Kg)	88 ± 5	200 ± 30	345 ± 18
Fe (mg/Kg)	503 ± 8	1362 ± 135	291 ± 9
Organic Carbon (%)	2.0 ± 0.1	5.8 ± 1.2	2.2 ± 0.2

Table 4.2. Nutrient element concentrations of soil collected from bridal creeper invaded areas (B) and reference areas (R) across four sites in south west Australia (mean ± s.e.). Two-way ANOVA p values are also presented for the differences between bridal creeper areas and reference areas as well as the interaction between site and area.

Site	**Glenlynn Conservation**		**Gairdner River**		**Quaalup Homestead**		**Quell Creek**		**Area[#]**	**Inter-action**
Area	**B**	**R**	**B**	**R**	**B**	**R**	**B**	**R**	**p**	**p**
Phosphorus (Colwell, mg/Kg)	7.5 ± 0.8	4.2 ± 0.4	8.8 ± 0.5	7.3 ± 0.4	9.7 ± 0.3	5.5 ± 0.6	16.8 ± 1.1	10.5 ± 0.6	<0.001	0.005
Phosphorus* (Bray #2, mg/Kg)	9.9 ± 2.1	4.1 ± 0.5	2.9 ± 0.4	1.2 ± 0.2	17.4 ± 3.2	2.9 ± 1.6	7.0 ± 0.6	1.4 ± 0.1	<0.001	n.s.
Nitrate* (mg/Kg)	5.5 ± 1.3	1.3 ± 0.3	2.3 ± 0.4	2.0 ± 0.0	2.0 ± 0.0	1.0 ± 0.0	2.2 ± 0.3	2.3 ± 1.0	<0.001	0.009
Ammonium* (mg/Kg)	11.0 ± 3.7	1.8 ± 0.4	3.3 ± 0.3	3.2 ± 0.3	3.0 ± 0.0	1.2 ± 0.2	5.7 ± 0.6	3.7 ± 0.6	<0.001	0.003
Potassium (mg/Kg)	273 ± 26	95 ± 18	404 ± 32	458 ± 16	185 ± 10	73 ± 7	311 ± 32	248 ± 32	<0.001	<0.001
Reactive Iron* (mg/Kg)	7357 ± 1099	2223 ± 613	1707 ± 477	437 ± 341	219 ± 6	111 ± 4	1817 ± 208	1222 ± 301	<0.001	0.044
Organic Carbon (%)	4.5 ± 0.3	2.5 ± 0.3	3.3 ± 0.2	3.3 ± 0.1	4.1 ± 0.2	1.6 ± 0.1	6.0 ± 0.1	3.9 ± 0.6	<0.001	<0.001
pH	6.7 ± 0.2	6.4 ± 0.2	6.4 ± 0.0	6.5 ± 0.0	5.9 ± 0.0	5.7 ± 0.0	6.6 ± 0.1	6.7 ± 0.1	n.s.	0.025

*Log 10 transformations applied.

[#]Significant values have been provided for the factor "area", even though significant interactions are evident for all but one phosphorus variable. The interactions were mainly caused by small differences in nutrient levels between areas at the Gairdner River (GR) site, however both phosphorus measurements (Bray # 2 and Colwell) and iron concentrations were consistently higher in bridal creeper areas (B) compared to reference areas (R) across the four sites.

Table 4.3. Phosphorus concentrations in dry weight, mg/g (mean ± s.e.) of aboveground growth of four species grown individually in three soil types.

	Reference soil	**Bridal creeper soil**	**Potting mix**
Bridal creeper	1.42 ± 0.02	1.92 ± 0.03	5.85 ± 0.33
Bluebell creeper	0.98 ± 0.10	1.65 ± 0.03	5.39 ± 0.10
Thomasia	1.71 ± 0.09	2.29 ± 0.16	9.04 ± 0.83
Veldt grass	0.53 ± 0.03	0.88 ± 0.08	3.50 ± 0.05

CHAPTER FIVE

EVIDENCE OF AN EXOTIC PLANT SPECIES DRIVING ECOLOGICAL CHANGE: *ASPARAGUS ASPARAGOIDES* INVASION INCREASES NUTRIENT CYCLING AND SOIL NUTRIENT AVAILABILITY

Key words: bridal creeper, decomposition, environmental weed, geophyte, litter, weed impacts

Abstract

In Australia many native plants have adapted to soils with low nutrients. Because of this low fertility, many plant communities are thought to be protected from invasion by exotic plants. However *Asparagus asparagoides* (L.) Druce (bridal creeper), a native to southern Africa invades undisturbed Australian plant communities adapted to low soil fertility. Being a geophyte, at the end of spring the aboveground growth of this weed ceases and its foliage senesces. *Asparagus asparagoides* foliage contains higher phosphorus and nitrogen concentrations compared to the native species in the invaded environment. The litterfall from the senescing plants retains a high nutrient content which is then rapidly leached as *A. asparagoides'* foliage quickly decomposes.

Asparagus asparagoides has the capacity to trap nutrients, firstly by the litterfall caught by bridal creeper shoots emerging from the soil, which were estimated at 75 to 115 shoots per m^2, and secondly through the interception of leached nutrients with its root architecture. *Asparagus asparagoides* has a dense tuberous root mat found only in the top 20 cm of the soil. Soils where *A. asparagoides* have invaded are now more fertile than adjacent *A. asparagoides* free areas. It is hypothesised that *A. asparagoides* has displaced many native woody shrubs and trees and as a consequence there has been a gradual shift in nutrient pools from aboveground plant biomass to the soil. Once the communities with the poorer soils have been invaded, *A. asparagoides* increases the soil fertility through increases in the rate of nutrient cycling. These changes to the soil fertility will leave a legacy that will have a dramatic effect on the restoration of areas

invaded by *A. asparagoides*, given that soil nutrient enrichment in Australia has already been shown to favour other exotic species.

Introduction

Exotic plant invasions can alter community composition, but there is also increasing evidence that invasive plants can alter ecosystem processes, including nutrient cycling (Vitousek, 1990). Richardson et al. (2000) reported that about 10% of all invasive exotic plants (the transformer species) can change the character and condition of native ecosystems. These environmental weeds can alter soil nutrient dynamics by differing to native species in biomass, productivity, tissue chemistry, plant phenology and plant morphology (Ehrenfeld, 2003). Environmental weeds frequently change the soil nutrient cycling process through increases in net primary production, increases in nutrient availability and production of litter with faster decomposition rates when compared to co-occurring native plants (Ehrenfeld, 2003). Changes to ecosystem processes can potentially influence many species within the invaded community (Vranjic et al., 2000b) and have important implications for the management of invasions and restoration of native communities (Corbin and D'Antonio, 2004; Ehrenfeld and Scott, 2001; Lindsay and French, 2005; Thorpe et al., 2006; Yelenik et al., 2004).

Examples of environmental weeds that change nutrient cycles include *Tradescantia fluminensis* Vell. in New Zealand, which has been shown to increase litter decomposition and to alter soil nutrient availability (Standish et al., 2004). In Hawaii, the litter of two exotic species is nutrient rich and decomposes at a faster rate compared to native litter. Soils below these exotic species have high concentrations of nitrogen (Matson, 1990). In Illinois, the rapid decomposition rate of the litter from the exotic species, *Rhamnus cathartica* L., has been implicated in causing soil enrichment (Heneghan et al., 2002). On the Balearic Islands in the Mediterranean Basin, Sala et al. (2007) established that the exotic geophyte, *Oxalis pes-caprae* L., was found in soil with high phosphorus availability compared to non-invaded soils and suggested that this geophyte also influenced nutrient cycling. In South Africa, *Acacia saligna* (Labill.) H.L. Wendl. and *Acacia cyclops* A. Cunn ex G. Don. (two Australian species) produce more litter with higher nitrogen levels than that of the native species (Witkowski, 1991), while in Australia, the leaves of *Chrysanthemoides monilifera* (L.) Norl. ssp. *rotundata*

(DC.) Norl. (a South African species) decompose faster than native species, which has been suggested to lead to changes in soil nutrient availability (Lindsay and French, 2004).

In Australia, many ecosystems are invaded by environmental weeds following nutrient enrichment caused by disturbances. However, the South African plant *Asparagus asparagoides* (L.) Druce (bridal creeper), can invade undisturbed native ecosystems (Hobbs, 1991; Raymond, 1995; Siderov and Ainsworth, 2004) and can persist in nutrient poor soil (see Chapters 4 and 7). However, unlike many native plants that normally grow in these nutrient poor environments (Adam et al., 1989), bridal creeper responds positively to increases in soil nutrients and bridal creeper invaded areas display increased levels of soil nutrients when compared to nearby native reference areas (Chapter 4). In addition, as soil nutrients were found to be higher in bridal creeper plots compared to plots where bridal creeper had been removed ten years previously (Chapter 7), it is hypothesised that bridal creeper can profoundly alter the soil nutrient characteristics following invasion.

Here I report on the proposed mechanisms by which bridal creeper could increase soil fertility. Bridal creeper is a geophyte with shoots climbing over native understorey trees and shrubs which it uses for support (Stansbury, 1999; Stansbury et al., 2007; Chapter 3 - Turner et al., 2008c). However, bridal creeper is deciduous and before the dry southern Australian summer commences, all aboveground growth senesces (Morin et al., 2006a) and leaves (cladodes) fall. Therefore, to determine if the growth habit of bridal creeper could lead to increases in soil nutrients, I investigated the differences in tissue chemistry, litter production and decomposition between bridal creeper and native species in south west Australia. In addition, litterfall, decomposition and foliage chemistry of native plants were also compared between invaded bridal creeper areas and nearby reference areas.

Methods

STUDY AREA

The majority of the study was undertaken across three sites within eucalypt woodlands across southern Western Australia (described previously, see Chapter 3 - Turner et al.,

2008c). One site was located in Glenlynn Conservation Reserve (GC). This reserve is surrounded by grazing land. The two other sites were located in and adjacent to a relatively remote national park, Fitzgerald River National Park (FRNP). The Quell Creek site (QC) was in an isolated area within FRNP. The third site was on the edge of FRNP, located next to the Gairdner River (GR) and is visited very infrequently by the public. An additional site was also used for part of the litterfall study being the Quaalup Homestead site (QH) which is a private wilderness retreat surrounded by FRNP (Anonymous, 1991).

Within each of these sites, areas invaded by bridal creeper have higher soil nutrients, mainly available phosphorus and reactive iron, when compared to nearby native reference areas that contained little or no bridal creeper (Chapter 4). Soil pH ranged from 5.9 to 6.6 in the bridal creeper invaded areas and from 5.7 to 6.7 in the reference areas. Bridal creeper cover in October 2004, across these study sites, ranged from 40.3 to 61.7% in the bridal creeper areas and 0.2 to 5.1% in the reference areas (Chapter 3 - Turner et al., 2008c).

FOLIAGE CHEMISTRY

Foliar nutrient levels of bridal creeper were firstly compared to the analysis of plants reported in Foulds (1993), who collected 368 plant species, across 696 samples, including 48 samples being from exotic species across southern Western Australia. In June 2005, when bridal creeper was actively growing, bridal creeper foliage was collected from three of the above sites (GR, QC and GC). At each site, six points within the bridal creeper stand were chosen haphazardly (but at least 2 m apart) and the terminal 10 cm of bridal creeper foliage was collected. Individual bridal creeper plants cannot be differentiated due to the entwining of the root mat. Two sub-samples from each site were bulked, so that three samples from each site were sent to CSBP Laboratories (W.A.) for chemical analysis. The concentrations of nitrogen (N) (Sweeney and Rexroad, 1987), chloride (Cl) (Zall et al., 1956), calcium (Ca), copper (Cu), phosphorus (P), potassium (K), magnesium (Mg), manganese (Mn), zinc (Zn) and iron (Fe) (McQuaker et al., 1979) were determined.

A Euclidean distance measure of dissimilarity, on log transformed and normalised measurements of foliage concentrations, was undertaken to construct a rank-similarity

matrix of bridal creeper compared to a suite of native plants analysed by Foulds (1993). From this an ordination plot (nMDS, Primer 6, Clarke and Warwick, 2001) was constructed to compare bridal creeper foliage with foliage concentrations of ten plant families reported in Foulds (1993) from south west Australia, except Fe which was not analysed by Foulds (1993).

Secondly, as the soil characteristics are different between bridal creeper areas and native reference areas (Chapter 4), native species were sampled from within both areas at the QC site. On 2/12/05, fresh plant material was collected from the dominant shrub species (within reference areas at QC), *Thomasia angustifolia* Steud. and the common tree species, *Eucalyptus occidentalis* Endl. Within each area, five individuals of each species were sampled by removing the leaves of a terminal 10 cm of the foliage. P and N concentrations were again determined using the above method. For each nutrient, the influence of species (*T. angustifolia* and *E. occidentalis*) and area (bridal creeper versus reference area) was analysed using a two-way analysis of variance (ANOVA) (GenStat, 2003).

Thirdly, as nutrients within foliage can be re-absorbed by a plant before abscission, senesced bridal creeper foliage was collected at GC on 30/11/05 and GR on 1/12/05 by catching falling cladodes after shaking bridal creeper at six points chosen haphazardly (but at least 2 m apart) at each site. Two sub-samples from each site were bulked, resulting in three samples from each site analysed to determine P and N concentrations using the above method. For each nutrient, the influence of site (GC and GR) and time of collection (green material collected June 2005 versus senesced material) was analysed using a two-way ANOVA (GenStat, 2003). No collection was made at QC at this time as bridal creeper had already dropped most of its foliage at this site.

ROOT CHEMISTRY

Nutrient concentrations in the bridal creeper root system (rhizome, tubers and roots) were measured when the plant was growing and when the plant had senesced. As with other geophytes, the storage organs (tubers) of bridal creeper reserve energy to support the production of foliage. It is bridal creeper's tuber reserves which enable it to survive over summer and then undergo rapid shoot development in the following autumn (Morin et al., 2006a).

In June 2005, when bridal creeper was actively growing, collections of root biomass were made at GC and GR and in June 2006, root biomass was collected at QC. At each site, six points were chosen haphazardly (but at least 2 m apart) within the bridal creeper areas and the root system dug up. Approximately 10 cm lengths of rhizome with tubers and roots attached were collected from each point. Soil was removed and two sub-samples from each site were bulked and the three samples from each site sent to CSBP Laboratories (W.A.) for chemical analysis. The concentrations of N and P were determined. This was repeated after bridal creeper had senesced. At GC on 30/11/05 and at GR and QC on 1/12/05, the root system was again collected and N and P concentrations determined using the above methods. For each nutrient, the influence of site (GC, GR and QC) and time of collection (when plant was actively growing in June versus collection made from senesced plants) was analysed using an ANOVA (GenStat, 2003). However, due to a significant interaction between sites and collection time for P concentrations, additional analysis involved using a series of one-way ANOVAs (see Quinn and Keough, 2002). The P concentration from each site was analysed separately with three one-way ANOVAs. Due to these multiple comparisons, an adjustment to the significance level was made under the Bonferroni Method, $\alpha = 0.017$ (three comparisons therefore 0.05/3) (see Quinn and Keough, 2002). Log10 transformations were applied where appropriate to meet the assumption of homogeneity of variances.

LITTERFALL

Given that bridal creeper senesces annually and the differences reported in plant species composition in invaded areas (Chapter 3 - Turner et al., 2008c), it could be expected that bridal creeper has changed the timing of the overall plant litterfall as well as the quality and quantity. Therefore, litterfall was captured using litter-traps and both dry weight and nutrient concentrations were measured in areas of bridal creeper and nearby native reference areas over a six month period. Litterfall was collected in circular funnels/traps (for example as used by Standish et al., 2004; and Witkowski, 1991). Funnels were 15.5 cm in diameter and 13 cm deep. To confirm the suitability of the traps, five painted eucalypt leaves were placed within ten random traps at the start of the experiment. These leaves remained in the traps over the collection period of three months, except for one trap which was knocked over by wildlife.

Each funnel contained mesh (1 x 1 mm) at the bottom. Fifteen funnels were placed haphazardly (but at least 2 m apart) in each bridal creeper area and native reference area across all four study sites, giving 30 traps per site and 120 traps in total. Funnels were staked and placed just above the forest floor. Funnels were kept just above the ground to keep the litter dry and to reduce decay. Traps were emptied approximately every three months. Traps were deployed before bridal creeper began to senesce in September 2005 and emptied after senescence in early December. Another collection was made approximately three months later in summer (that is December to February). At this time bridal creeper is not growing, but native species have their highest litterfall. Therefore, litterfall at the study sites was measured for spring and summer. Collections were made for a full year, however only the first two quarterly collections are reported due to the biological control agent, the bridal creeper rust, causing early defoliation of bridal creeper during the last two quarters (see Chapter 8).

Collected litter was oven dried for four days at 70^{o}C and dry weights determined. P and N concentrations of the bulked litter per area at each site were then determined using the above method. For biomass, the influence of time (first or second quarter) and area (bridal creeper versus reference area) was analysed using a two-way ANOVA (GenStat, 2003). A square root transformation was applied to meet the assumption of homogeneity of variances. For each nutrient, the influence of time and area was also analysed using a two-way ANOVA. As bridal creeper fully senesces in spring and does not grow in summer, one-way ANOVAs were also undertaken (bridal creeper versus reference area) for biomass, N and P for spring only.

LITTER DECOMPOSITION

Litter decomposition rates were measured between bridal creeper invaded areas and reference areas as well as between species, bridal creeper and native, by using litter bags (for example as used by Emery and Perry, 1996; Heneghan et al., 2002; and Standish et al., 2004). Decomposition was estimated from the biomass lost from litterbags containing either bridal creeper or one of two native eucalypt species common to the area. Native shrubs were not included given the lack of native shrubs at the sites (Chapter 3 - Turner et al., 2008c). As bridal creeper cladodes are very fragile and break down rapidly, fresh litter (freshly fallen leaves) was not available in sufficient quantity, therefore green material was used to measure decomposition.

Cladodes of bridal creeper and leaves of *Eucalyptus rudis* Endl. were collected approximately two months before commencement of the experiment and air dried within the laboratory. This eucalypt species is a common species found at two sites, GC and GR. After two months, the biomass was placed within mesh bags (10 cm x 20 cm, mesh size 1.5 mm), with 3.0 $\pm$ 0.005 g (mean $\pm$ s.e.) of air dried material per bag. This amount was chosen as it was sufficient to fill the litterbag. Fifty six bags for each species were prepared for two sites, GC and GR. In June 2005, at each site, 24 bags were placed within the litter on mineral soil. Twelve bags were placed within the bridal creeper areas at each site and 12 within the native reference areas. Three stakes, at least 5 m apart, within each area, had four litterbags of each species attached with string.

The biomass in the remaining eight bags for each species was dried at 70^{o}C to determine initial dry weights. The initial biomass per bag of bridal creeper was estimated at 2.78 $\pm$ 0.01 g (mean $\pm$ s.e.) and 2.86 $\pm$ 0.01 g for *E. rudis*. P and N concentrations of the initial litter were determined using the above method. Approximately every three months the sites were revisited and a bag of each species was collected from each stake. The biomass was removed from the bags, any soil removed and the biomass dried at 70^{o}C to determine dry weight. Material from each species collected from each area (three bags) was then bulked and P and N concentrations of the litter were again determined using the above method.

The litter decomposition measurement was repeated at a third site, QC except that the local eucalypt, *Eucalyptus occidentalis* was used and the material placed at the site in October 2005. The initial biomass per bag of bridal creeper was estimated at 2.74 $\pm$ 0.01 g and 2.78 $\pm$ 0.03 g for *E. occidentalis.*

The influence of time (four quarterly collections) and area (bridal creeper versus reference area) on biomass loss was analysed using two-way ANOVAs (GenStat, 2003) for each species. In addition, as the litterbags were placed out at QC at a different time, these bags were analysed separately. As there was no difference between areas, samples at each site were analysed together to determine which species decomposed faster. The influence of time (four quarterly collections) and species (bridal creeper versus native eucalypt) was analysed using a two-way ANOVA at each site. If significant differences

were found in any of the above analyses, it was followed by a pair wise Tukey comparison test (GenStat, 2003). At the end of the experiment (approximately 12 months), a two-way ANOVA was also undertaken to determine if the remaining percentage of biomass, and mass of N or P was different as well as if it differed between bridal creeper and the eucalypt species across the three sites.

LITTER STANDING CROP (BIOMASS ON FOREST FLOOR)

The litter standing crop was collected in October 2004, before bridal creeper had senesced at the sites GR and GC for a comparison of accumulated litter on the forest floor between invaded and uninvaded areas. A metal quadrat (18 cm x 18 cm) was pressed into the soil and all litter above the soil was collected. Ten haphazard collections (but at least 2 m apart) were made within each area at each site. Soil was removed from the litter which was then dried at 70^{o}C for four days to determine dry weights. A further litter collection was made at QC in October 2005. The influence of site (GR, GC and QC) and area (bridal creeper versus reference area) on litter standing crop was analysed using a two-way ANOVA (GenStat, 2003).

SEED CHEMISTRY

Nutrient concentrations of N, P, K, Mg, Cu, Mn and Fe of seeds of bridal creeper, collected from QH on 13 September 2006 and in a Tuart woodland in Yanchep National Park (north of Perth, 31.533S, 115.683E) on 17 October 2006, were determined and compared to seeds from native *Grevillea* spp. collected in southern Western Australia and reported by Hocking (1986) as well as seeds from another South African exotic geophyte, *Gladiolus caryophyllaceus* (N. L. Burman) Poir., also collected in southern Western Australia and reported by Hocking (1993). Bridal creeper seeds were not available at this time from the main study sites due to the biological control agent, the bridal creeper rust, preventing flowering and therefore fruit production (see Chapter 8). Approximately 200 bridal creeper fruits were collected from each of these two sites. Bridal creeper fruits were pressed through a sieve to remove the pulp and the seeds were then washed, dried at 70^{o}C for three days before being separated into three sub-samples per site and then sent to CSBP Laboratories (W.A.) for chemical analysis.

Results

FOLIAGE CHEMISTRY

Assuming a normal distribution, the 95% confidence intervals for nutrient concentrations of green bridal creeper foliage was 19.6 to 26.0 mg/g for N; 1.3 to 3.0 mg/g for P; and 14.9 to 42.9 mg/g for K. Therefore, this foliage appeared to contain greater concentrations of N, P and K when compared to native plants collected from southern Western Australia and reported by Foulds (1993) (Table 5.1). When nine nutrient concentrations were analysed simultaneously, the nutrient concentrations in bridal creeper foliage are dissimilar to plant families growing in southern Western Australia (Figure 5.1).

There was significantly more N found in the native *T. angustifolia* compared to *E. occidentalis* ($F=95.76$; d.f. 1,16; $p<0.001$, Table 5.2), but there was no difference in N concentrations in native plants collected from bridal creeper and reference areas ($F=0.65$; d.f. 1,16; $p=0.432$). In contrast, there was no significant difference between P concentrations in the native species ($F=2.49$; d.f. 1,16; $p=0.134$), however P concentrations were higher in the native plants growing in the bridal creeper areas, compared to the reference areas ($F=5.1$, d.f. 1,16; $p=0.038$, Table 5.2). Even so, the P levels were still lower than that of bridal creeper foliage and similar to that of other native species (Table 5.1).

For N concentrations of green and senesced bridal creeper foliage, there was no significant difference between the sites GR and GC ($F=2.77$; d.f. 1,8; $p=0.135$), however there was a significant difference between the N concentrations of green bridal creeper foliage and senesced foliage ($F=71.46$; d.f. 1,8; $p<0.001$, Table 5.3). For P concentrations, there was no significant difference between the two sites ($F=1.73$; d.f. 1,8; $p=0.224$) or between green bridal creeper foliage and senesced foliage ($F=1.70$; d.f. 1,8; $p=0.229$, Table 5.3).

ROOT CHEMISTRY

The nutrient concentrations were higher in the root system when bridal creeper was actively growing compared to the root system of recently senesced plants. There was no significant difference in N concentrations in the root systems between sites ($F=1.94$; d.f.

2,12; p=0.187), however there was a significant difference between the N concentrations in the root systems of actively growing plants compared to senescing plants (F=18.11; d.f. 1,12; p=0.001, Table 5.4). For P concentrations, there was a significant interaction between the time of collection and site (after log10 transformation, F=12.23; d.f. 2,12; p=0.001). At GC, there was no significant difference in P concentrations between collection times (after log10 transformation, F=0.30; d.f. 1,4; p=0.614). However at the other two sites, there were significant differences in P concentrations between collection times (for GR, after log10 transformation, F=40.91; d.f. 1,4; p=0.003; for QC, after log10 transformation, F=16.00; d.f. 1,4; p=0.016).

LITTERFALL

The biomass of litterfall was similar in bridal creeper and reference areas (after a square-root transformation F=1.78; d.f. 1,12; p=0.207) and between spring and summer (F=4.05; d.f. 1,12; p=0.067). However, there was an increase in the amount of litterfall in bridal creeper areas during the time when bridal creeper senesces, being the first three months of measurements. The litterfall was significantly higher in bridal creeper invaded areas, when bridal creeper senesces in spring, compared to reference areas (F=16.35; d.f. 1,6; p=0.007, Figure 5.2). This litterfall was also higher in P and N compared to the litterfall of nearby reference areas at this time (Table 5.5). There were significant interactions in litter nutrient concentrations between spring and summer collections (for N F=44.94; d.f. 1,12; p<0.001; and for P F=18.81; d.f. 1,12; p<0.001). However, P and N were consistently higher in the litterfall from bridal creeper areas in spring, with both N (F=114.18; d.f. 1,6; p<0.001) and P (F=34.81; d.f. 1,6; p<0.001) significantly higher in litterfall collected from bridal creeper areas across the four sites at that time (Table 5.5).

LITTER DECOMPOSITION

The loss of biomass was not different for bridal creeper foliage nor eucalypt foliage when comparing bridal creeper invaded areas or nearby native reference areas. For the decomposition of bridal creeper foliage at GR and GC there was no significant difference between areas (F=0.14; d.f. 1,40; p=0.715), however there was a significant difference across collection periods (F=7.36; d.f. 3,40; p<0.001). The biomass of the first collection was significantly greater than the final three collections. The remaining biomass from the latter three collections was not significantly different. For the

decomposition of bridal creeper foliage at QC, again there was no significant difference between areas ($F=2.90$; d.f. 1,16; $p=0.108$), however again there was a significant difference in the weight of the remaining biomass across collection periods ($F=68.81$; d.f. 3,16; $p<0.001$). All collections periods were significantly different except between the third and fourth (final) collection.

The decomposition of *E. rudis* foliage at GR and GC was similar between areas ($F=0.82$; d.f. 1,40; $p=0.371$), but differed across collection periods ($F=23.73$; d.f. 3,40; $p<0.001$). The weights of the remaining biomass across all collections periods were significantly different except between the second and third collection. The decomposition of *E. occidentalis* foliage at QC was also not different between areas ($F=3.12$; d.f. 1,16; $p=0.097$), but differed across collection periods ($F=94.16$; d.f. 3,16; $p<0.001$). All collections periods were significantly different except between the third and fourth (final) collection.

As the decomposition for bridal creeper and *Eucalyptus* spp. were not different between areas (as determined by percentage loss of biomass), samples at each site were analysed together (with areas combined) to determine which species decomposed faster. At GR, bridal creeper decomposed faster than the native species ($F=148.92$; d.f. 1,40; $p<0.001$, Figure 5.3a) and there was also a significant difference across collection periods ($F=36.96$; d.f. 3,40; $p<0.001$). All collection periods were different, except for the second and third collections. At GC, bridal creeper also decomposed faster than the native species ($F=177.10$; d.f. 1,40; $p<0.001$, Figure 5.3d) and there was also a significant difference across collection periods ($F=14.58$; d.f. 3,40; $p<0.001$). The first collection period was different to the other collection periods and the second collection period was different to the fourth (final) collection. Also at QC, bridal creeper decomposed faster than the native species ($F=875.26$; d.f. 1,40; $p<0.001$, Figure 5.3g) and there was also a significant difference across collection periods ($F=145.52$; d.f. 3,40; $p<0.001$). All collection periods were significantly different.

Across the three sites, between 33 to 68% of bridal creeper biomass was lost in the first three months, with approximately 25% of the original bridal creeper biomass remaining after 12 months (Figures 5.3a, 5.3d, 5.3g). Between 46 to 72% of all N was lost from the bridal creeper litter in the first three months (Figures 5.3b, 5.3e, 5.3h) and 69 to 87%

of all P was also lost from the bridal creeper litter also in the first three months (Figure 5.3c, 5.3f, 5.3i). Higher percentages of biomass, N and P were lost from bridal creeper foliage compared to the natives after 12 months ($F=4707.8$; d.f. 1,12; $p<0.001$, Figure 5.4). However, there was no significant difference in the percentage of remaining biomass, or mass of N or P ($F=406.8$; d.f. 2,12; $p=0.103$, Figure 5.4). N and P loss paralleled biomass loss with neither being lost at a greater rate than the others.

LITTER STANDING CROP (BIOMASS ON FOREST FLOOR)

There was no difference in the standing crop of litter between areas ($F=0.00$; d.f. 1,54; $p=0.948$, Figure 5.5). However, there was a significant difference between sites ($F=7.43$; d.f. 1,54; $p=0.001$).

SEED CHEMISTRY

Assuming a normal distribution, the 95% confidence intervals for nutrient concentrations of bridal creeper seed was 26.4 to 30.4 mg/g for N; 4.3 to 5.0 mg/g for P; 11.6 to 12.0 mg/Kg for Cu; and 78.9 to 159.3 mg/Kg for Fe. Therefore, bridal creeper seeds appeared to have lower P and Cu concentrations compared to seeds from native *Grevillea* spp. (n=9) collected from southern Western Australia and reported by Hocking (1986) (Table 5.6). Bridal creeper seeds appeared to have higher N, P and Fe concentrations when compared to *Gladiolus caryophyllaceus*, another South African geophyte growing in southern Western Australia (Table 5.6).

Discussion

The outcomes of this research have important implications towards our understanding of invasions in Australia. Ehrenfeld (2003) listed nine traits from exotic plants that are thought to affect soil nutrient cycling processes. Bridal creeper exhibits at least four of these traits in contrast to the native species it has replaced. 1) Tissue Type – with an herbaceous weed replacing woody plants. Bridal creeper is a climbing herb which has been shown to replace native woody trees and shrubs (Chapter 3 - Turner et al., 2008c; Chapter 2 - Turner and Virtue, 2006). 2) Life History - bridal creeper is different to most native plants, with most of the native plants as well as bridal creeper being perennial, but in contrast, bridal creeper is a geophyte and all of the aboveground growth of bridal creeper senesces every year (Morin et al., 2006a; 7% of the estimated

native flora are geophytes in SW Australia - Parsons and Hopper, 2003). 3) Vegetative Spread/Roots - bridal creeper is also able to vegetatively spread through branching rhizomes (Morin et al., 2006a) and its root architecture can minimise nutrient loss (Chapter 6 - Turner et al., 2006). 4) Tissue Chemistry - I have now demonstrated that bridal creeper foliage has higher levels of nutrients compared to native species, and my data suggests that these nutrients are recycled through the litterfall and decomposition.

FOLIAGE CHEMISTRY

Nutrient analysis of bridal creeper foliage indicated that it contained greater concentrations of P, as well as N and K when compared to native plants. The accumulation of P in plant biomass can become a potential source of soil P following litterfall (Grierson et al., 2004). However, in eastern Australia Lindsay and French (2005) established that large proportions of P and N were reabsorbed before abscission by both the exotic species, *Chrysanthemoides monilifera* ssp. *rotundata* and the native species. In contrast to this, the full complement of P within the foliage of bridal creeper appears to be returned annually in litterfall, with no difference in P concentrations found between the green foliage and senesced foliage. This is not unusual in deciduous species. In California, Gray (1983) reported that an evergreen shrub was more effective at re-translocating N and P before abscission compared to drought-deciduous species and overall it has been suggested that evergreens are more efficient than deciduous species at resorbing P (Killingbeck, 1996). Nutrients which are not resorbed must be circulated through litterfall (Aerts, 1996) and the mobility of nutrients will therefore be dependent on the rate of decomposition of this litterfall (Attiwill, 1968). Inorganic nutrients within litter are then made available to plants through leaching or mineralisation by microbes (Lindsay and French, 2005).

ROOT CHEMISTRY

Based on the results from the foliage chemistry, some N may be reabsorbed by bridal creeper before dropping its foliage (Table 5.3), however it is more likely that N was leached from the dead foliage when still on the plant waiting for leaf drop. It appears that bridal creeper does not resorb N or P from the foliage before senescing as indicated by the results from the root chemistry which showed that the nutrient concentrations of the storage organs were equal to or lower in plants that had recently senesced compared to the root systems in the plants that were actively growing.

As bridal creeper does not store P, it suggests that bridal creeper must have other mechanisms to guarantee P acquisition when aboveground growth commences in autumn. This could also relate to its invasiveness into relatively intact vegetation and possible mechanisms are discussed further below.

LITTERFALL

During spring 2005, bridal creeper areas had litterfall with greater biomass, N and P compared to that of reference areas. Even though these levels are high, these nutrient levels are probably under-estimated for bridal creeper areas due to the potential leaching of nutrients from the delicate bridal creeper litter by rain before the collection of material.

Higher levels of organic carbon have been found in the soil in bridal creeper areas at three of the four study sites compared to the reference areas (Table 4.2). Plant roots and the soil mineral material compete for the supply of available P (Attiwill and Weston, 2003), however organic matter can block P adsorption sites in acidic soils (Haynes and Mokolobate, 2001). Besides bridal creeper dropping nutrient rich litter, the increased organic matter dropped in spring may also increase the availability of P by blocking P adsorption sites in the soil. Usually only small amounts of P are available to plants in acidic soils as there is high phosphate adsorption and strong interactions with active forms of Fe and aluminum (Haynes and Mokolobate, 2001; Iyamuremye and Dick, 1996). During decomposition of organic matter, organic acids are released with potential P adsorption sites blocked, such as citric acid and malic acid (Haynes and Mokolobate, 2001), which in turn increase the availability of P in the soil (Attiwill and Weston, 2003). Another example is oxalic acid, which has also been shown to increase available P, when released from senescent *Salsola tragus* L. leaves (Cannon et al., 1995), and also proposed as the mechanism for P cycling in *Oxalis pes-caprae* leaf litter (Sala et al., 2007).

LITTER DECOMPOSITION

All the foliage of bridal creeper senesces each year and this foliage decomposes rapidly compared to the native species. Nutrients are also rapidly leached into the soil from this nutrient-rich bridal creeper litter. The difference in rates reported here could be even

higher as green native material was used in the litterbags, and this could have overestimated the rate of the native litter decomposition, as nutrients in the native species are normally reabsorbed from the leaves before being dropped (Lindsay and French, 2005). Interestingly, higher P concentrations were found in native plants growing in bridal creeper areas compared to the nearby reference areas. Resorption efficiency of eucalypts have been shown to decrease with increased levels of P availability within the soil (Hawkins and Polglase, 2000), therefore native eucalypt litter within bridal creeper areas (that contain elevated levels of available P in the soil) may be contributing to the increased cycling of P. However, the elevated P levels in the foliage of *E. occidentalis* in bridal creeper areas were still considerably lower than that of bridal creeper (see Tables 5.1 & 5.2) and eucalypts in this study decomposed slower (Figure 5.4) and lost P at a slower rate when compared to bridal creeper. However to investigate the differences in the nutrient recycle strategies, further tests with isotopes are recommended.

My results reported here are not unusual for a deciduous species, as the decomposition rate and release of N and P from the litter tends to be faster from deciduous species than from evergreen species (for example see Decker and Boerner, 2006; Schlesinger and Hasey, 1981). However, in contrast to my bridal creeper study where there was no difference found in decomposition rates between invaded and reference areas, litter below the exotic plant, *T. fluminensis* decomposed nearly twice as quickly as litter placed away from *T. fluminensis* (Standish et al., 2004). The differences measured in my study relate to the quality of bridal creeper. As 69 to 87% of P in the litter was removed within three months as well as 46 to 72% of N, these nutrients would be available when bridal creeper began to re-shoot just before the break in the dry season around March each year.

LITTER STANDING CROP (BIOMASS ON FOREST FLOOR)

In 2004, bridal creeper cover within the bridal creeper areas at these study sites, ranged from 40.3 to 61.7% (Chapter 3 - Turner et al., 2008c), which based on the relationship reported by Turner and Virtue (Figure 2.1 - 2006), equates to approximately 75 to 115 bridal creeper shoots per m^2 . This large number of stems could trap any litterfall from bridal creeper or any other species present (see also Stephens et al., 2008). Yet, there was no difference in the standing crop (floor biomass) of litter between areas. The

measurements were taken before bridal creeper senesced and based on the decomposition study most of the bridal creeper litter dropped 12 months previously would have already decomposed. In contrast, areas with *T. fluminensis* had a lower standing crop to that of non-invaded areas (Standish et al., 2004). In addition, Heneghan et al. (2004) reported more than six times the litter in un-invaded areas compared to invaded areas with the exotic, *Rhamnus cathartica*. Most of the litterfall collected in my study was in summer and from the tree species. To date, bridal creeper has only been shown to displace the lower understorey trees and shrubs (Chapter 3 - Turner et al., 2008c) and native ground-cover plants (Stephens et al., 2008).

ROOT SYSTEM – OPPORTUNITIES FOR FURTHER RESEARCH

Mycorrhizal associations between bridal creeper and any fungi have not been investigated (Morin et al., 2006a), however the roots and tubers of bridal creeper form a dense, continuous mat with dry weights of the belowground biomass at my study sites ranging from 2.3 to 3.7 kg/m^2 (Chapter 6 - Turner et al., 2006). This biomass is only found between the soil surface and to a depth of 20 cm (but mainly in the top 5 cm) into the soil and therefore given the architecture of these root mats, bridal creeper is in a position to capture nutrients leached from the litter above them. Lambers et al. (2006) suggested that such root mats can minimise nutrient losses by scavenging nutrients directly from decomposing litter.

Any nutrients that entered the system would be trapped and then recycled. This could explain the higher nutrient levels found in plots where bridal creeper was not controlled compared to areas where bridal creeper was controlled following a wild fire (see Table 7.2). Nutrient availability in the soil increases for a short-time following fire (Handreck, 1997; Hobbs and Huenneke, 1992), however bridal creeper may be able to trap and recycle these nutrients before they are leached away. It is also hypothesised that as bridal creeper has displaced many native woody shrubs and trees, any nutrients from the decomposing or burnt native woody shrubs and trees would also be trapped by the root mats. This could lead to a gradual shift in nutrient pools from aboveground plant biomass to the soil.

It has been suggested that bridal creeper can invade undisturbed native areas (Hobbs, 1991; Raymond, 1995; Siderov and Ainsworth, 2004). In addition, when bridal creeper

was grown in field collected soil low in nutrients (both N and P), it was still able to produce the same number of tubers compared to other bridal creeper plants grown in other field collected soil with higher nutrients (Chapter 4). However, bridal creeper also showed positive responses to increases in P when N was kept low. This would suggest that bridal creeper does not require elevated N or P levels for invasion to take place, but does benefit when P is increased (Chapter 4). Bridal creeper seeds had high P concentrations compared to another South African geophyte, therefore when germinating in low P soils, I suggest that bridal creeper has an advantage over this other exotic geophyte and could more readily establish in the nutrient poor soils. This advantage would increase as bridal creeper seed is also dispersed in bird faeces (Thomas and Miller, 2000) which in turn would also be an additional source of nutrients.

Many soils with low available P however, do contain other reserves of P that are fixed in forms that are unavailable to most plant species (Grierson et al., 2004; Haynes and Mokolobate, 2001). As mentioned above, P may be strongly adsorbed in acidic soils or it could also be precipitated as Al or Fe phosphate minerals (Iyamuremye et al., 1996). Within low nutrient soils, roots of some plants exude organic acids, forming an important role in their nutrient acquisition of nutrients such as P and Fe (Dakora and Phillips, 2002). These exudates convert the fixed P into soluble forms that can then be used by plants (Grierson et al., 2004) and the production of root exudates, including organic acids such as citric and malic acid, under low availability of P have been suggested to increase the availability of P (Attiwill and Weston, 2003). Caffeic acid is another example that makes both Fe and P available for plant uptake by increasing their solubility (Dakora and Phillips, 2002). These three organic acids are all found in the roots of a species in the same genus as bridal creeper, *Asparagus officinalis* L. (Hartung et al., 1990). Given that both available P and reactive Fe were found to be higher in bridal creeper invaded soils compared to nearby reference areas (Table 4.2), it is hypothesised that bridal creeper can exude organic acids as a response to low P.

If organic acids can make both Fe and P available for plant uptake by increasing their solubility, additional support that bridal creeper can produce such acids comes from the large levels of Fe (7,901 mg/Kg) found in bridal creeper's roots (Table 6.1 - Turner et al., 2006). Gardner et al. (1983) suggested that P acquisition in *Lupinus albus* through

root exudates lead to Fe accumulation in its root system. Fe is a micronutrient, so if Fe in the soil reaches high levels and is not needed by the plant in such high concentrations, yet can not be excluded from the plant, some plants ameliorate this situation by removing Fe away from sites of active metabolism and usually store the element in their root system (Fitter and Hay, 2002; Shaw, 1989). This could suggest that bridal creeper can make both Fe and P available for its uptake by increasing their solubility. This is not new for exotic plants, with Thorpe (2006) suggesting that root exudates produced by the exotic, *Centaurea maculosa* Lam., enabled this species to acquire more P compared to that of the native species.

Further research is needed on the ability of bridal creeper to access P. In the glasshouse experiment, when bridal creeper was grown in a relatively low nutrient soil, collected from the reference area at Quell Creek (QC) (Chapter 4), the P concentration of this foliage was relatively high, being 1.42 $\pm$ 0.02 mg/g (mean $\pm$ s.e.), compared to only 0.98 $\pm$ 0.10 mg/g for the native bluebell creeper (Table 4.3). This P concentration in bridal creeper was also higher than the 0.7 mg/g for native plants generally (Table 5.1) and the 0.69 $\pm$ 0.02 mg/g for *Thomasia* and 0.64 $\pm$ 0.02 mg/g for *E. occidentalis* reported for native plants growing in the reference area at QC (Table 5.2). Two further experiments are therefore warranted to test the ability of bridal creeper to access additional P; (i) growing bridal creeper seedlings in a hydroponic situation, with low and high concentrations of P; and (ii) growing bridal creeper seedlings in sand with different forms of P added, such as Fe phosphate. The first experiment would measure the response of bridal creeper to low levels of P including identifying exudates produced by the plant. The second experiment could determine which forms of P bridal creeper can access, including that of Fe phosphate.

SYNTHESIS OF CHAPTER

Many reviews or studies that investigated the effects of environmental weeds on soil nutrient cycling have concentrated on changes to nitrogen (for example see Ehrenfeld, 2003; Lindsay and French, 2005). This may be important especially for those exotic species that fix atmospheric nitrogen (for example acacias reported by Witkowski, 1991) however, given that within many parts of Australia, plants have adapted to soils low in phosphate (Adam et al., 1989; Beadle, 1953; Beadle, 1966), P may be more or equally as important. With native species re-absorbing P before litterfall and the slow

release of the P that is left in their litter (Attiwill, 1968), P nutrient pools are kept low. In the past this has protected sites from the invasion of plants that require higher P concentrations. In invasion ecology within Australia, it has been suggested that nutrient enrichment of low-fertility soils was a prerequisite for exotic plant invasions (Lake and Leishman, 2004). However, with the ability to change soil functions, certain exotic plants may have an important characteristic that renders that species capable of invading intact communities (Ehrenfeld et al., 2001).

The results from Chapter 4 of increased soil nutrients below bridal creeper could be interpreted that bridal creeper has a preference for soils of high fertility. This could be the case especially for bridal creeper invasions along roadsides or urban parks, but as bridal creeper can also invade undisturbed native ecosystems (Hobbs, 1991; Raymond, 1995; Siderov and Ainsworth, 2004), can grow in nutrient poor soil (Chapters 4 and 7), and can cause a rapid turnover and capture of nutrient-rich litter, all suggest that bridal creeper can modify the soil characteristics.

The ability to change the soil conditions may be an important characteristic that enables exotic plants to invade and then dominate ecosystems (Ehrenfeld et al., 2001; Fogarty and Facelli, 1999). When the fitness of potential competitors is reduced, relative to the plant species that has altered the soil conditions, plant-soil feedback may contribute to monocultures of these transforming exotic species (van der Putten, 1997). Given many native plants are adapted to low soil P within Australia (Beadle, 1953; Beadle, 1966) and native species richness decreases following increase in P (Adam et al., 1989), which is in contrast to bridal creeper that responds positively to increases in P (Chapter 4), it seems plausible that this feedback hypothesised above has contributed to the monocultures of bridal creeper found within Australian native ecosystems.

Information on the mechanisms that change ecosystem processes is also important when restoring a site following weed control (Heneghan et al., 2004). If bridal creeper can slowly enrich nutrient poor soil, this will have important implications for restoration of these invaded sites. Where ecosystem properties have been altered, it is likely that both control of the weed and restoration of the altered properties will be necessary if a return to a pre-invasion state is desired (Gordon, 1998). Even if the biological control programme of bridal creeper within Australia is successful (Morin et al., 2006b) the

legacy of the invader may persist long after the exotic species has been controlled (Corbin and D'Antonio, 2004), with elevated nutrient levels in the soil persisting. An important restoration goal of bridal creeper invaded areas will be to reduce the elevated nutrient levels. However, methods for reducing available P are not well established (Marrs, 2002). After fertiliser application, Heddle and Specht (1975) established that much of the P was retained in the soil even 22 years after application. In many instances changes in nutrient availability and species composition may be irreversible (Evans et al., 2001).

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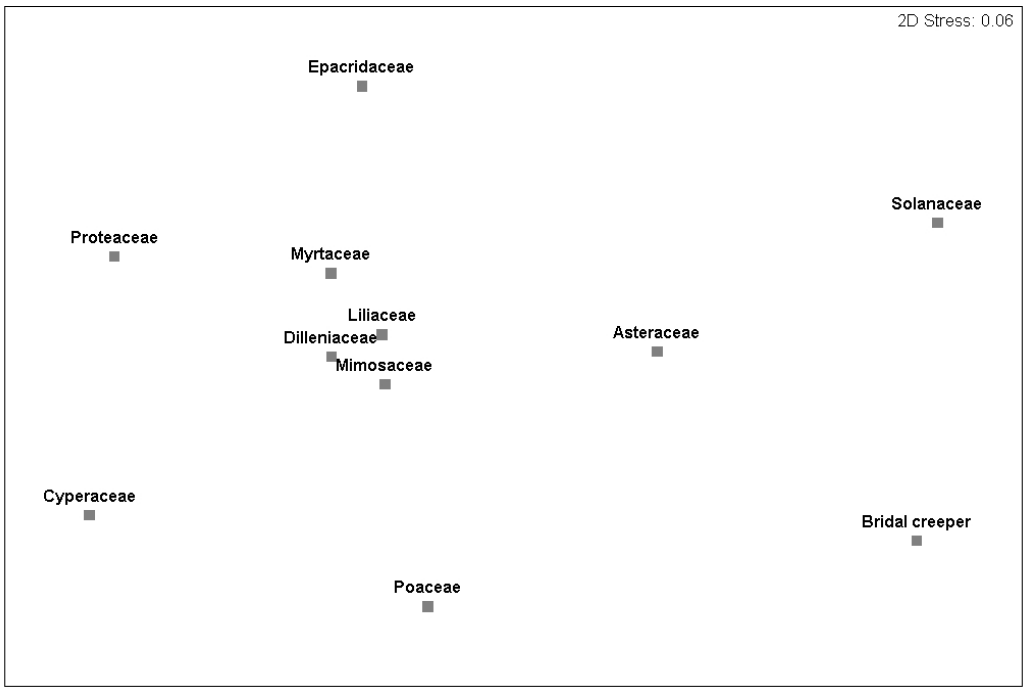

Figure 5.1. Ordination plot (nMDS) of plant families and bridal creeper based on nine nutrients (N, P, K, Ca, Mg, Cl, Cu, Zn & Mn) from bridal creeper foliage samples collected from QC, GR and GC and plant families also collected in southern Western Australia by Foulds (1993).

The relative distances between squares represent the degree of dissimilarity of foliage nutrients. (Nutrient concentrations were log transformed and normalised, followed by a Euclidean distance measure of dissimilarity. Also refer to Table 5.1)

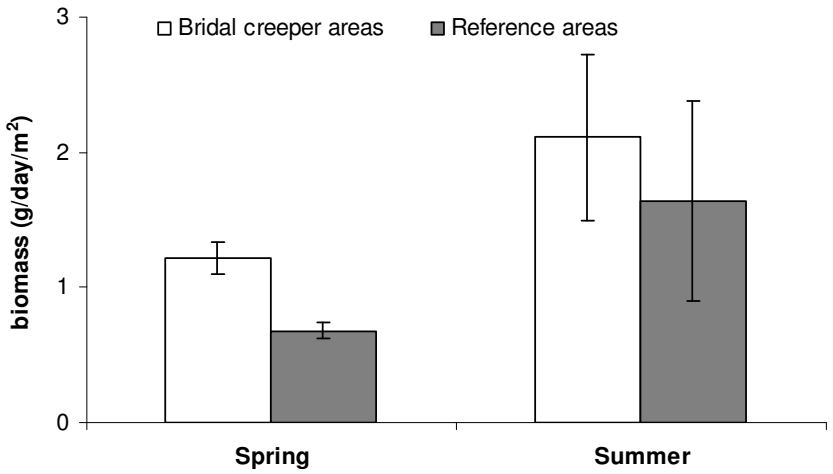

Figure 5.2. Average litterfall (± s.e.) rates (including bridal creeper) in spring (September – November) and summer (December – February) across four sites in south west Australia.

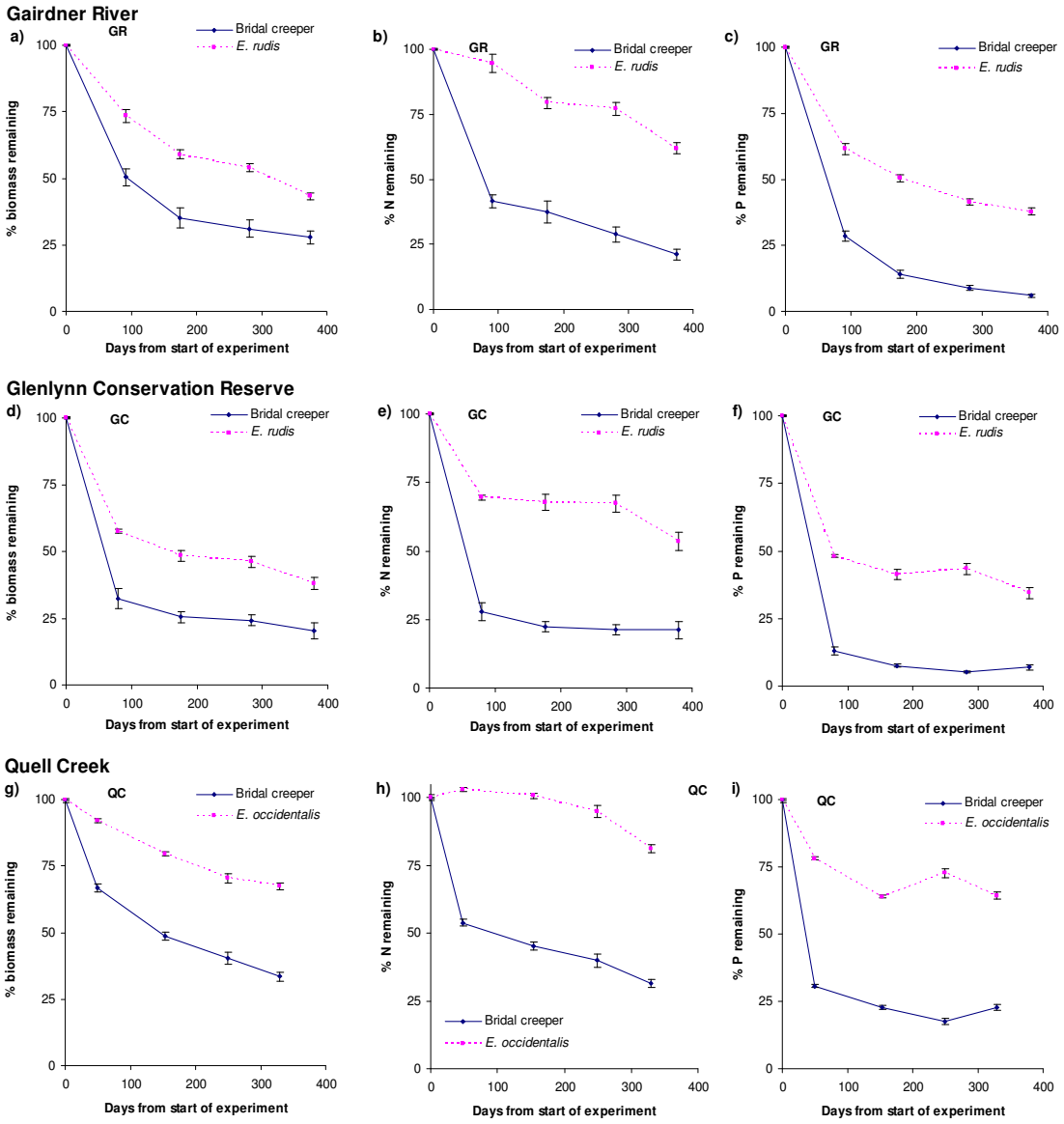

Figure 5.3. Percentage loss of biomass and nutrients, N and P (± s.e.) from the decomposition of bridal creeper and two native eucalypts, *Eucalyptus rudis* and *Eucalyptus occidentalis* across three sites in south west Australia.

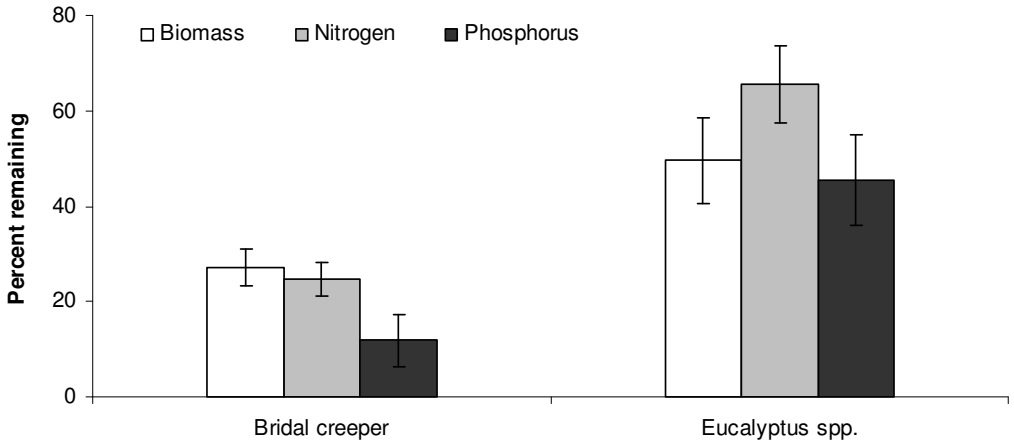

Figure 5.4. The average percentage (± s.e.) of remaining biomass; and mass of N and P after approximately 12 months of decomposition across the three sites.

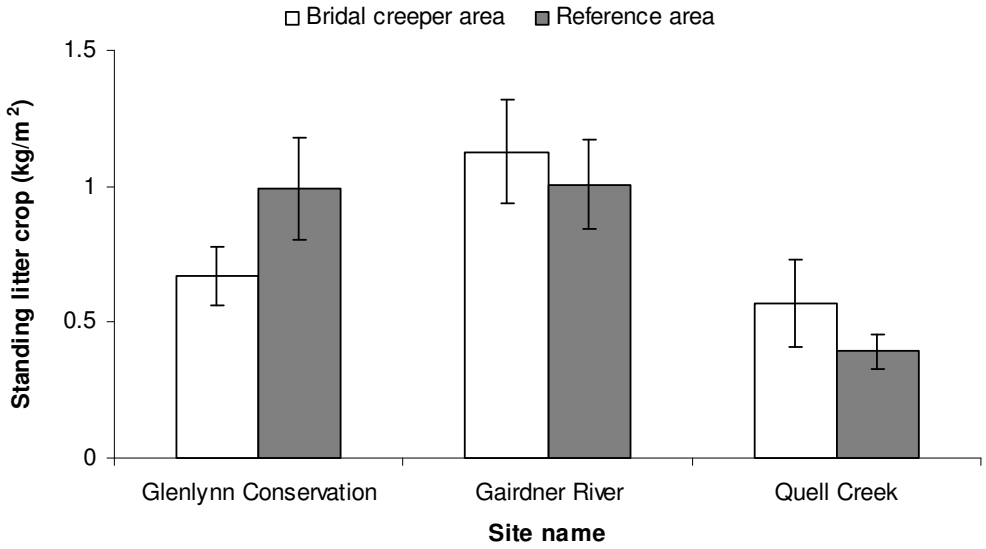

Figure 5.5. Litter biomass (± s.e.) found on the forest floor just before bridal creeper senesces.

Table 5.1. Nutrient element concentrations of aboveground shoots of bridal creeper (dry weight, mean ± s.e.) collected from GC, QC & GR compared to mean nutrient element concentrations of aboveground shoots of native and exotic plants collected from southern Western Australia.

		Bridal creeper	Native species*	Exotic species*
N	(mg/g)	22.8 ± 1.6	9.7	13.2
P		2.1 ± 0.4	0.7	1.7
K		28.9 ± 7.1	7.7	16.4
Mg		3.4 ± 0.4	2.0	3.9
Cu	(mg/Kg)	6.3 ± 0.7	3.9	4.0
Mn		75.5 ± 12.4	69.0	50.0
Fe		130.6 ± 30.1	-	-

*data analysed from Foulds (1993), based on 368 plant species, across 696 samples, including 48 samples being from exotic species.

Table 5.2. Nutrient element concentrations of aboveground shoots of two native species found at QC (dry weight, mean ± s.e.).

Species	Nutrient	Bridal creeper area	Reference area
T. angustifolia	N (mg/g)	16.64 ± 7.44	16.09 ± 7.20
	P	0.74 ± 0.03	0.69 ± 0.02
E. occidentalis	N	11.12 ± 0.36	12.42 ± 0.38
	P	0.71 ± 0.02	0.64 ± 0.02

Table 5.3. Nutrient element concentrations of aboveground shoots of bridal creeper (dry weight, mean ± s.e.) collected from GC & GR, comparing fresh material collected in winter 2005 and senesced material collected at the start of summer.

		Green bridal creeper foliage (June)	**Senesced bridal creeper foliage (Nov/Dec)**
N	(mg/g)	24.18 ± 1.48	13.60 ± 0.60
P		1.70 ± 0.16	1.24 ± 0.30

Table 5.4. Nutrient element concentrations of belowground root system of bridal creeper (dry weight, mean ± s.e.) collected from GC, QC & GR, comparing when the plant was actively growing and when the plants had senesced at the start of summer.

		Actively growing plants (June)	**Senesced plants (Nov/Dec)**
N	(mg/g)	14.78 ± 0.88	9.30 ± 1.35
P		0.81 ± 0.07	0.48 ± 0.07

Table 5.5. N and P concentrations (dry weight, mean ± s.e.) of total litterfall trapped between September and November 2005 (in spring when bridal creeper senesces and drops its foliage) and December 2005 to February 2006 (summer, when bridal creeper is not growing), across four sites (QC, GC, GR & QH) in both bridal creeper invaded areas and nearby reference areas.

		Bridal creeper areas (Sept–Nov 05)	**Reference areas** (Sept–Nov 05)	**Bridal creeper areas** (Dec 05–Feb 06)	**Reference areas** (Dec 05–Feb 06)
N	(mg/g)	16.41 ± 0.75	7.24 ± 0.42	8.07 ± 0.45	8.14 ± 0.98
P		1.36 ± 0.18	0.26 ± 0.05	0.38 ± 0.05	0.15 ± 0.06

Table 5.6. Nutrient element concentrations of bridal creeper seeds (in dry weight, mean ± s.e.), collected from QH and Yanchep National Park compared to other south west Australian seeds from native *Grevillea* spp. (n = 9) reported by Hocking (1986) and seeds from another exotic geophyte, *Gladiolus caryophyllaceus* reported by Hocking (1993).

		Bridal creeper (Mean ± s.e)	***Grevillea* spp.** (Range)	***Gladiolus caryophyllaceus*** (Mean ± s.e.)
N	(mg/g)	28.4 ± 1.0	28.8 – 45.2	19.1 ± 1.0
P		4.6 ± 0.2	6.1 – 14.8	1.8 ± 0.1
K		6.3 ± 0.3	3.9 – 66.6	15.7 ± 0.9
Mg		2.0 ± 0.1	1.6 – 7.5	1.1 ± 0.1
Cu	(mg/Kg)	11.8 ± 0.1	16.0 – 57.2	9.5 ± 0.6
Mn		38.1 ± 3.4	27.7 – 255.7	4.5 ± 0.3
Fe		119.1 ± 20.5	35.9 – 152.6	32.8 ± 2.8

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CHAPTER SIX

A BARRIER TO THE RECOVERY OF BRIDAL CREEPER (*ASPARAGUS ASPARAGOIDES* (L.) DRUCE) INFESTED SITES: THE RESIDUAL IMPACTS OF THE ROOT SYSTEM

Key words: allelopathy, decomposition, geophyte, nutrients, tubers, weed impacts

Abstract

Bridal creeper is an environmental weed in Australia that has the potential to dominate native vegetation both above and belowground. Its extensive rhizomes and storage tubers form underground mats that comprise up to 87% of total plant biomass. Even after control, the dead root system can remain in the soil for many years. Therefore, this study aimed to i) measure the quantity, nutrient levels and decomposition of the belowground biomass of bridal creeper; and ii) determine the impact of both live and dead root material on early plant growth. In Western Australia, the belowground dry weight of bridal creeper was estimated at 2.99 $\pm$ 0.32 kg m^{-2} (mean $\pm$ s.e.) across four sites. This biomass was concentrated in the top 20 cm of the soil profile. The nutrient concentrations in this belowground biomass were similar to other geophytes that grow in Western Australia. The decomposition of bridal creeper's dead belowground biomass was measured using field-buried litterbags. After a rapid loss of about 40% of biomass in the first three months, decomposition slowed dramatically, indicating that decomposition may take many years following weed control. In addition, using a site of earlier removal trials in South Australia, the belowground biomass was measured at 1.4 $\pm$ 0.2 kg m^{-2}, still nine years after control.

The effects of bridal creeper's root biomass (both live and dead) on the growth of a native species were investigated in a glasshouse experiment using potted plants. The

relative growth rate of the Western Australian native, *Billardiera heterophylla* (Labill.) L.Cayzer & Crisp, was not affected by the presence of bridal creeper roots, however its root to shoot ratio was significantly decreased when grown in the presence of either live or dead bridal creeper roots. In a laboratory experiment, aqueous solutions of fresh bridal creeper roots inhibited the development of roots in three common vegetable species, while aqueous solutions of dead and decomposing bridal creeper roots only had a minimal impact on the root growth of one of these species. The above studies show that the root biomass can stay in an ecosystem for many years after control and that the dead bridal creeper roots can still have an impact on other species by occupying space that would normally be re-colonised by other plants. Weed control methods and restoration activities will need to take into account the residual impact of bridal creeper.

Introduction

Invasive geophytes are found in most regions of the world (Raymond, 1999), including within Australia and New Zealand (Williams and West, 2000). In certain regions of Australia, including the south west, they are becoming an increasing concern in native ecosystems (Humphries et al., 1993). They can form dense underground mats of bulbs, corms, tubers and rhizomes that can crowd out native vegetation (Humphries et al., 1993). In south west Australia, many South African geophytes have spread widely, including various species of *Freesia*, *Gladiolus*, *Ixia*, *Sparaxis*, *Watsonia*, and *Oxalis* (Pate and Dixon, 1982), even though this region has a high native geophyte diversity, with 496 native monocot geophyte species found in south west Australia or 7% of the estimated native flora (Parsons and Hopper, 2003). Yet, few studies have investigated the significance of geophytes as environmental weeds (Raymond, 1999).

The widespread form (see Kleinjan and Edwards, 1999) of *Asparagus asparagoides* (L.) Druce (bridal creeper), is a serious environmental weed in Australia and has been associated with displacing native plant species (Chapter 3 - Turner et al., 2008c; Chapter 2 - Turner and Virtue, 2006). Native to southern Africa, this geophyte has storage organs (tubers) that reserve energy to support the production of foliage. Once established bridal creeper has the potential to dominate native vegetation both above and belowground, and in Australia the root system can represent more than 87% of the plant's total biomass (Raymond, 1996).

The perennial belowground system of bridal creeper consists of many tubers (modified roots) densely packed along a central rhizome (underground stem) (Morin et al., 2006a). In its native range, the rhizome is 5.4 $\pm$ 1.7 mm (mean $\pm$ s.e.) in diameter (Kleinjan and Edwards, 1999). In Australia, the rhizome is also approximately 5 mm in diameter and the tubers are normally 8 to 20 mm wide (Morin et al., 2006a), with the distal end of the tubers continuing as conventional roots. The root system of bridal creeper plants become intertwined and form mats just below the soil surface (see Kleinjan and Edwards, 1999 for description of the root system when grown in its native range). In the hot, dry summer, aboveground growth of bridal creeper ceases and its foliage senesces. The tuber reserves enable the plant to survive over summer and then undergo rapid shoot development the following autumn (Morin et al., 2006a).

In many parts of Australia, bridal creeper is now actively managed through both herbicide applications and biological control. Even after bridal creeper has been controlled, residues from old root systems of bridal creeper could still pose a barrier to the recovery of managed sites and therefore needed to be investigated. Turner and Virtue (Chapter 2 - 2006) observed that dead tubers remained in trial plots eight years after the weed had been killed with herbicide. Turner and Virtue (2006) suggested that the persistence of these dead tubers may have affected native seedling establishment and may have formed a barrier to the recovery of the invaded area following weed control. In New Zealand it was also reported that following control, a large amount of dead root biomass from another *Asparagus* species, the South African *A. scandens* Thunb., could also impede the growth of other plants until the root biomass broke down (Timmins and Reid, 2000). Therefore, this Chapter reports on the decomposition of the belowground biomass of bridal creeper as well as the impacts that the decomposing belowground biomass could have on other plants. The belowground biomass of bridal creeper from four established populations was estimated and the rate at which the belowground biomass of bridal creeper decomposes in the field was measured. As root chemistry has been suggested to be the primary controller of root decomposition (Silver and Miya, 2001), the nutrient levels of the belowground biomass were also determined.

The impacts from actively growing and decomposing belowground biomass of bridal creeper were also determined in a series of controlled experiments. In Chapter 4 it was

established that bridal creeper seedlings were a poor competitor, with the relative growth rate of two native species not changing in the presence of bridal creeper. However, older bridal creeper plants have significantly more belowground biomass. Therefore, the impact of the root system (both dead and alive) from mature bridal creeper plants on the growth rate and root allocation of a native plant was measured. In addition, a laboratory experiment was also undertaken to measure the allelopathic effects of live and decomposing root material, as other species of *Asparagus* have been shown to have allelopathic impacts (Hazebroek et al., 1989). Aqueous root extracts from live *A. officinalis* L. and *A. racemosus* Willd. have been shown to inhibit seed germinations of lettuce, *Lactuca sativa* L. (Hazebroek et al., 1989) and another *Asparagus* species, *A. curillus* Buch.-Ham. ex Roxb. also has potential allelopathic compounds in its roots (Sati and Sharma, 1985). Extracts of root residues from *A. officinalis* killed ten years previously were also able to cause significant inhibition of root growth of garden cress, *Lepidium sativum* L., even though decaying *A. officinalis* root tissue was found to be approximately 90% lower in weight (Blok and Bollen, 1993).

Methods

STUDY AREA

Four main sites across southern Western Australia (W.A.), where bridal creeper had yet to come under substantial attack from the biological control agents (see Chapter 3 for full site description) were used in this study. The first site was located in Glenlynn Conservation Reserve (GC) (34.002S, 116.155E) with the other three sites all located in or adjacent to Fitzgerald River National Park. The Quell Creek site (QC) (34.254S, 119.414E) was an isolated area within the park. The Quaalup Homestead site (QH) (34.263S, 119.410E) was in private property that was surrounded by the park. The Gairdner River site (GR) (34.373S, 119.427E) was in local government land, which was managed as part of the park.

BELOWGROUND BIOMASS

All future references to root biomass in this Chapter relate to the total belowground biomass including the associated tubers and rhizomes. Root biomass of bridal creeper was sampled from the four study sites. In March 2005 at each site, 20 random soil cores,

9.5 cm in diameter, were taken within relatively homogeneous stands of bridal creeper to a depth of 20 cm. Soil was sieved through 1 cm mesh and the root biomass of bridal creeper was removed. To determine the dry weight of each sample, the biomass was washed to remove soil, dried at 70^{o}C for seven days, and then weighed.

ROOT CHEMISTRY

In June 2005, when bridal creeper was actively growing, collections of the root biomass were made at GC and GR and in June 2006 root biomass was also collected at QH and QC. Methods and results for nitrogen and phosphorus concentrations for the root biomass for three sites, GC, GR and QC, have already been described in Chapter 5. At each site, six points were chosen haphazardly (but at least 2 m apart) within bridal creeper areas and the root system dug up. Approximately 10 cm lengths of rhizome with tubers and roots attached were collected from each point. The root system had the soil removed and two samples from each site were bulked, resulting in three samples from each site being sent to CSBP Laboratories (W.A.) for chemical analysis. The concentrations of nitrogen (Sweeney and Rexroad, 1987), phosphorus, potassium, magnesium, manganese and iron (McQuaker et al., 1979) were determined. The nutrient levels were then compared to other studies on geophytes.

ROOT DECOMPOSITION

The buried litterbag technique was used to determine the decomposition of the belowground biomass. Silver and Miya (2001) investigated 152 studies on root decomposition, and of these 87% used this buried litterbag method. The roots collected in March 2005 to determine biomass for the sites GR and GC (as described above) were left in the laboratory for two months after the dry weights were determined. This root biomass was then placed within mesh bags (10 cm x 20 cm, mesh size 1.5 mm), with 17.8 $\pm$ 0.2 g (mean $\pm$ s.e.) per bag. This amount was chosen as it was sufficient to fill the litterbag and mimic the tight packing of the root system. Forty two bags were prepared for the two sites (GC and GR). At each site in June 2005, four stakes at least 5 m apart, had four litterbags attached with string. These 16 bags per site were buried 5 cm below the soil surface within the existing live bridal creeper root mat at the site from which the original root biomass was collected. The root biomass of the five bags remaining from each site was again dried at 70^{o}C to determine initial dry weights. In September 2005, additional root material was collected from the third site, QC, dried at

70°C for seven days then kept in the laboratory until mid October 2005, when the root material was placed into the field using the same methods as above. Again, 16 bags were placed at this site. The root biomass in another five bags was dried at 70°C to determine initial dry weights.

Approximately every three months the sites were revisited and four bags per site, one from each stake, were collected. The biomass was removed from the bags, washed and dried at 70°C to determine dry weight. Results were analysed with simple linear regression as well as a one-way analysis of variance (ANOVA) (GenStat, 2003). The one-way ANOVA determined if there was a difference in the average biomass of the four bags collected for each site (three replicates being sites), across the four quarterly collections.

As this litterbag study only ran for approximately 12 months at each site, belowground biomass of bridal creeper in plots where bridal creeper had been killed with herbicide in October 1997 in South Australia (see Turner and Virtue, 2006 - Chapter 2 for description of site and methods) were sampled nine years later. In September 2004, the cover of bridal creeper averaged 45.2% in the centre of the 20 experimental control plots, while in another 20 removal (herbicide) plots, bridal creeper cover only averaged 1.8% (centre 1 m^{-2} plots - Turner and Virtue unpub.). In September 2006 in the centre of each of these plots, a core 15 cm in diameter was taken to a depth of 20 cm. Soil was sieved through 1 cm mesh and the root biomass of bridal creeper was removed. To determine the dry weight of each sample, the biomass was washed and dried at 70°C for seven days, and then weighed.

ALLELOPATHIC IMPACTS OF LIVE AND DECOMPOSING ROOTS

To test the inhibitory activity of fresh and decomposing root biomass, seed germination and root growth was compared across four plant species. Three treatments were used, a control of distilled water, an aqueous extract from freshly collected bridal creeper root systems from GR and thirdly, an aqueous extract from dead root systems that have been in the field at GR for 12 months as part of the above decomposition study. Before commencing the experiment, the root systems of bridal creeper were washed and then placed in an oven to dry at 70°C for seven days.

The testing of allelopathic effects was based on the methods of Blok and Bollen (1993). Two aqueous extracts were made with 10 g of dried root material (either freshly collected root system or dead/decomposing root system) added to 200 mL of distilled water. Tubers and rhizomes were cut into 1 cm portions then placed with the distilled water into a blender. The slurry was blended for 2 minutes then allowed to sit for 30 minutes, before being blended again for 2 minutes. The slurry was then filtered through filter paper (Whatmann 1, 110 mm ø). Solution was then shaken by hand for one minute. Filter paper was placed in 60 Petri dishes (85 mm diam) and then moistened with 4 mL of either the distilled water or one of the aqueous root extracts. Five dishes of each treatment were assigned to receive seeds of one of four vegetable species: cress (*Lepidium sativum* L.; 10 seeds per dish); radish (*Raphanus sativus* L.; 5 seeds per dish); tomato (*Lycopersicon esculentum* Mill.; 5 seeds per dish); and lettuce (*Lactuca sativa* L.; 10 seeds per dish). The dishes were sealed with paraffin to prevent desiccation.

Native seeds were not used in this experiment, given their long dormancy and the difficulties of germinating many native plants that require smoke or heat shock to promote germination. Radishes were chosen as they have been suggested as a suitable plant to test soil toxicity to plants (Bodman and Sharman, 1993). As root aqueous extracts of *A. officinalis* have been shown to inhibit root growth of cress (*Lepidium sativum*) (Blok and Bollen, 1993), cress was again chosen for this study. Aqueous extracts of *A. officinalis* roots have also been shown to inhibit seed germination in tomato (*Lycopersicon esculentum*) and aqueous extracts of both *A. officinalis* and *A. racemosus* roots have inhibited germination in lettuce (*Lactuca sativa*) (Hazebroek et al., 1989) and therefore these two species were also used in my experiment. Cress, lettuce and radish seeds were obtained from Mr Fothergill's Seeds Pty Ltd. Tomato seeds were obtained from D.T. Brown & Co Ltd.

Petri dishes were placed in a growth chamber with 12 hour dark/light cycle and set at 15^{o}C for one week. For each seed that germinated in that week, the root length was measured at the end of the seven days. For each species, the effect of the aqueous solution on root length was evaluated using a one-way ANOVA. Pair wise comparisons across the three treatments were made using Tukey's test (GenStat, 2003). If not all

seeds germinated, the percentage of germination was also compared across treatments, also with a one-way ANOVA.

ALLELOPATHIC IMPACTS OF BRIDAL CREEPER SEEDLINGS

A second allelopathic experiment used live bridal creeper seedlings that had two tubers developed. These plants were grown in a glasshouse from seed collected from QC. Paper towel was placed on the bottom of 500 mL food containers and 12 mL of distilled water was added. A control consisted of containers with only distilled water and the other treatment also contained a single bridal creeper seedling with the soil removed. The tubers and roots of the bridal creeper seedlings were placed in the bottom of the container and the stem was left to rest up against the side, ensuring cladodes (leaves) did not touch the moistened paper towel. There were five containers with water and five with a bridal creeper seedling. Ten lettuce seeds were placed in each container and sealed with a lid. They were placed in a growth chamber as described above for seven days. This was repeated with another ten containers each containing ten cress seeds, with five of the containers also containing a bridal creeper seedling. For each species a one-way ANOVA was also undertaken on root lengths (GenStat, 2003). For each of these analyses, log10 transformations were applied to meet the assumption of homogeneity of variances.

IMPACT OF BRIDAL CREEPER ROOTS ON A NATIVE SPECIES

In a glasshouse experiment, the influence of bridal creeper's belowground biomass (both dead and alive) was assessed on the native species, *Billardiera heterophylla* (Labill.) L.Cayzer & Crisp (Pittosporaceae) (bluebell creeper). Belowground biomass of bridal creeper was collected from QC in October 2005. All soil was removed from the root system then half of this biomass was placed in pots with potting mix, placed in a glasshouse and allowed to re-establish. This material was used as the live root biomass in this experiment. The other half of this biomass was placed on a laboratory bench. Foliage that shot from this biomass was removed weekly to draw down the tubers. At the end of January 2006, this root biomass was placed in an oven to dry at 70^{o}C for seven days. This ensured that this biomass was killed. Once removed from the oven, the dead biomass was placed back in the laboratory until the start of the experiment.

Bluebell creeper is found in south west Western Australia (W.A.) (Traeger et al., 2004) and had previously been observed at all four of the study sites. Bluebell creeper fruits were collected in September 2004 from Meelup Regional Park (33.563S, 115.071E). Seeds were removed from the fruits and stored in the laboratory until 30 December 2005. Seeds were germinated using a method developed by Williams et al. (unpublished data). On 7 February 2006, germinated bluebell creeper seeds were placed in seedling trays in the glasshouse.

At the end of March 2006, either dead root biomass of bridal creeper, live root biomass of bridal creeper or no bridal creeper biomass was placed with potting mix (see Chapter 4 for description of potting mix) in rectangular pots, 39 cm by 29.5 cm, with a height of 20 cm. Eighteen pots were prepared. The first six were approximately half filled with the live root biomass, another six approximately half filled with dead root biomass and the final six filled with just potting mix. On 12 April 2006, all aboveground growth of bridal creeper in the pots with the live root biomass was cut off. In each pot across the three treatments, three bluebell creeper plants were placed in the centre of each pot in a triangle 15 cm apart. Another 10 bluebell creeper plants were destructively harvested to determine initial weights.

Every week, the aboveground shoots of bridal creeper were removed from the treatment with the live root biomass. This was to ensure that only the impacts of bridal creeper from its belowground biomass were measured. The removal of bridal creeper foliage was assumed to only have a minimal impact on the live root mass as bridal creeper's tuber reserves are not easily depleted (Morin et al., 2006a) and bridal creeper plants mechanically defoliated every five weeks for eight months still produced a few tubers and regrowth still occurred (Raymond, 1999). My experiment ran for 70 days during which time the temperature in the glasshouse ranged from 5 to 25^{o}C. At completion, bluebell creeper plants were dried at 70^{o}C for six days, before total dry weights were determined. Root to shoot ratios were also determined by comparing the below and aboveground weights of bluebell creeper. Also, at the end of the experiment, the bridal creeper root system was removed from the pots, and to determine the dry weight of the bridal creeper roots within each pot, the biomass was washed to remove soil, dried at 70^{o}C for seven days, and then weighed. The live root biomass was estimated to average

1.5 kg m^{-2} $\pm$ 0.4 (mean $\pm$ s.e.) and the dead root biomass was estimated to average 1.4 kg m^{-2} $\pm$ 0.2.

The relative growth rate (RGR) of bluebell creeper was calculated. RGR is the increase in plant material per unit of material per unit of time (Hunt, 1978). RGRs were calculated using the classical method (Evans, 1972; Hunt et al., 2002). The RGR of bluebell creeper was analysed, with the influence of bridal creeper (live roots, dead roots or absent) using a one-way ANOVA. A second one-way ANOVA was also undertaken for the root to shoot ratios of bluebell creeper. If significant differences were found in any of the above analyses, it was followed by a pair wise Tukey comparison test (GenStat, 2003).

Results

BELOWGROUND BIOMASS AND CHEMISTRY

Mean dry weights of the belowground biomass at four sites in W.A. ranged from 2.3 to 3.7 kg m^{-2} (Figure 6.1). The nutrient concentrations in the belowground biomass were similar to other species, except for the high iron (Fe) levels (Table 6.1).

ROOT DECOMPOSITION

The decomposition (loss) of the belowground biomass was rapid in the first three months, however the amount of biomass lost then slowed dramatically with no significant change across the four quarterly collections ($F=2.82$; d.f. 3,8; $p=0.107$, Figure 6.2). After approximately 12 months, an average of 47.2% $\pm$ 1.9 (mean $\pm$ s.e.) of the original biomass remained.

In South Australia, at Owen, within the plots where bridal creeper had been controlled nine years earlier (see Chapter 2), 1.4 kg m^{-2} $\pm$ 0.2 of belowground biomass of bridal creeper remained. At this same site, in plots where bridal creeper was not killed, the belowground biomass was estimated at 3.2 kg m^{-2} $\pm$ 0.5.

ALLELOPATHIC IMPACTS OF LIVE AND DECOMPOSING ROOTS

All lettuce seeds germinated across the aqueous treatments, however the lettuce roots did not develop when germinated in a solution of fresh bridal creeper roots. Due to this,

there was a significant difference in root lengths ($F=129.51$; d.f. 2,12; $p<0.001$), however there was no significant difference in root lengths of lettuce seedlings that germinated in either distilled water or the solution containing the decomposing root material.

All cress seeds germinated across the treatments and again the roots on the germinated cress seedlings did not develop when growing in the solution of fresh bridal creeper roots. There was a significant difference in cress root length between all treatments, with seedlings in distilled water having longer roots than those germinating in the solution of dead bridal creeper roots ($F=538.55$; d.f. 2,12; $p<0.001$, Figure 6.3a).

Only 50.7% of radish seeds germinated across treatments, but there was no significant difference in rate of germination in the different solutions ($F=0.50$; d.f. 2,12; $p=0.619$). There was a difference in root lengths of the radish seeds that germinated ($F=89.39$; d.f. 2,12; $p<0.001$). Roots did not develop when placed in the solution of fresh/live bridal creeper roots and there was no significant difference between root lengths of radish seedlings that germinated in either distilled water or the solution containing the decomposing root material.

An average of 97% of tomato seedlings germinated, but there was no difference across solutions ($F=2.61$; d.f. 2,12; $p=0.114$). In contrast to the other species, the roots of tomato seedlings developed in the solution of fresh bridal creeper roots, but these roots were significantly shorter than roots on seedlings that developed in distilled water or in the solution of decomposing root material ($F=6.36$; d.f. 2,12; $p=0.013$, Figure 6.3b). There was no significant difference between root lengths of tomato seedlings that germinated in either distilled water or the solution containing the decomposing root material.

ALLELOPATHIC IMPACTS OF BRIDAL CREEPER SEEDLINGS

Lettuce and cress seedlings had slightly, but not significantly, shorter roots when germinating next to a bridal creeper seedling. The roots of lettuce seedlings averaged 25.0 mm $\pm$ 1.6 (mean $\pm$ s.e.) when grown in a container with a bridal creeper seedling, while lettuce seedlings averaged 28.5 mm $\pm$ 0.6 when grown in just distilled water (after a log10 transformation $F=4.39$; d.f. 1,8; $p=0.069$). The roots of cress seedlings averaged

33.4 mm ± 3.1 when grown in a container with a bridal creeper seedling, while cress seedlings averaged 43.3 mm ± 4.0 when grown in just distilled water (after a log10 transformation F=4.04; d.f. 1,8; p=0.079).

IMPACT OF BRIDAL CREEPER ROOTS ON A NATIVE SPECIES

There was a significant difference in the root to shoot ratio of bluebell creeper (F=21.58; d.f. 2,15; p<0.001, Figure 6.4). The root to shoot ratio was significantly higher for plants growing in pots without any bridal creeper biomass, however there was no difference in root to shoot ratios of bluebell creeper when grown with either live or dead bridal creeper root systems (Figure 6.4). There was no significant difference in the RGR of bluebell creeper when grown in a pot with or without bridal creeper root biomass (F=1.70; d.f. 2,15; p=0.216).

Discussion

The total belowground biomass of bridal creeper in Western Australia is considerable when compared to the belowground biomass of a bridal creeper invasion in Victoria, with only 0.84 kg m^{-2} reported for an invasion in Mornington Peninsula National Park (Raymond, 1996). The belowground biomass of bridal creeper also appears to be high when compared to the belowground biomass reported for two other geophytes (Iridaceae) from their native range in South Africa. The biomass of these geophytes was also found mainly in the top 20 cm of the soil, with greater than 90% of the total root biomass found in the upper section of the soil, yet this biomass only averaged 0.18 kg m^{-2} (Higgins et al., 1987). However, Jackson et al. (1996) compiled a database of 250 root studies that were undertaken around the world and established that for sclerophyllous shrubs, 67% of their total root biomass was found in the upper 30 cm of the soil and this amount of biomass was approximately 3.2 kg m^{-2}. Therefore, the biomass of bridal creeper roots in this study does not seem high when compared to sclerophyllous shrubs. Also, Low and Lamont (1990) established that root biomass in *Banksia* scrub-heath in south west Australia was 2.27 kg m^{-2} in the upper 30 cm of the soil profile. Therefore, given the tight packing of the bridal creeper root mat, bridal creeper's root biomass may have replaced or displaced the area previously occupied by the roots of native shrubs.

Unfortunately, the space occupied by bridal creeper within the soil will remain occupied by these bridal creeper roots, even after this weed has been killed. This could prevent native shrub recovery, given that the bridal creeper root biomass will take many years to decompose and this will continue to have an impact on other plants. Within this Chapter, it has been established that the dead root material of bridal creeper will impact on the root to shoot ratio of the native bluebell creeper and the root length of cress seedlings. These impacts could remain for some time, as this study has also shown that the decomposition rate of the bridal creeper's root biomass slows dramatically after three months (Figure 6.2).

Other studies have also suggested that decomposition rate of belowground tissue of bridal creeper may hinder native plant recovery (Chapter 2 - Turner and Virtue, 2006), with a considerable amount of root biomass still evident at this site in South Australia nine years after bridal creeper had been killed with herbicide applications. However, Meney et al. (2002) reported that underground biomass of bridal creeper in an urban park, in Perth Western Australia, breaks down within just two years. However, their results appear to be from an observation only, without any actual measurements taken.

Like the amount of bridal creeper root biomass found in the upper soil profile, the decomposition of bridal creeper's root biomass does not appear to be that different to other plant species. For example, Silver and Miya (2001) also reported an exponential rate of decay for roots, following their analysis of root decomposition studies undertaken around the world. In my study, after 12 months, 47.2% $\pm$ 1.9 (mean $\pm$ s.e.) of the original bridal creeper root biomass remained. Using the global dataset reported by Silver and Miya (2001), it can be established from other studies that used the litterbag technique, an average of 50.2% of the biomass remained after 12 months for roots <2 mm in diameter (n=69) and an average of 59.5% of the biomass remained for roots between 2 to 5 mm (n=62).

The nutrient concentrations in the root biomass of bridal creeper were also similar to other geophytes especially those collected by Pate and Dixon (1982) in Western Australia. Although, Pate and Dixon (1982) did not specify which were native or non-native species or provide a measure of the variation (for example a standard error) across the 94 species they sampled, nitrogen, phosphorus and potassium concentrations

of bridal creeper all fell within the mid range of the histograms that they presented. Unfortunately, they also did not measure or report on Fe concentrations. Bridal creeper appears to have high levels of Fe, especially when compared to the other two geophytes from southern Africa (Table 6.1).

Aboveground foliage of bridal creeper had higher levels of nitrogen, phosphorus and potassium compared to the belowground parts, but more iron was found in the root system compared to the foliage of bridal creeper (Tables 5.1 and 6.1). Iron is very important for photosynthesis and the formation of chlorophyll (Amaro-Lopez et al., 1995; Epstein, 1972). The high levels of Fe reported here could explain how bridal creeper is able to rapidly produce aboveground growth in autumn and re-shoot even after many defoliation episodes. The high iron concentrations could also relate to the iron concentrations in the soil where the root biomass was collected. Iron concentrations ranged from 219 mg kg^{-1} to 7,357 mg kg^{-1} in the soil in the bridal creeper areas at these study sites (Table 4.2). These soil concentrations were higher than nearby native reference areas that contained little or no bridal creeper. Iron is usually referred to as a trace element as plants normally require small quantities of this micronutrient (Shaw, 1989). As discussed in the previous Chapter, when metals like Fe cannot be excluded from entering the plant and reach high concentrations, mechanisms have evolved that enable plants to tolerate these levels. For example, plants may remove these metals away from sites of active metabolism and store them, usually in the root system (Fitter and Hay, 2002; Shaw, 1989). Therefore, the high concentrations of Fe in the bridal creeper root system could relate to the long term accumulation of Fe.

ALLELOPATHY

In contrast to *A. officinalis* and *A. racemosus* (Hazebroek et al., 1989), aqueous solutions of live bridal creeper root system did not inhibit seed germination, but had a significant effect on root development. Shafer and Garrison (1986) incorporated root tissue of *A. officinalis* into soil. They found that small quantities (2 or 4 g per 100 g soil) could inhibit lettuce and delay seedling emergence of other species. However, the toxicity diminished after 50 days following the incorporation of the roots. Larger quantities of root (6 g) remained toxic after 90 days. This may be similar to my allelopathic study with live and decomposing roots, with the root system that was decomposing for a period of 12 months before commencement of the study having only

a small impact on one species, while the material from fresh root biomass impacted across all four species. This could indicate that toxicity of dead bridal creeper roots could decrease with time, even if the biomass takes many years to decompose.

Hartung et al. (1990) established that many organic acids were found in the roots of *A. officinalis* and suggested that in combination, these organic acids could inhibit seed germination and root development of other plant species. In this study, bridal creeper did not inhibit germination but impacted on the root development of other species. Therefore, further chemical analysis of the bridal creeper root biomass is warranted given that allelopathic compounds may be present in its root system. Unknown organic compounds in the roots may also be having a wider range of impacts besides the allelopathic impacts and include phosphorus acquisition, impacts on the microbial communities in the soil and also discouraging invertebrate feeding on the root system.

PHOSPHORUS ACQUISITION

Many of the organic compounds found in *A. officinalis* have been previously reported to be important in allelopathic interactions (see Hartung et al., 1990). In Chapter 5, it was also suggested that bridal creeper roots may exude these compounds as a way to access additional phosphorus in the soil. If bridal creeper does exude similar chemicals as *A. officinalis*, it could have a double effect, with allelopathic impacts on other plant species while bridal creeper increases its own growth rate through additional phosphorus acquisition. Increases in phosphorus have already been shown to increase the growth rate of bridal creeper (Chapter 4). However, allelopathic effects require further study as this impact of bridal creeper has not been fully established in this study, with the variation in root lengths of vegetable seedlings germinating in the presence or absence of bridal creeper seedlings (as opposed to the aqueous solutions) not significantly different. Therefore, the experiment with bridal creeper seedlings should be repeated over a longer period. However, given the impacts from the aqueous solution of fresh root material, this hypothesis does seem plausible.

BREAKDOWN OF ROOT SYSTEM BY OTHER ORGANISMS

Microbial activity may be also inhibited due to the compounds found in the root system. The organic compounds found in *A. officinalis* are also microbial toxins (Hartung et al., 1990), and could impact on any microbial activity on the decomposing roots. These

compounds may also discourage invertebrate feeding on the root system, which would be important for biological control if agents were excluded from attacking the root system due to the chemistry of the roots. Although an unidentified weevil was found on the tubers of the Western Cape form of *Asparagus asparagoides* (Kleinjan and Edwards, 2006), surveys for potential biological control agents that were undertaken in the past in the native range in South Africa have failed to identify any organisms that directly attacked the root system of the widespread form of *Asparagus asparagoides* (bridal creeper) (Kleinjan et al., 2004a) and no invertebrate feeding has been observed on the roots of bridal creeper in Australia (personal observation).

IMPLICATIONS FOR RESTORATION

In the longer-term glasshouse experiment, the root to shoot ratio of the native bluebell creeper was reduced in the presence of large quantities of bridal creeper root biomass (both dead and alive), but the RGR was unchanged. The impact of live and dead bridal creeper roots had a similar impact. The native plant put more allocation to shoots at the expense of roots when grown in the presence of both live and dead bridal creeper root biomass. This could have serious impacts on the native plant, given its ability to access both nutrients and moisture would be compromised, even when growing with dead bridal creeper roots. This experiment showed that the residual effects of the invader can remain for some time. Although unintentional, the dead root biomass used in my glasshouse experiment was 1.4 kg m^{-2} $\pm$ 0.2 (mean $\pm$ s.e.) and at the South Australian Owen site, where bridal creeper was controlled nine years previously (see Chapter 2), the root biomass also averaged 1.4 kg m^{-2} $\pm$ 0.2. Given the result of my glasshouse experiment, it could be argued that this dead root biomass at the site in South Australia would still be having an impact at the site.

This study has shown that the belowground biomass and the decomposition rate of bridal creeper roots may pose a problem for many years after its control. The main impact from bridal creeper belowground biomass detailed in this Chapter is not an allelopathic one, but a competition for space. The space within the soil remains occupied by deceased bridal creeper following control and this has a similar impact to live bridal creeper plants (that is competition for space which would then exclude the re-colonisation of native shrubs after control). Willis et al. (2003) suggested that fire could be used to deplete the tubers reserves by destroying the new seasons foliage in autumn

followed by treating the re-growth with herbicide. Also, the biological control agent, *Puccinia myrsiphylli* (Thuem.) Wint., acts as a resource sink through the absorption of nutrients (Morin et al., 2006b) and this has been shown to significantly reduce bridal creeper's vegetative growth as well as decreasing the belowground biomass (Morin et al., 2002; Turner et al., 2004). Different weed management methods will have different effects on the amount of root biomass that remains after control and restoration activities will need to take this into account as well as the residual effect of the invader that will remain after control.

Bridal creeper's root system can impact on the root allocation of other plants even after bridal creeper has been killed. Impacts after control appear to be due to space limitations and not allelopathy. However, given that this root system will take many years to decompose this impact will remain for some time. Bridal creeper control at new infestations must be a priority so as to prevent the large build up of root biomass.

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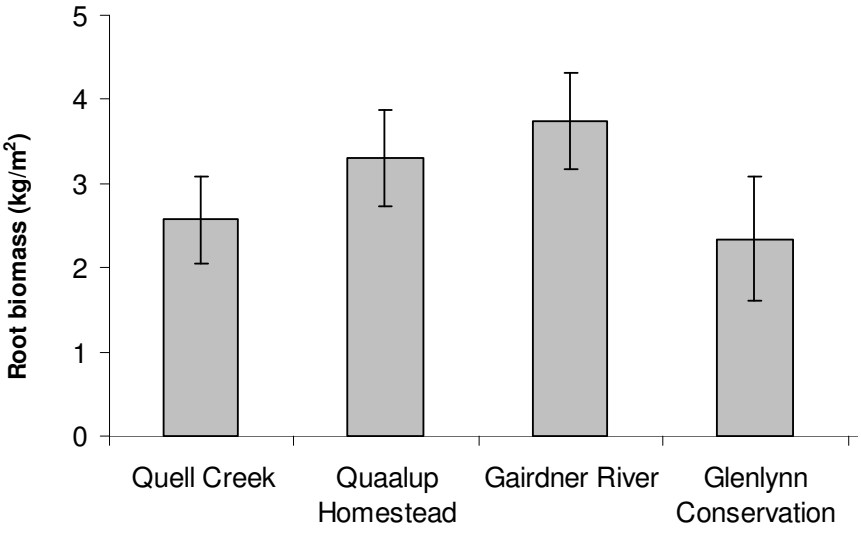


Figure 6.1. Dry weight of bridal creeper's total belowground biomass (mean $\pm$ s.e.) across four Western Australian sites.

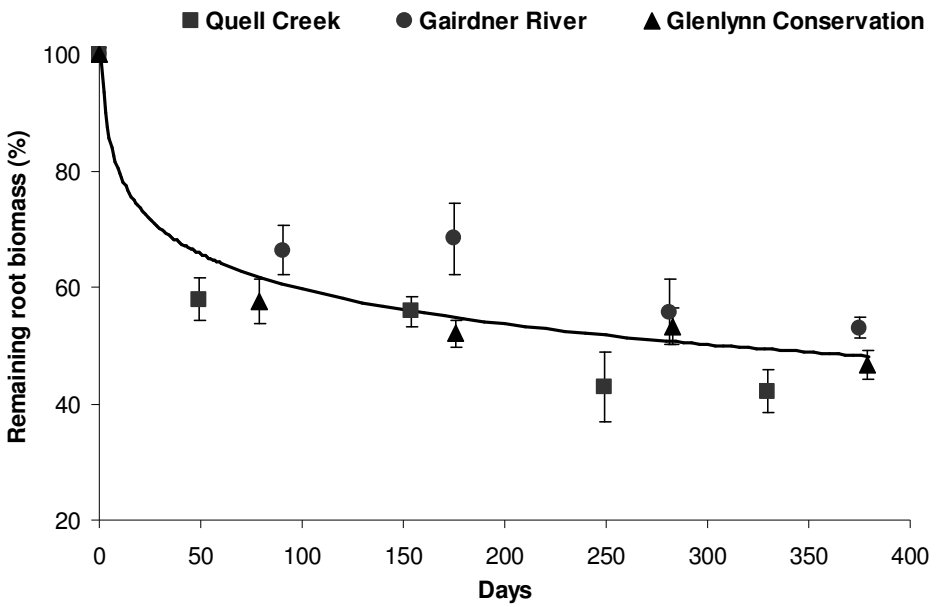
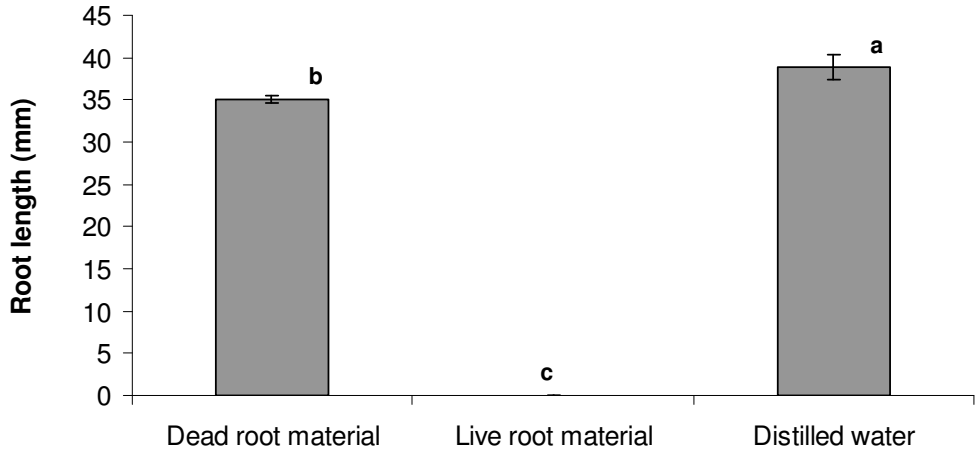


Figure 6.2. Decomposition of bagged bridal creeper belowground biomass across three Western Australian sites.

A significant negative relationship was evident across combined sites; $y = -8.66\ln(x) + 99.56$; $R^2=0.91$; $F=134.6$; d.f. 1,13; $p<0.001$.

a) - Cress seedlings



b) - Tomato seedlings

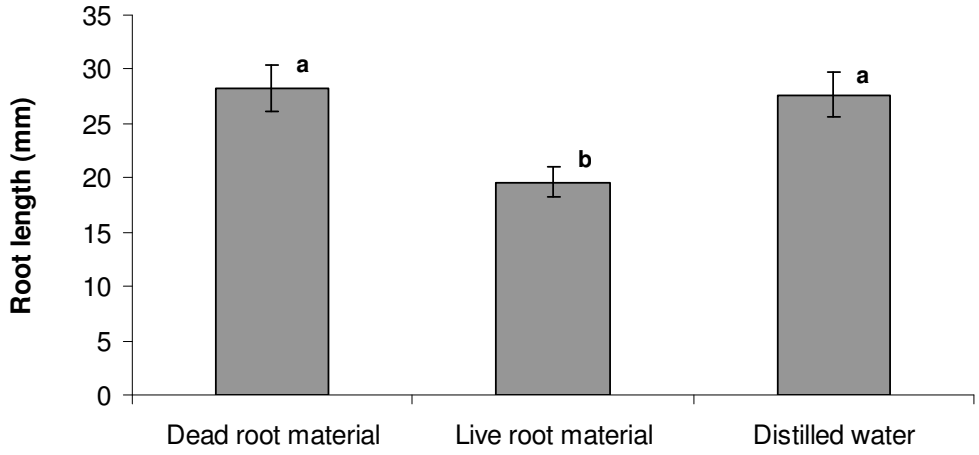


Figure 6.3. Average root length (± s.e.) of a) cress seedlings and b) tomato seedlings that germinated in solutions containing bridal creeper root material or a control of distilled water.

The same letter above bars indicates the root lengths that were not significantly different in *post hoc* Tukey tests.

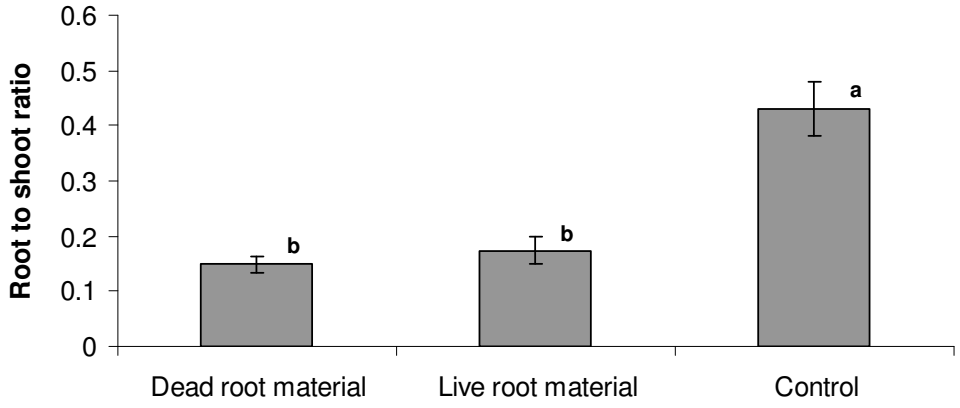


Figure 6.4. Average (± s.e.) root to shoot ratio of a native bluebell creeper when grown in pots with or without the presence of bridal creeper roots.

The same letter above bars indicates that the root to shoot ratios were not significantly different in *post hoc* Tukey tests.

Table 6.1. Nutrient element concentrations of the belowground root system of bridal creeper (dry weight, mean ± s.e.) collected from GC, QC, GR and QH and of the belowground storage organs and roots of other species.

Plant species (family)	**Location of collection**	**Nitrogen mg/g**	**Phosphorus mg/g**	**Potassium mg/g**	**Magnesium mg/g**	**Manganese mg/kg**	**Iron mg/kg**	**Source**
A. asparagoides, widespread form (Asparagaceae)	Southern W.A.	14.8 ± 0.4	1.0 ± 0.2	9.2 ± 0.5	3.1 ± 0.6	281 ± 111	7901 ± 633	This study
A. racemosus (Asparagaceae)	Northern W.A.	3.0	0.8	12.7	6.8	-	-	(Pate and Dixon, 1982)
94 geophyte species across 30 plant families	across all W.A.	13.1	1.2	17.1	1.8	-	-	(Pate and Dixon, 1982)
Haemanthus pubescens L.f. (Amaryllidaceae)	South Africa	13.5	11.8	19.6	0.2	59	280	(Ruiters, 1995)
Sparaxis grandiflora Ker Gawl. (Iridaceae)	South Africa	6.1	1.0	7.0	1.5	56	47	(Ruiters and McKenzie, 1994)
Anemone nemorosa L. (Ranunculaceae)	Sweden	-	-	15.2	3.9	941	2700	(Tyler, 1976)

- represents that the parameter not reported.

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CHAPTER SEVEN

TEN YEAR POST-FIRE RESPONSE OF A NATIVE ECOSYSTEM IN THE PRESENCE OF HIGH OR LOW DENSITIES OF THE INVASIVE WEED, *ASPARAGUS ASPARAGOIDES*

Key words: bridal creeper, environmental weeds, soil nutrients, succession, weed impacts

Abstract

Bridal creeper, *Asparagus asparagoides* (L.) Druce, is a major environmental weed in southern Australia. Being a geophyte, it has annual shoot growth with a large tuberous root mat belowground. It is capable of displacing native vegetation and has been targeted for control in Australia, especially using biological control. Previous studies on the impact of this environmental weed have suggested that without further restoration, invaded areas could take many years to recover. As fire can be used as a restoration tool, given it can stimulate the regeneration of some native Australian plants, this study aimed to determine the response of a native plant community for the first ten years following a fire, with and without the presence of bridal creeper.

Following a wildfire in March 1996, plots were established in a mallee remnant in South Australia. In October 1996, bridal creeper was controlled in half the plots using glyphosate. In 2006, there was still a significant difference in the density of bridal creeper, with 33.4 $\pm$ 5.0 (mean $\pm$ s.e.) emerging shoots m^{-2} in the untreated plots compared to 9.1 $\pm$ 1.2 shoots m^{-2} in the controlled plots. However at the same time, there was no significant difference in the native plant assemblages or with the number of native plant species between plots with high or low bridal creeper density, except for small shrubs, creepers and climbers which had higher cover in the untreated plots. A difference in soil nutrients was also evident. The soil where bridal creeper was not

controlled had significantly higher ammonium, potassium and organic carbon, compared to where bridal creeper was controlled. This study site, in the early stages of post-fire succession appears to be resistant to the impacts of bridal creeper, and from other weed species, with acacias and other native trees and shrubs dominating the site. It is therefore concluded that fire can be an important restoration tool that could be used in conjunction with weed management. Fire can be used to stimulate the regeneration of some native Australian plants and speed up the recovery of bridal creeper-invaded ecosystems, provided that bridal creeper and other weeds are kept at a low post-fire density, naturally or through targeted control.

Introduction

In Australia, bridal creeper is a Weed of National Significance (WONS) (Thorp and Lynch, 2000). A garden escapee, this geophyte is able to invade undisturbed native ecosystems (Hobbs, 1991; Raymond, 1995) and impacts or threatens many native plant species (see Downey, 2006; Fox, 1984; Sorensen and Jusaitis, 1995; Willis et al., 2003; Willis et al., 2004). For example, bridal creeper is the primary threat to the largest remaining population of the endangered shrub, *Pimelea spicata* R.Br. in the south-west of Sydney (Willis et al., 2003). Community impacts are also evident, with plant assemblages in areas invaded by bridal creeper in south west Australia containing 52% fewer native plant species compared to nearby native reference areas, that contained little or no bridal creeper (Chapter 3 - Turner et al., 2008c). In an eight year removal experiment, Turner & Virtue (Chapter 2 - 2006) established that bridal creeper could reduce biomass and abundance of native plants. However within this eight year timeframe, there was no significant change detected in native plant species richness following bridal creeper removal and only one saltbush, *Enchylaena tomentosa* R.Br., and native grasses showed significant increases in cover.

Luken (1997) recommended that management activities aimed at removing exotic plant species should involve the manipulation of both exotic and native species. Turner and Virtue (Chapter 2 - 2006) suggested that the minimal recovery of native species in their study could relate to a lack of suitable environmental conditions for germination and establishment of native species. Turner et al. (Chapter 3 - 2008c) also suggested that recovery of invaded sites may not occur after bridal creeper control. They established

that the readily germinable seed bank below bridal creeper in south west Australia contained very few native species compared to exotic species. Further studies were recommended to investigate the role of fire as a restoration tool following bridal creeper control; given that fire has an important role in the regeneration of some Australian native communities (Bell et al., 1993; Fisher, 1999; Shea et al., 1979). For example, seeds of a large number of native leguminous shrubs, such as acacias, require heat before germination occurs (Bell et al., 1993; McCaw, 1998; Shea et al., 1979) and therefore these species would not have been recorded in the readily germinable seed bank measured in Chapter 3. The use of fire as a restoration tool could help increase the germination rate of native species and may help tip the balance back towards native species, by increasing the ratio of native to exotic germinations (Chapter 3 - Turner et al., 2008c).

Turner and Virtue (Chapter 2 - 2006) also observed that dead bridal creeper tubers remained in the experimental plots eight years after the weed had been killed with herbicide, and this may have also impacted on native species recovery. Turner et al. (Chapter 6 - 2006) established that this belowground biomass, with its slow decomposition, may pose a problem for many years after control. As a way to deplete this root system, Willis et al. (2003) recommended that fire could be used to destroy the new season's foliage in autumn, followed by treating the re-growth with herbicide. However, Carr (1996) suggested that fire was not an appropriate management tool for bridal creeper as it stimulated bridal creeper growth and invasion. Fire has also been reported to promote the spread and density of a number of other exotic plant species (Adams and Simmons, 1991; Briese, 1996; Duggin and Gentle, 1998; Milberg and Lamont, 1995). In addition, when smoke water was used to promote the germination of the seed bank collected from bridal creeper sites (Chapter 3), it assisted in the germination of both native and exotic species. Therefore, the use of fire in bridal creeper management needed to be investigated given that it could promote further weed invasions.

The biology of bridal creeper has recently been described (see Morin et al., 2006a). In its native range in southern Africa, it mainly occurs as an understorey species and is usually found scrambling or climbing up other plants (Kleinjan and Edwards, 1999). Within Australia, bridal creeper has the potential to dominate native vegetation both

above and belowground, with climbing annual shoots and extensive belowground storage tubers (Raymond, 1996). However, simply reducing the presence of bridal creeper may not guarantee successful restoration of invaded areas and additional restoration efforts may be needed to ensure the protection of native vegetation (Chapter 3 - Turner et al., 2008c).

This paper reports on a complementary study to that of Turner & Virtue (Chapter 2 - 2006) which determined the impact by bridal creeper, by measuring the response of vegetation following the removal of bridal creeper. Similarly, the aim of this study was to measure the impact by bridal creeper on plant species and to measure their response to bridal creeper removal. However unlike the Turner & Virtue (2006) study, this study was conducted following a wild fire. Therefore, the study reported in this Chapter aimed to investigate the successionary pathway that occurred over the first ten years post-fire within a mallee community, with or without the presence of bridal creeper. As nutrient availability in the soil increases following fire (Handreck, 1997; Hobbs and Huenneke, 1992), this study also measured the impact of bridal creeper and of the fire on the soil nutrient status.

Methods

STUDY AREA

The study was undertaken in Meningie Hill Reserve, a mallee remnant community, south-east of Adelaide near the township of Meningie, South Australia 35°41'S, 139°21'E. Native vegetation within the reserve is dominated by an overstorey of *Eucalyptus diversifolia* Bonpl. and *E. incrassata* Labill., with large shrubs being mainly *Acacia* spp. and *Melaleuca lanceolata* Otto. In March 1996, a wildfire occurred in part of the reserve, burning most of the aboveground vegetation (including bridal creeper) except for woody trunks of the mallee eucalypts. The study site has calcareous, sandy soil with a south-westerly aspect.

Methods followed here were similar to Turner & Virtue (Chapter 2 - 2006), who undertook an eight year bridal creeper removal study near Owen, north of Adelaide. In August 1996, 30 (3 m × 3 m) plots were chosen, where the fire had burnt five months previously and where there was also an even coverage of bridal creeper. Bridal creeper

had re-sprouted from the belowground root system following the fire. Bridal creeper was then controlled in half the plots in October 1996, using 33% Roundup® (360 g/L glyphosate) with 2% Pulse Penetrant® (1,020 g/L polyether modified polysiloxane), applied by hand with a sponge to minimise off-target contact with native plants. These 15 plots were labelled as 'removal plots' and the untreated 15 plots were labelled as 'bridal creeper plots'. Between August 1996 and May 2006, vegetation was periodically sampled within the plots. In August 1996, the number of shoots of bridal creeper was recorded. This was repeated in November 1998 and May 2006. From April 1997, as native plants began to recover (re-sprouting and germinating) from the fire, the presence of all other plant species within the plots was recorded as well as the percentage areal shoot cover of each species. This was repeated in May 2002 and May 2006. At the end of the experiment in May 2006, the biological control agent, the bridal creeper rust was observed to be at an early stage of establishment at the study site.

Soil measurements were also taken in May 2006. From the centre of each of the 30 plots, soil cores were taken from below the bridal creeper tuber mats. Soil cores 5 cm deep and 5 cm in diameter were taken 5 cm below the litter layer. Cores from three proximal plots of the same treatment were bulked and any large organic matter was removed, such as tubers and other roots. Five samples per treatment were then forwarded in airtight containers to CSBP Laboratories (WA) for chemical analysis. Nitrogen (NO_3^- and NH_4^+), extractable phosphorus, potassium, organic carbon and pH were measured.

Also in May 2006, the soil sampling was repeated in a third treatment, an unburnt area adjacent to the burnt plots that had a similar pre-fire coverage of bridal creeper. Five additional soil samples were taken from this unburnt area. Ten 1 m × 1 m quadrats were selected in the unburnt section of the reserve, based on an even and dense cover of bridal creeper. The number of shoots of bridal creeper was recorded and two soil cores were taken from each quadrat and bulked. Soil samples from two quadrats were further bulked and a total of five samples from this unburnt area were also forwarded to CSBP Laboratories for analysis. Except for the number of shoots of bridal creeper, no other vegetation was measured within this unburnt area.

Statistical analysis was carried out using GenStat (2003). Transformations were applied when appropriate, via a log10 transformation, to meet the assumption of homogeneity of variances. If significant differences were found in the above soil analyses, it was followed by a pair wise Tukey comparison test (GenStat, 2003). Multivariate analysis was also used to compare the plant assemblages sampled in May 2006, to compare differences between removal (herbicide treated in the burnt area) plots and bridal creeper plots (untreated in the burnt area) (Primer 6, Clarke and Warwick, 2001). A Bray-Curtis similarity index on square-root transformed percentage cover of all plant species (excluding bridal creeper) was calculated to construct a rank-similarity matrix (see Clarke, 1993; Clarke and Warwick, 2001). ANOSIM (Analysis of Similarity) was used to determine differences in community composition between these herbicide treated and herbicide un-treated plots within the burnt area.

Results

Before treatments were applied, the number of bridal creeper shoots was not different between bridal creeper plots and removal plots in the burnt area ($F=0.75$; d.f. 1,28; $p=0.395$). In August 1996, the bridal creeper (untreated) plots had 29.7 ± 3.9 shoots m^{-2} (mean $\pm$ s.e.), while the removal plots had 25.5 ± 3.0 shoots m^{-2} prior to being treated with herbicide (Figure 7.1). Following the treatment and ten years later in 2006, there was a significant difference in the density of bridal creeper ($F=26.28$; d.f. 1,28; $p<0.001$), with 33.4 ± 5.0 emerging shoots m^{-2} in the bridal creeper (untreated) plots compared to 9.1 ± 1.2 shoots m^{-2} in the removal (herbicide treated) plots. The maximum number of bridal creeper shoots in a bridal creeper plot was 77.9 ± 12.4 shoots m^{-2}.

Six months after the herbicide treatment was applied, in April 1997, the mean cover of native plant species was similar between bridal creeper plots and removal plots (Figure 7.2). In May 2006, there was no significant difference in the number of native plant species between treatments (Table 7.1). There were also no significant differences in cover of individual groups of native or exotic plant species, except for native small shrubs and native climbers and creepers, where their cover was higher in the bridal creeper (untreated) plots (Table 7.1 and Figure 7.2). In contrast, the year immediately following the application of glyphosate (1997) there was no significant difference in the cover of these native small shrubs ($F=0.17$; d.f. 1,28; $p=0.684$, Figure 7.2) and the cover

of these native climbers and creepers (log10 transformed; F=0.45; d.f. 1,28; p=0.509, Figure 7.2) between bridal creeper plots and the removal plots. In 1997, native small shrubs averaged 1.02% $\pm$ 0.30 in the bridal creeper plots and 0.84% $\pm$ 0.30 in the treated removal plots, while native climbers and creepers averaged 2.47% $\pm$ 1.36 in the bridal creeper plots and 1.34% $\pm$ 0.41 in the removal plots.

In May 2006, there was no significant difference in the native plant assemblages between treatments (ANOSIM R=0.017; p=0.274, Figure 7.3). Acacias and large shrubs and trees dominated both treatments in 2006. Combined cover of these large woody native plants within the bridal creeper plots averaged 46.5%, while in the removal plots this averaged 55.0%; yet there was no significant difference between treatments (Table 7.1).

Even though no differences were detected in the native plant assemblages, the soil in the burnt area beneath the herbicide untreated plots (bridal creeper plots) had significantly more ammonium, potassium and organic carbon compared to the burnt, removal (herbicide treated) plots, ten years after the fire (Table 7.2). The additional plots sampled in the unburnt area, which contained bridal creeper, had a significantly higher pH and lower organic carbon and ammonium in comparison to the burnt bridal creeper plots. The areas where the soil was sampled had different abundances of bridal creeper, with the burnt bridal creeper and unburnt plots having approximately eight and twenty times the number of shoots found in the burnt removal plots respectively (Table 7.2). In the burnt area, the bridal creeper centre sub-plot (1 m x 1 m) had 38.2 $\pm$ 7.2 shoots m^{-2} (mean $\pm$ s.e.); the removal centre sub-plot had 4.8 $\pm$ 1.0 shoots m^{-2}; while in the unburnt area, the ten additional quadrats averaged 94.0 $\pm$ 9.4 shoots m^{-2}.

Discussion

Originally the aim of this experiment was to investigate the successionary pathway that occurred ten years post-fire in a mallee community, with or without the presence of bridal creeper. However, bridal creeper had begun to recover in the removal (herbicide treated) plots, to a density of 9.1 $\pm$ 1.2 shoots m^{-2} in 2006. This was still significantly lower than in the untreated plots, therefore this study measured the response of the plant community following a fire in the presence of high and low densities of bridal creeper.

However, the density of this invasive weed did not influence the post-fire response of vegetation within this mallee ecosystem, with acacias and other native trees and shrubs dominating the site 10 years post-fire.

An invader may have a large effect in one area, but a negligible effect in other areas (Byers et al., 2002). In portions of the adjacent, unburnt area, bridal creeper density was relatively high, similar to that observed at the Owen site (referred to in Chapter 2 - Turner and Virtue, 2006) which had an average of 87.8 $\pm$ 8.8 shoots m^{-2} in 2004 (mean $\pm$ s.e.; Turner and Virtue unpub.). However, whilst not directly measured, individual shoots were shorter throughout the whole Meningie site compared to Owen, with the former site appearing to have less bridal creeper aboveground biomass and rarely having tall 'curtains' of bridal creeper shoots. The whole study site at Meningie may be less suitable for bridal creeper compared to the Owen site. Hester and Hobbs (1992) established a strong correlation between soil phosphorus and abundance of exotic species. The Owen site had available soil phosphorus in the range of 10.8-13.8 mg/Kg (Table 2.4 - Turner and Virtue, 2006), compared to 3.6-6.0 mg/Kg at the Meningie site (Table 7.2). Lower soil phosphorus, combined with reduced aboveground biomass, may partly explain the lack of competitive effects observed in this post-fire experiment. However, in some parts of the unburnt area at this Meningie study site, there were low levels of phosphorus (Table 7.2) and bridal creeper abundance was relatively high, averaging 94.0 $\pm$ 9.4 shoots m^{-2}. Therefore, at this Meningie study site, bridal creeper was still able to achieve a high abundance in some of the unburnt area that had relatively low soil nutrients. Therefore, it is likely that the native vegetation, being the primary post-fire successional species such as acacias, were able to at least partially suppress bridal creeper in the areas that were burnt.

It appears, from the several studies reported in this thesis that have investigated the response of plant communities to bridal creeper control, that impacts and the recovery of native vegetation as well as the response of secondary invaders are site specific and depend on the history of the site and its current successionary state. At the Owen site in South Australia, Turner and Virtue (Chapter 2 - 2006) reported an increase in biomass of chenopods but overall there was no difference in the number of species following bridal creeper control. There was also an increase in the exotic *Oxalis pes-caprae* L. eight years after this control. Similar to this Meningie study, four sites in a southern

Western Australia study, showed no overall significant increase in exotic cover following bridal creeper control (Chapter 8). In the Western Australia study, in bridal creeper invaded plots, cover of other exotic species (excluding bridal creeper cover) increased from 4.2% in 2004 to 12.8% in 2006 following the biological control of bridal creeper; however this was comparable to the exotic cover in the nearby uninvaded reference plots at the same time in 2006 (Chapter 8 - Turner et al., 2008b). Yet, at one of the Western Australia sites, Quell Creek, Turner et al. (2008b) reported an increase in exotic cover from 0.03% to 23.4% following the biological control of bridal creeper.

In this Meningie study, native small shrubs, creepers and climbers had higher cover in the bridal creeper plots compared to the removal (herbicide treated) plots (Table 7.1). These species could be responding to the higher nutrients found below bridal creeper. In Western Australia, at the same study site mentioned above, Quell Creek, Turner et al. (Chapter 8 - 2008b) also reported that native climbers had increased from 0.07% to 5.0% and that this cover of native climbers was higher than the nearby native reference plots at the same time in 2006, being only 0.8% (Turner et al., 2008b). In this Western Australia study, at Quell Creek, the bridal creeper invaded plots had higher soil nutrients than the nearby native reference plots (see Table 4.2) and following biological control, native climbers had six times greater cover in the higher nutrient soil (Chapter 8). This is also supported by a glasshouse trial that established that a native climber, a *Billardiera* species (bluebell creeper), had increased growth rates with increases in soil fertility (Figure 4.2).

An alternative hypothesis for the higher cover of native small shrubs, creepers and climbers in the bridal creeper plots compared to the removal (herbicide treated) plots at this Meningie site is that they may have been accidentally killed by the herbicide application in the removal plots during the initial bridal creeper removal in 1996. Whilst due care was taken to only target bridal creeper, there may have been inadvertent contact with some regenerating native species. However, it is assumed that the off-target impacts were minimal given that there was no significant difference in the cover of native small shrubs, creepers and climbers in 1997, a year following the application of glyphosate. Even so, the differences in cover of these native species may not be ecologically significant (although statistically significant between treatments in 2006),

given the differences recorded relate to a difference in cover of only one to two percent between treatments and between 1997 and 2006 (Figure 7.2).

Nutrient availability in the soil is usually only increased for a short time following fire (Handreck, 1997; Hobbs and Huenneke, 1992). Bridal creeper may be able to permanently capture and retain the nutrients released during the fire by trapping nutrients and organic material with its dense tuberous root mat (Chapter 6 - Turner et al., 2006) and recycling them through its annual senescence (Chapter 5). This may explain the differences in nutrient levels between the burnt bridal creeper plots and the burnt removal plots in this study (Table 7.2). Carr (1996) suggested that fire was not an appropriate management tool for bridal creeper as it stimulated bridal creeper growth and invasion. Given this, fire should not be used as a sole control measure for bridal creeper, as bridal creeper will re-shoot and trap the nutrients released during the fire. This could over time transform the community and move it further away from its restoration goals. Therefore, fire is only suitable if used in conjunction with other restoration and control techniques, such as those recommended by Willis et al. (2003).

It seems plausible that the native vegetation was able to suppress bridal creeper and other weeds in the burnt study area, for the ten years following the single disturbance event, being a wild fire. However, in the absence of future fires, it has been reported that populations of native legume species (including acacias) decline, as adults die at the end of their normal life span of approximately four to 15 years without seedling recruitment (Fogarty and Facelli, 1999; McCaw, 1998; Shea et al., 1979). Therefore this site may become more vulnerable to invasion at a later successional stage. The burnt areas where bridal creeper was not controlled could be more vulnerable to invasion by other weeds or to an increase in the density of bridal creeper, given the differences observed in the soil nutrients (for example see Lake and Leishman, 2004). Following the decline of early post-fire species, such as acacias, areas with the higher nutrient levels may be replaced with those species (native and exotic) that respond more favourably to higher nutrient soils. These would include a suite of exotic species.

Biological control agents have been released in Australia to control bridal creeper (Morin et al., 2006b; Chapter 8 - Turner et al., 2008b). Briese (1996) suggested that fire and biological control may not be compatible strategies for weed management in native

areas, although a personal observation in a Tuart woodland in Yanchep National Park (north of Perth, 31.533S, 115.683E) following a high intensity fire in January 2005, indicate they can be compatible. The biological control agent, the bridal creeper rust (*Puccinia myrsiphylli* (Thuem.) Wint.) exhausts the fleshy tuberous root system of bridal creeper (Morin et al., 2002; Turner et al., 2004). At Yanchep National Park, it appeared that the fire, following five years of biological control, was able to burn most of the senesced root system. In addition, in November 2005, the biological control agents were observed to have re-colonised bridal creeper plants that had survived or germinated since the fire. However, more research into this area is needed, given that fire is a natural occurrence in most Australian ecosystems and weeds that have invaded these native ecosystems are increasingly becoming targets for biological control (McFadyen, 1998).

Because fire is a disturbance, it may increase the chances of weed invasion (Adams and Simmons, 1991; Fox and Fox, 1986; Milberg and Lamont, 1995). However, no exotic species benefited following the fire or following the control of bridal creeper during this study at Meningie. Exotics other than bridal creeper only averaged a maximum of 3.45% cover (Table 7.1) and native species dominated suggesting that fire did not decrease the site's resilience. Weed species present at the site but remaining at low density included *Ehrharta calycina* Sm., *Brassica tournefortii* Gouan and *Freesia* sp. Thomson and Leishman (2005) found that fire did not promote invasion into areas that were non-nutrient enriched. This is supported by Hester and Hobbs' (1992) suggestion that fire does not necessarily increase weed invasion and was a useful management tool in remnant vegetation in Western Australia. The Meningie study was undertaken at only one site however and further research is recommended, given that the outcomes may vary across sites depending on timing of fire, fire intensity, pre-fire invasion status and soil quality.

Fire can be an effective tool when used in conjunction with other control techniques (Willis et al., 2003). However, in highly disturbed roadside remnants and those areas that have elevated soil nutrient levels, the use of fire may promote exotic species (for example see Milberg and Lamont, 1995; Thomson and Leishman, 2005). The degree of weed invasion could change depending on fire frequency and intensity as well as season of the burn, for example a spring versus autumn burn (Hobbs and Huenneke, 1992).

This study indicates that fire can be an important restoration tool to stimulate the regeneration of native Australian plants and speed up the recovery of bridal creeper invaded ecosystems, provided that bridal creeper and other weeds are kept at a low post-fire density, naturally or through targeted control. Research into the use of fire for restoration of bridal creeper invaded sites was listed as a high national priority that was to be addressed under the bridal creeper national (WONS) strategic plan (Gannaway and Virtue, 2006). Further research is now needed to confirm the suitability of fire across a range of bridal creeper sites throughout southern Australia.

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Figure 7.1. The abundance of bridal creeper across the period of the study.

The bridal creeper plots (untreated with herbicide) and the removal plots (herbicide treated) were all located within the burnt area of the study site. The removal plots were treated with glyphosate two months following the 1996 measurements. Bridal creeper abundance was not recorded in the years not shown. In 2006, there was a significant difference in the density of bridal creeper between bridal creeper plots and removal plots ($F=26.28$; d.f. 1,28; $p<0.001$).

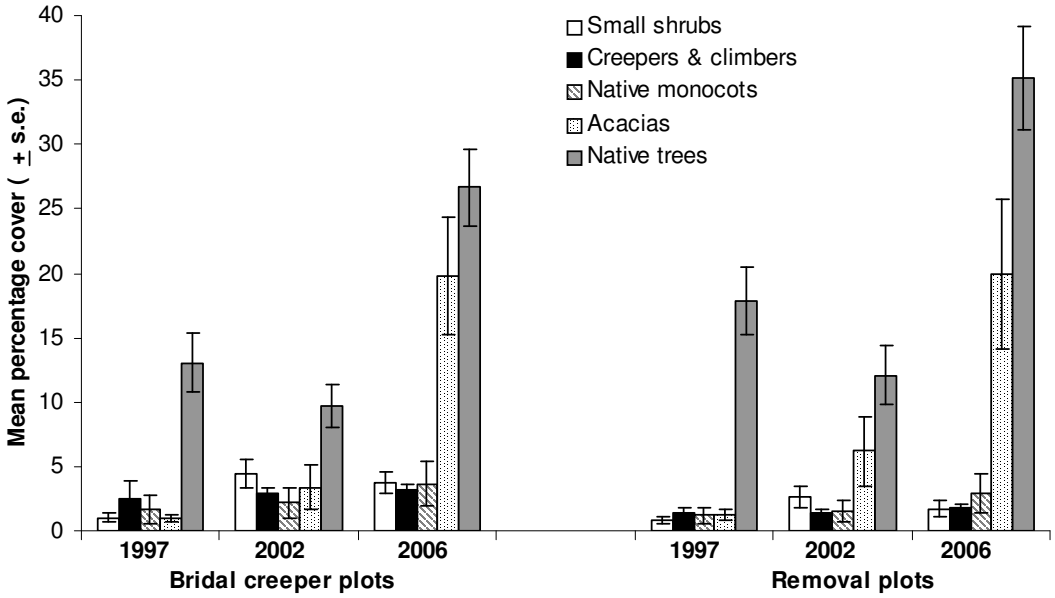

Figure 7.2. Percentage cover of native species in 1997, just after the treatment was applied, and in 2002 and 2006 at the completion of the experiment.

Bridal creeper plots are the untreated plots. Native trees are a combination of *Eucalyptus diversifolia* Bonpl., *E. incrassata* Labill. and *Melaleuca lanceolata* Otto. Acacias are a combination of *Acacia paradoxa* DC. (primarily), *A. pycnantha* Benth. and *A. longifolia* (Andrews) Willd. Native monocots are mainly a combination of *Dianella revoluta* R.Br., *Xanthorrhoea caespitosa* D.J. Bedford and orchids. Creepers and climbers were dominated by *Billardiera cymosa* F.Muell. and *Carpobrotus modestus* S.T.Blake. Small shrubs were dominated by *Thomasia petalocalyx* F. Muell., with fewer *Rhagodia* sp., *Dampiera* sp. and *Hibbertia* sp.

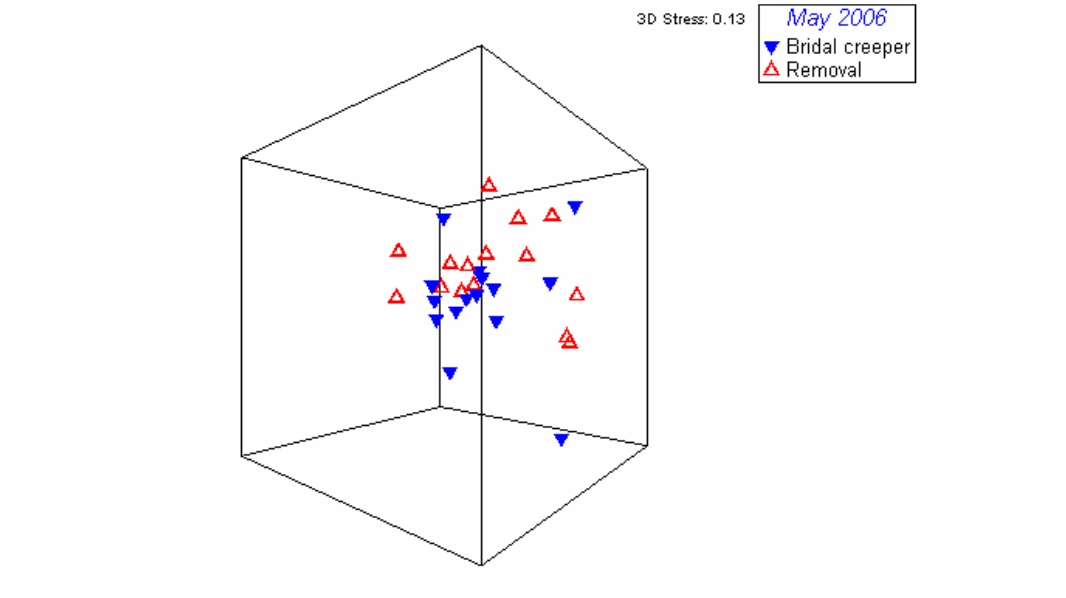

Figure 7.3. Individual plots shown in a three-dimensional ordination (non-metric multi-dimensional scaling).

The relative distance between plots (represented by triangles) represent the degree of dissimilarity of plant assemblages between plots at the end of the study period in May 2006. Analysis of similarity revealed no significant difference between bridal creeper plots (untreated) or removal plots (herbicide treated): Sample statistic (Global R): 0.017, p=0.274.

Table 7.1. Differences in number of native species per plot (mean ± s.e.) and plant cover (%) between treatments in May 2006[A].

Variable	Bridal creeper (untreated) plots	Removal (treated) plots	F	p
No. of native species	11.20 ± 0.62	10.33 ± 0.41	1.36	0.253
Cover of:				
Native small shrubs[C]	3.73 ± 1.08	1.68 ± 0.61	5.46	0.027[B]
Native creepers & climbers	3.16 ± 0.47	1.82 ± 0.28	7.16	0.012[B]
Native monocots	3.65 ± 1.70	2.95 ± 1.50	0.19	0.668
Native acacias	19.75 ± 4.59	19.89 ± 5.79	0.67	0.419
Other native trees & large shrubs	26.70 ± 2.97	35.14 ± 4.03	2.84	0.103
Exotic grasses and bulbs[D]	3.45 ± 1.20	1.45 ± 0.27	3.06	0.091

[A] The analysis of variance models with treatment (n=15) as the only factor. A log10 transformation was applied to all variables, except no. of native species and native trees and large shrubs before the analysis.

[B] Statistically significant ($p<0.05$).

[C] See Figure 7.2 for description of native groups.

[D] Exotic grasses and bulbs were dominated by veldt grass (*Ehrharta calycina* Sm.) and *Freesia* sp.

Table 7.2. Differences in mean (± s.e.) soil variables between treatments in May 2006[A]. In 2006, the abundance of bridal creeper differed between plots and therefore the abundance is also documented below.

Soil variable	Burnt bridal creeper plots	Burnt removal (herbicide treated) plots	Unburnt bridal creeper area	F	p
Nitrate (mg/Kg)	5.60 ± 1.57	5.20 ± 0.20	2.60 ± 0.60	3.70[B]	0.056
Ammonium (mg/Kg)	5.80 ± 1.46[b]	2.40 ± 0.24[a]	2.60 ± 0.24[a]	5.75[B]	0.018
Phosphorus (mg/Kg)	6.00 ± 1.22	3.80 ± 0.20	3.60 ± 0.40	3.02[B]	0.087
Potassium (mg/Kg)	165.6 ± 28.9[b]	83.8 ± 7.0[a]	101.2 ± 5.8[ab]	6.06	0.015
Organic carbon (%)	4.29 ± 0.43[b]	1.87 ± 0.18[a]	1.64 ± 0.32[a]	20.02	<0.001
pH	6.86 ± 0.24[b]	7.62 ± 0.21[ab]	8.10 ± 0.18[a]	8.75	0.005
Bridal creeper (shoots m^{-2})	38.2 ± 7.2[*]	4.8 ± 1.0[*]	94.0 ± 9.4		

The burnt bridal creeper plots (untreated with herbicide) and the removal plots (herbicide treated) were all located within the burnt area of the study site

[A] The analysis of variance models with treatment (n=5) as the only factor.

[B] Log10 transformation applied.

[*] This abundance relates to the centre 1 x 1 m of the plot, where the soil cores were taken.

Different letters after s.e. relate to significant difference at 0.05 based on Tukey Multiple Comparisons Tests.

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CHAPTER EIGHT

IMPLICATIONS OF SUCCESSFUL BIOLOGICAL CONTROL OF BRIDAL CREEPER (*ASPARAGUS ASPARAGOIDES* (L.) DRUCE) IN SOUTH WEST AUSTRALIA

Key words: conservation, evaluation, reference sites, succession, weed substitution

Abstract

The assessment of environmental weed control programmes must encompass more than measurements of weed density reduction. Measurements are also needed on the vegetation that replaces the target weed. Bridal creeper (*Asparagus asparagoides* (L.) Druce) has invaded a variety of habitats across southern Australia. The only viable option for widespread control is the use of biological control agents. I report that the biological control agent, the bridal creeper rust (*Puccinia myrsiphylli* (Thuem.) Wint.), is having a significant impact on bridal creeper in south west Australia. However, following the biological control of bridal creeper, with a reduction in bridal creeper cover from 49.9% $\pm$ 4.4 (mean $\pm$ s.e.) to 10.2% $\pm$ 2.7, there has been little change in native plant cover. At one site however, the cover of other exotic species had increased from 0.03% $\pm$ 0.03 to 23.4% $\pm$ 6.7 following the biological control of bridal creeper. Also at this same site, native climbers increased from 0.07% $\pm$ 0.07 to 5.0% $\pm$ 2.2.

Although there was a reduction in cover of bridal creeper, it may take many years for the belowground tuberous mats of this weed to be exhausted at sites where bridal creeper has been present over the longer term. Another major barrier to restoring invaded areas is the invasion or increase in density of other exotic plant species. However, at other sites where bridal creeper is at the early stages of invasion or at sites that are yet to be invaded by bridal creeper, the biological control programme will aid in

the protection of these sites from the ecological impacts of bridal creeper. At sites where bridal creeper has been established for a long period of time, a more holistic approach is needed in conjunction with the successful biological control of bridal creeper. This should include the identification of sites with high conservation value, where biological control should be used in combination with other restoration techniques. This would involve targeting all undesirable exotic species while encouraging native species recovery.

Introduction

Serious environmental weeds have an impact on native biodiversity, and control measures, including biological control, are sought to reduce these impacts. Monitoring of community-level effects should accompany biological control releases into native ecosystems (Lesica and Hanna, 2004; Lonsdale et al., 2001), as the desired outcome of biological control should include the indirect effects of increased diversity and abundance of native species (Denslow and D'Antonio, 2005). To measure these effects a biological control programme needs to be evaluated beyond assessing an agent's release, establishment and the subsequent decrease in the target weed, to showing that the impacts to native biodiversity have been reduced.

In Australia, the environmental weed bridal creeper, a Weed of National Significance (WONS) (Thorp and Lynch, 2000), has been targeted for biological control (Morin et al., 2006b). In June 2000, the bridal creeper rust, *Puccinia myrsiphylli*, which destroys the tissue of bridal creeper's cladodes and causes early defoliation, was approved for release (Morin et al., 2002). Kleinjan et al. (2004b) have documented its life cycle in South Africa and Morin et al. (2006b) have documented the life cycle and the initial impact of this agent within Australia. The biological control agent, bridal creeper rust, has now been released at more than 1,700 sites across southern Australia (Morin et al., 2006b). Of the three biological control agents that have been released in Australia to control bridal creeper, the bridal creeper rust has readily established throughout southern Australia and is causing a significant and rapid reduction in bridal creeper density (Morin and Edwards, 2006; Morin et al., 2006b).

Before the bridal creeper rust could impact significantly on the density of bridal creeper, the impacts of bridal creeper were determined at four sites in south west Australia. Areas invaded by bridal creeper contained fewer native species than nearby reference areas (Chapter 3 - Turner et al., 2008c). The plots established during this study were continued and vegetation was monitored following the release of the bridal creeper rust at these sites. The response of the plant communities following the initial stage of the biological control of bridal creeper is reported here.

Methods

This study was undertaken at four sites across south west Australia. Within each site, plots were established in stands of bridal creeper and in nearby reference areas. These reference areas were within native vegetation with little or no bridal creeper present (see Chapter 3 - Turner et al., 2008c for full description of sites and plots). Reference areas represent the target for restoring invaded sites (Blossey, 2004; Chapman, 1999).

In 2004, each of the four sites contained relatively homogeneous stands of bridal creeper of a sufficient size to accommodate at least two 10 x 1 m plots, separated by at least 10 m. Two of the sites had larger bridal creeper infestations, allowing for three plots to be established within each bridal creeper stand, while at the other two sites, two plots were established. This represented a total of ten bridal creeper plots. Each of these plots were paired to a reference plot (also 10 x 1 m) located directly adjacent to the bridal creeper areas and at least 10 m away from other plots.

Plots within both bridal creeper and reference areas were established in October 2004. At this time, all vascular plant species were identified and percentage areal shoot cover of the understorey (to a maximum height of 1.5 m) was estimated visually for each species within each plot. The methods and results for this survey are presented in Chapter 3 - Turner et al. (2008c). During October 2004, when the first vegetation surveys were undertaken, all sites were either free of the bridal creeper rust or there was only a small amount of infection (<5% cladode damage), with the rust colonising two of the sites in that year (P. Turner, unpublished data). As these sites were yet to come under substantial attack from the rust, in June 2005 the rust was released in the centre of

each bridal creeper stand at each site. Additional rust spores may have also naturally dispersed into sites, given that other releases had been made nearby.

In September 2006, the sites were revisited and all vascular plant species were identified and the cover of the understorey estimated, again using the same methods as described above. For a before and after comparison, across the four invaded (bridal creeper) areas, one-way analysis of variances (ANOVA) were undertaken to compare the change in cover of exotic and native plants between the two surveys. In addition, the influence of site (GC, QC, QH and GR) and area (bridal creeper or reference) on percentage cover and species number, measured in 2006 following the release of the biological control agent, of both exotic and native species, was analysed using two-way ANOVAs (GenStat, 2003).

Results

Between 2004 and 2006, average bridal creeper cover had decreased from 49.9% $\pm$ 4.4 (mean $\pm$ s.e.) to 10.2% $\pm$ 2.7 within the bridal creeper areas (Figure 8.1). Even in the reference areas, bridal creeper cover had decreased from 2.3% $\pm$ 0.9 in 2004 to 0.6% $\pm$ 0.1 in 2006.

As bridal creeper cover decreased, the cover of other exotic species increased, although this was not significant ($F=3.56$; d.f. 1,6; $p=0.108$). In the bridal creeper invaded plots, the cover of other exotics increased from 4.4% $\pm$ 1.6 in 2004 to 13.8% $\pm$ 2.9 in 2006 (Figure 8.2 and Table 8.1). However, this was comparable to the exotic cover in the reference plots at the same time in 2006 (10.0% $\pm$ 2.7). There was no change in the cover of native species ($F=0.75$; d.f. 1,6; $p=0.420$), with total native cover in bridal creeper plots in 2004 averaging 22.0% $\pm$ 4.0 and in 2006 cover was 26.8% $\pm$ 3.5.

In 2006 following the initial stages of control, there were on average 6.6 $\pm$ 0.7 exotic species in bridal creeper plots and 6.3 $\pm$ 0.5 in reference plots, which was not significantly different ($F=0.09$; d.f. 1,12; $p=0.774$, Figure 8.3a and Table 8.1). In 2004 before control, there were on average 3.6 $\pm$ 0.8 exotic species in bridal creeper plots and 4.0 $\pm$ 0.6 in reference plots, which was again was not significantly different ($F=0.34$;.d.f. 1,12; $p=0.572$, Figure 3.2b). In 2006, the cover of all exotic species

excluding bridal creeper in reference areas was 10.0% ± 2.7, compared to 13.8% ± 2.9 in the bridal creeper areas. There was however, a significant interaction between site and area for cover of exotic species (F=4.7; d.f. 3, 12; p=0.021, Figure 8.3b). The cover of all exotic species excluding bridal creeper, was not statistically different in 2004, with exotic cover in reference areas being 10.1% ± 3.4, compared to 4.4% ± 1.6 in the bridal creeper areas (after square root transformation F=4.11; d.f. 1, 12; p=0.065, Figure 3.2c).

The significant interaction between site and area for cover of exotic species in the 2006 survey was mainly influenced by the changes in cover at one site. In the most isolated site, Quell Creek (QC), there was a dramatic increase in the cover of other exotic species. At this site, although bridal creeper cover had decreased from 60.3% ± 7.3 to 9.8% ± 2.3, cover of other exotics had increased from 0.03% ± 0.03 to 23.4% ± 6.7, compared to only 3.8% ± 0.5 in the reference areas in 2006 (Figure 8.3b). The main exotic species that increased in the bridal creeper area at QC was fleabane (*Conyza bonariensis* (L.) Cronquist). In 2006, fleabane had 15.4% ± 7.5 cover in bridal creeper plots at QC and 0.3% ± 0.2 cover in the reference plots.

In 2004, both the mean number of native plant species and the percentage cover of all native understorey plants were significantly lower in bridal creeper areas compared to reference areas (F=82.66; d.f. 1,12; p<0.001, Figure 3.3a and F=30.31; d.f. 1,12; p<0.001, Figure 3.3b respectively). In 2006 following the initial stages of control, both the mean number of native plant species and the percentage cover of all native understorey plants were still significantly lower in bridal creeper areas compared to reference areas (F=21.75; d.f. 1,12; p<0.001, Figure 8.4a and F=12.64; d.f. 1,12; p=0.004, Figure 8.4b respectively). In 2006, bridal creeper plots averaged 9.0 ± 1.6 native species while reference plots averaged 15.7 ± 0.7, while the cover of native understorey was 26.8% ± 3.5 in the bridal creeper plots and 42.4% ± 3.9 in the reference plots (Table 8.1). But again at QC, native climbers had increased from 0.07% ± 0.07 in 2004 to 5.0% ± 2.2 in 2006. In contrast, in reference plots at QC in 2006, native climbers averaged only 0.8% ± 0.3.

Discussion

The biological control programme for bridal creeper is already being considered as one of the most successful in Australia (Morin and Edwards, 2006) and my study supports this. In less than two years there has been a dramatic decrease in the cover of bridal creeper at my sites. Even the small bridal creeper cover observed in 2004 in the reference areas has been reduced. As the bridal creeper rust reduces and in most cases prevents flowering and fruiting of bridal creeper (Morin et al., 2006b and personal observation), it is highly likely that this biological control programme has lead to the protection of these reference sites and will prevent the invasion of bridal creeper into new areas. Therefore, sites that are at an early stage of bridal creeper invasion and sites where bridal creeper could potentially invade, but has yet to do so, would most likely be protected from the impacts of bridal creeper due to this biological control programme.

While studies of the response of native plant communities to weed biological control are rare, the few studies that have undertaken this monitoring have had varying results (Denslow and D'Antonio, 2005), with results depending on individual site conditions (Lesica and Hanna, 2004). Denslow and D'Antonio (2005) reported that in some cases there was an increase in native species diversity, while other cases showed that biological control led to the replacement of the target weed with secondary invaders. The Quell Creek site, and a site reported in Turner and Virtue (Chapter 2 - 2006) had increases in cover of other exotic species following the control of bridal creeper. The latter site had an increase in the exotic *Oxalis pes-caprae* L. eight years after herbicide control. Thus both sites will require additional restoration, in the form of further weed control of secondary invaders, following the control of bridal creeper.

The bridal creeper rust has had a significant impact on bridal creeper across my four sites in south west Australia. Although long-term monitoring is needed to fully evaluate the response of other plant species to the control of bridal creeper, these early results already suggest that both exotic species and a set of native species (especially at Quell Creek) benefit from the control of bridal creeper. Given that it has only been a relative short time to measure the response of vegetation, a companion to this study is presented in Chapter 9 which documents the changes in ant assemblages at these sites over this same period. In the past in Australia, ants have been used as bioindicators to evaluate

land degradation and restoration processes and to assist in the assessment of ecosystems (Andersen, 1990). This is possible as ants are highly sensitive to environmental variables and respond rapidly to environmental change. In addition, a three year bridal creeper rust exclusion experiment, which I helped establish in Western Australia in June 2005, and which has also been established in New South Wales (Morin et al., 2006b), will complement this study when completed.

I also await the results from long term monitoring on the vegetative growth and reproduction of bridal creeper that was established before and after the release of the biological control agents. Permanent trellises were established in 1999 across southern Australia to gather these data (Morin et al., 2002; Stansbury et al., 2007). However, what is evident from my study is the value of reference sites and these may be more useful than, or at least complement, before and after comparisons. For example when comparing bridal creeper plots, in 2004 the exotic cover was 4.4% and following control it had increased to 13.8% (Table 8.1). It could be argued that there has been a three-fold increase in exotic cover. However, the exotic cover in 2006 in the reference areas was comparable to the 2006 measurements in the bridal creeper plots. Similarly, it can be shown that the number of native species in the bridal creeper plots had nearly doubled during the two years (4.9 to 9.0 – Table 8.1). Yet, 15.7 native species were found in the reference areas in 2006. As each sampling year would have experienced different climatic events, this would confound any before and after comparisons. For example, in Chapter 3 it was established that eighteen exotic species, being autumn and winter germinating annual herbs or grasses, were absent in the 2004 vegetation survey, but were found in the seed bank. Exotic species which were rare or absent in the 2004 vegetation survey, but were in larger numbers in the seed bank and more abundant in the 2006 surveys included exotic grasses such as *Bromus diandrus* Roth and other autumn and winter germinating annual herbs (Wheeler et al., 2002), such as *Arctotheca calendula* (L.) Levyns (cape weed) and *Anagallis arvensis* L. (pimpernel).

One of the main goals of the bridal creeper biological control programme in Australia was to reduce bridal creeper densities to a level at which infestations no longer threaten native biodiversity (Morin et al., 2002). However, when the results from this study are coupled with other studies, indications are that further restoration will be needed, at least at some sites. Many barriers to the recovery of the native vegetation exist in bridal

creeper invaded areas, including bridal creeper's dense tuberous root mat that can remain in the soil long after control (Chapter 6 - Turner et al., 2006), a germinable seed bank in invaded areas that contains a large number of exotics (Chapter 3 - Turner et al., 2008c), as well as elevated soil nutrients in invaded areas (Chapter 4). In Australia, soil nutrient enrichment has been shown to favour exotic species and many exotic species in the seed bank at these study sites will readily germinate (Chapter 3 - Turner et al., 2008c). In contrast, many native species may require specific conditions for germination (see Chapter 2 - Turner and Virtue, 2006; and Chapter 7 - Turner and Virtue, in press). Given this, biological control needs to be coupled with other restoration techniques.

Ecosystem restoration was identified as the main priority for bridal creeper management in Australia following the National Asparagus Weeds Management Workshop in November 2005 (Gannaway and Virtue, 2006). It was suggested that this restoration could be applied within high priority biodiversity areas that were invaded by this weed. However, to date these areas have not been identified. Yet a method for identifying these high conservation areas is available and has been demonstrated for two other WONS (Turner et al., 2008a) and the first step in this approach has already been trialled for *Asparagus* weeds (Downey, 2006). The biological control of bridal creeper in south west Australia has been successful. Failure to identify these high priority areas as well as the additional restoration that may be required at each site may see many sites change from bridal creeper dominance to dominance by secondary, exotic invaders following the successful biological control of bridal creeper.

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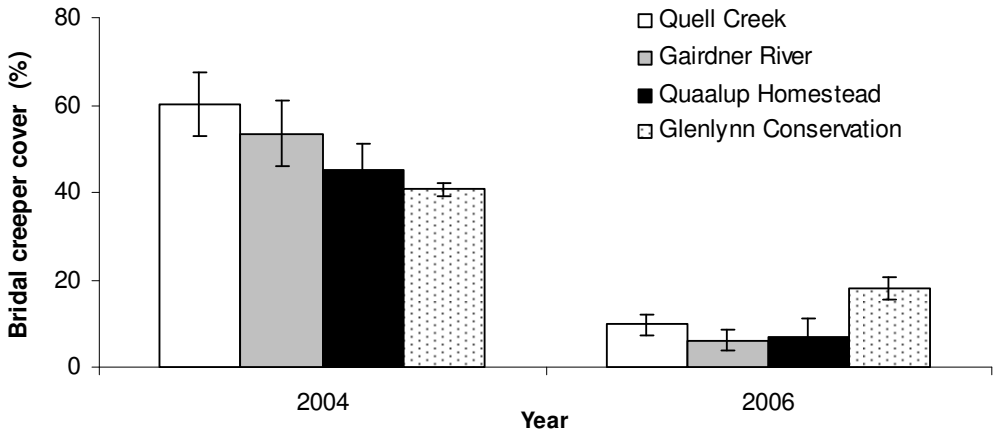


Figure 8.1. Change in bridal creeper cover (mean $\pm$ s.e.), before and after the arrival and release of the bridal creeper rust at four sites in south west Australia.

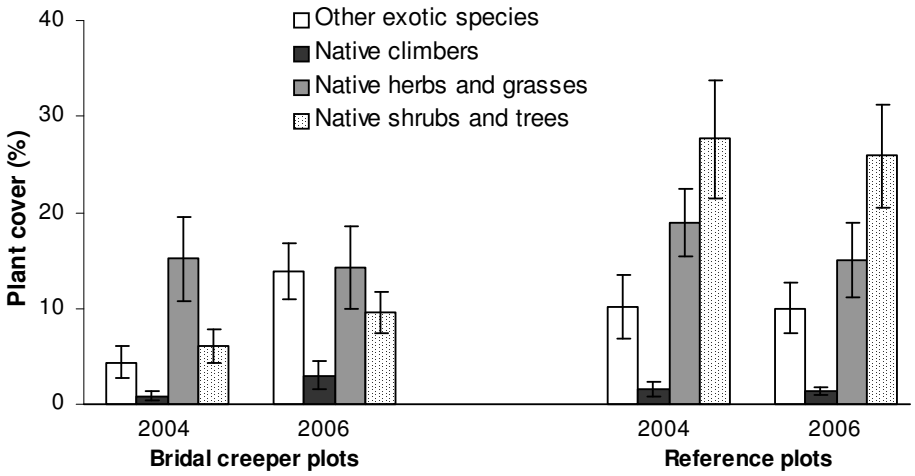
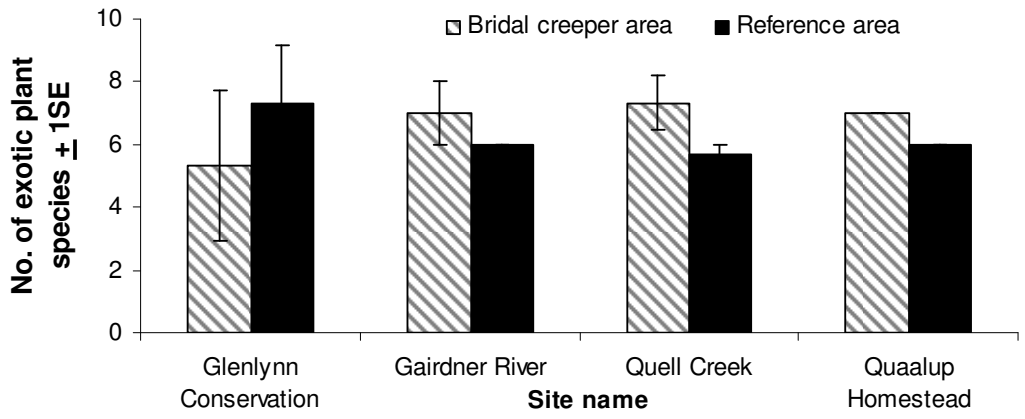


Figure 8.2. Change in plant cover (mean ± s.e.) before and after the arrival and release of the bridal creeper rust, averaged across all plots.

a)



b)

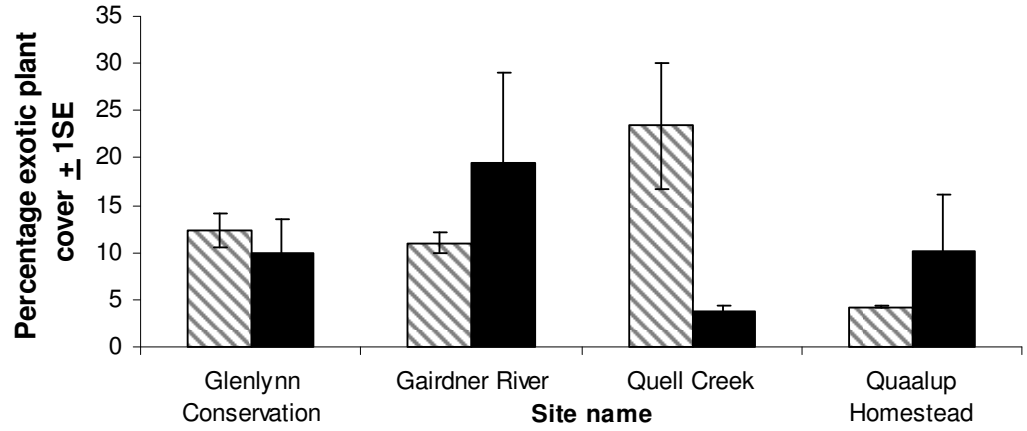


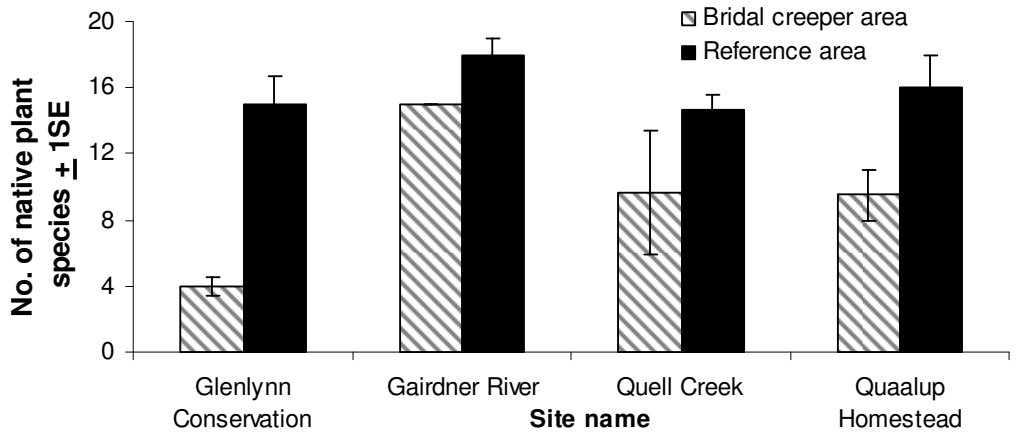
Figure 8.3. a) Mean number of exotic plant species (excluding bridal creeper) per 10 m^2 in 2006, following the biological control of bridal creeper.

See Figure 3.2b for comparison of exotic richness pre-control in 2004. There was no variation between plots in areas where error bars are not shown.

b) Mean percentage cover of other exotic species (excluding bridal creeper) in 2006, following the biological control of bridal creeper.

See Figure 3.2c for comparison of cover pre-control.

a)



b)

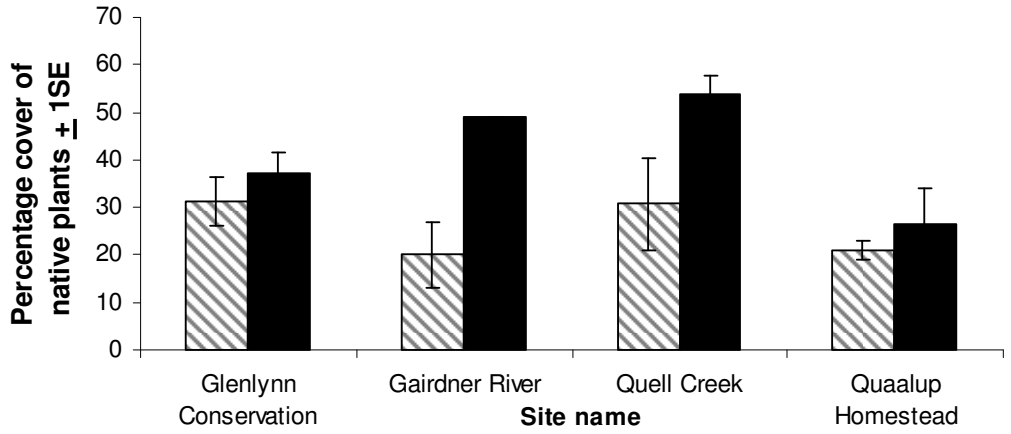


Figure 8.4. a) Mean number of native species per 10 m^2 across the sites following the biological control of bridal creeper.

See Figure 3.3a for comparison of native richness pre-control in 2004. There was no variation between plots in areas where error bars are not shown.

b) Mean percentage cover of all native plants in 2006, following the biological control of bridal creeper.

See Figure 3.3b for comparison of cover pre-control.

Table 8.1. Mean (± s.e.) number and cover of plant species in 2004 before biological control of bridal creeper and in 2006, after the initial reduction in bridal creeper following the release of the bridal creeper rust.

	Bridal creeper plots		**Reference plots**	
	2004	**2006**	**2004**	**2006**
No. of exotics[*#]	3.6 ± 0.8	6.6 ± 0.7	4.0 ± 0.6	6.3 ± 0.5
Cover of exotics[*]	4.4% ± 1.6	13.8% ± 2.9	10.1% ± 3.4	10.0% ± 2.7
No. of natives[#]	4.9 ± 0.7	9.0 ± 1.6	10.3 ± 0.9	15.7 ± 0.7
Cover of natives	22.0% ± 4.0	26.8% ± 3.5	48.1% ± 4.5	42.4% ± 3.9

[*]Excluding bridal creeper

[#]Per 10 m^2

CHAPTER NINE

IMPACT OF WEED INVASION AND SUBSEQUENT WEED CONTROL ON ANTS AS BIOINDICATORS OF ECOLOGICAL CHANGE

Key words: environmental weeds, Formicidae, Hymenoptera, impacts, invertebrates, monitoring, reference sites

Abstract

Asparagus asparagoides (L.) Druce (bridal creeper) is an environmental weed across southern Australia. While impacts on native vegetation have been established, the impacts on animals are not well known. This study investigated the impact of bridal creeper on ants (Hymenoptera: Formicidae) in south west Australia. Ants are recognised as bioindicators of environmental change in Australia. As bridal creeper is being actively managed, ant assemblages could be an indicator of ecosystem restoration success. Ants are also important seed dispersers of native plants and therefore any impact by bridal creeper on ant assemblages may affect the recovery of native plants following the control of this weed.

Across four sites, 200 pitfall traps were placed within bridal creeper invaded areas and in nearby native reference areas. Ants were trapped before and after the biological control of bridal creeper. Neither the invasion of natural habitats by bridal creeper in south west Australia nor subsequent biological control of the weed impacted on the biodiversity of ants, with the mean number of ant genera and overall ant abundance not significantly different between bridal creeper areas and native reference areas before or after biological control. Before biological control, the only difference between bridal creeper areas and reference areas was the abundance of the functional group Opportunists. This impact was no longer evident following biological control. As ants are important seed dispersers of many Australian native plants, it appears that ant assemblages will not be a barrier to native plant recovery in bridal creeper invaded sites, given that there was only a minimal impact by bridal creeper and that no impact was evident due to weed control. However, results from this and similar studies question the

general applicability of using ants as bioindicators of ecological change caused by weed invasion.

Introduction

While environmental weeds have been acknowledged as a major threat to biodiversity (Adair and Groves, 1998; Coutts-Smith and Downey, 2006), the majority of impact studies in Australia have focused on plant communities and ignored the impact on animals (Adair and Groves, 1998). In particular, little is known about the impact of environmental weeds on invertebrate communities (Clay and Schneider, 2000; French and Eardley, 1997; French and Major, 2001; Gerber et al., 2008). Yet changes to plant community composition, through both weed invasion and weed control, have multitrophic effects (Levine et al., 2003; Turner and Downey, 2008). Therefore, a more complete picture of the impacts of environmental weeds can be gained by considering the responses of organisms in other trophic levels during plant removal (Wardle et al., 1999). However given the limited resources available to manage environmental weeds, the need to determine impacts must be balanced against the need to implement management practices on the ground (Grice et al., 2004), therefore it is not practical to determine impacts across all groups of biodiversity and ecosystem processes. Thus an efficient way to investigate the impacts of environmental weeds would be to use consistent bioindicators of ecosystem health (Byers et al., 2002).

Ants are regarded as the dominant terrestrial invertebrate group in the Australian environment due to their great abundance, diversity and functional importance (Andersen, 1990; Burbidge et al., 1992; Hoffmann and Andersen, 2003). Their predictability of responses to disturbances has made them by far the most commonly used invertebrate bioindicator in Australian land management (Andersen et al., 2004; Hoffmann and Andersen, 2003). As bioindicators, ants have been used to evaluate land degradation and restoration processes and to assist in the assessment of ecosystems (Andersen, 1990; Majer et al., 2004).

Ants are suitable bioindicators because they interact with many other parts of ecosystems, are functionally important at all trophic levels, are readily sampled, respond rapidly to environmental change and are highly sensitive to environmental variables

(Andersen, 1990; Burbidge et al., 1992; Underwood and Fisher, 2006). For example, ants are involved with seed dispersal as well as with changes in soil structure and nutrient availability (Majer et al., 2002). In addition in mine restoration, the recolonisation by ants have been correlated with other invertebrate groups (Majer et al., 2002; Majer et al., 2004). Ants are also correlated to the soil microbial biomass (Andersen and Sparling, 1997; Majer et al., 2002) and in rehabilitated bauxite mines in Western Australia, Majer et al. (1984) established a positive association of ant species richness and diversity with plant richness and diversity, and percentage litter cover. Given this, there is the potential to use surveys of ants as surrogates of ecosystem function (Majer et al., 2002) and as a potential indicator of changes to other groups of biodiversity.

In addition to being indicators of ecosystem health, some ant species are also important dispersal agents of Australian native plants and therefore would play an important role in ecosystem restoration. The dispersal and survival of many Australian plant seeds are intimately linked with the ant fauna of the region (Majer et al., 2002) and seeds of approximately 1,500 Australian vascular plant species (mostly shrubs) are regularly dispersed by ants (Berg, 1975). These species are known as myremecochorous with ant-attracting elaiosomes on their seed or fruit (Berg, 1975). These elaiosomes are special oil-rich food bodies attached to the seed (Hughes and Westoby, 1992; Shattuck, 1999). Seed dispersing ants, such as those of the genus *Iridomyrmex* are often attracted to and then disperse these seeds (Shattuck, 1999). Seed collection by ants can alter the local abundance and distribution of native plants (Grimbacher and Hughes, 2002). Seeds are redistributed both vertically and horizontally by ants following seed-fall (Shea et al., 1979). If weed invasion impacts negatively on an ant community, it is likely to influence the ability of native plant species to compete in weed infested communities because some native plants rely on ants for seed burial which protects their seeds from fire and predators (French and Eardley, 1997).

This study investigated the impacts of the environmental weed bridal creeper (*Asparagus asparagoides* (L.) Druce) on ant communities across four sites in south west Australia. Given that bridal creeper has impacted on the native understorey ground covers (Stephens et al., 2008) and the shrub and tree layer (Chapter 3 - Turner et al., 2008c), as well as impacting on nutrient cycling (Chapter 5), it would be expected that

invasion by bridal creeper would also be reflected in a changed ant community. The biological control of bridal creeper has commenced in Australia (Morin et al., 2006b; Chapter 8 - Turner et al., 2008b) and in addition to evaluating the impact of environmental weeds, the effectiveness of weed control can also be successfully evaluated by monitoring ant communities (Clay and Schneider, 2000).

By monitoring the build-up in ant richness and successional changes in ant community composition, ants can provide a measure of ecological restoration (Schnell et al., 2003). As a predictive framework has been developed based on ant functional groups in relation to ant responses to environmental stress and disturbance (Andersen et al., 2004; Majer et al., 2004), impacts on ant functional groups have been investigated as part of this study. The use of functional groups in the past has provided a framework for analysing ant community responses to disturbance in the absence of reliable information of individual ant species (Hoffmann and Andersen, 2003). Functional groups are of most use in situations where disturbance causes substantial change in habitat structure, particularly in the ground layer. Given the change in the structure of vegetation in bridal creeper areas, with understorey shrubs and trees being replaced by bridal creeper (Chapter 3 - Turner et al., 2008c), ant functional groups have been incorporated into this study. Therefore, the objectives of this study were:

1. to determine the impacts of bridal creeper on ant community structure and functional groups, by undertaking a multi-site comparison (see Adair and Groves, 1998) between areas with bridal creeper and reference areas,
2. to characterise the temporal changes in ant community structure before, during and after the initial stage of the biological control of bridal creeper, and
3. to determine the impacts of the initial stage of the biological control of bridal creeper on ant community structure and functional groups, by undertaking a multi-site comparison between bridal creeper areas and reference areas following biological control.

Methods

STUDY AREA

This study was undertaken at the same four sites across south west Australia and over the same time period referred to in Turner et al. (Chapter 8 - 2008b; and Chapter 3 -

2008c). Within each site, 10 x 1 m plots were established in stands of bridal creeper or in nearby reference areas. These reference areas were within native vegetation with little or no bridal creeper present (see Chapter 3 - Turner et al., 2008c for full description of sites and plots). These reference areas represent the target for restoring invaded sites (Blossey, 2004; Chapman, 1999). Each plot which was established in the bridal creeper area was paired to a plot (also 10 x 1 m) in a reference area located directly adjacent to the bridal creeper area, but at least 10 m away from other plots.

Plots within both bridal creeper and reference areas were established in October 2004. At this time, all vascular plant species were identified and percentage areal shoot cover of the understorey (to a maximum height of 1.5 m) was estimated visually for each species within each plot. The methods and results for this survey are presented in Turner et al. (Chapter 3 - 2008c). In June 2005 the biological control agent, the bridal creeper rust, was released in the centre of each bridal creeper stand at each site (Chapter 8). In September 2006, the sites were revisited and all vascular plant species were identified and the cover of the understorey estimated. The results from this second vegetation survey are reported in Turner et al. (Chapter 8 - 2008b). An initial stage of bridal creeper control was reached after the release of the bridal creeper rust. Between 2004 and 2006, average bridal creeper cover had decreased from 49.9% $\pm$ 4.4 (mean $\pm$ s.e.) to 10.2% $\pm$ 2.7 (Figure 8.1) within bridal creeper areas across the four study sites.

ANT PITFALL TRAPPING

A pitfall trap was placed in the ground every 1 m along the 10 m side of each plot. As two sites (GC and QC) had three plots in both bridal creeper areas and reference areas, 60 traps were used in total at each of these sites. Forty traps were used at QH and GR, given there was a total of four plots at each of these sites. Each trap was a plastic screw top vial, 6.5 cm in diameter and 10 cm deep. Traps were filled with 100 mL of water and a few drops of detergent to break the surface tension of the water. Each trap was placed in the soil so that it was flush with the soil level. Traps remained closed for at least seven days following placement in the ground. The 200 traps across the four sites then had their lids removed and these traps remained opened continuously for six days. When collected after six days, each trap was immediately replaced with a new sealed (un-opened) trap, waiting for the next sampling period. This was done to minimise disturbance.

Three sampling events were undertaken in spring, in October 2004, September 2005 and September 2006, when bridal creeper is usually at its highest density and cover. Two sampling events were also undertaken in summer, in February 2005 and December 2005. Although bridal creeper was senesced during the summer periods, this is the season when ants are normally more active within the study region (Majer, 1985). The ten pitfall traps in each plot were pooled. All ants collected in the traps were placed in 70% ethanol solution for later identification. Ants were identified to genus level (Shattuck, 1999). Ant genera were then assigned to functional groups (Table 9.1) as described in Andersen (1995) and referring to Hoffmann and Andersen (2003), Schnell et al. (2003) and Majer et al. (2004).

IMPACT OF BRIDAL CREEPER

The impact of bridal creeper on ant genus richness and ant abundance was determined by comparing the ant assemblages collected in October 2004 from the bridal creeper areas and the reference areas (similar to the analysis undertaken for the vegetation survey described in Turner et al., 2008c). The influence of site and area for ant genus richness and ant abundance, were analysed using two-way analysis of variances (GenStat, 2003). Individual plots (10 traps) sampled in October 2004, before biological control commenced at the sites, were used in the analysis. Transformations were applied when appropriate, via a log10 transformation, to meet the assumption of homogeneity of variances.

The ant assemblages between invaded and reference areas from the October 2004 survey were also compared using multivariate statistics (Primer 6, Clarke and Warwick, 2001). As the sampling intensity was not equal across the four sites, following the combination of plots in each area at each site, the abundances of ant genera were standardised by totals (see Clarke and Warwick, 2001). For each area sampled across all sites, a rank-similarity matrix was then constructed using a Bray-Curtis similarity index on square-root transformed standardised ant abundances (see Clarke, 1993; Clarke and Warwick, 2001). An analysis of similarity (ANOSIM Primer 6) then determined differences between invaded and reference areas. This analysis was also repeated for the abundances of ant functional groups.

The average plot abundance of individual functional groups, within each area, was also analysed using one-way analysis of variances (GenStat, 2003). Each area within a site was treated as one replicate, therefore ant abundances within plots within the same area at the same site were averaged. This gave a total of eight replicates, four from each area. A log10 transformation was applied when appropriate to meet the assumption of homogeneity of variances.

To determine if there was a relationship between native plant species richness (as reported in Chapter 3) and ant genus richness in October 2004, across the 20 plots (located in both areas), a simple linear regression analysis was undertaken. This was also repeated to determine if there was a relationship between native plant cover and the abundance of ants.

IMPACT OF THE BIOLOGICAL CONTROL OF BRIDAL CREEPER

The influence of site and area for ant genus richness and total ant abundance, were also analysed using two-way analysis of variances (GenStat, 2003) by comparing the ant assemblages collected in September 2006 from the bridal creeper areas and the reference areas. The cover of bridal creeper had decreased to 10.2% $\pm$ 2.7 (mean $\pm$ s.e.) within the bridal creeper areas at the time of this ant survey (Figure 8.1).

Multivariate statistics (Primer 6, Clarke and Warwick, 2001) were again used to compare ant assemblages between invaded and reference areas from the September 2006 survey, at the end of the study to determine the impact of this initial stage of biological control. Following the combination of plots in each area at each site, the abundances of ant genera were standardised by totals. For each area sampled across all sites, a rank-similarity matrix was then constructed using a Bray-Curtis similarity index on square-root transformed standardised ant abundances (see Clarke, 1993; Clarke and Warwick, 2001). An ANOSIM then determined differences between invaded and reference areas. This analysis was also repeated for ant functional groups. The average plot abundance of individual functional groups, within each area, was also analysed using one-way analysis of variances for the September 2006 survey (GenStat, 2003).

Results

This study sampled a total of 13,803 ants across 31 genera. Ant genus richness (Figure 9.1a) and ant abundances (Figure 9.1b) were comparable between bridal creeper areas and reference areas during each of the five collection periods.

IMPACT OF BRIDAL CREEPER

In October 2004, ant genus richness was not different between sites ($F=1.73$; d.f. 3,12; $p=0.213$) or between bridal creeper areas and reference areas ($F=0.92$; d.f. 1,12; $p=0.356$, Figure 9.2a). Ant abundances were significantly different between sites (log10 transformation; $F=6.54$; d.f. 3,12; $p=0.007$), but there was no difference between areas (log 10 transformation; $F=0.21$; d.f. 1,12; $p=0.685$, Figure 9.3a).

Ant assemblages were not different. Multivariate analysis indicated there were no significant differences between invaded areas and reference areas in October 2004, when comparing ant genera ($R=-0.25$; $p=0.914$) or ant functional groups ($R=0.094$; $p=0.229$). The three most abundant functional groups were Dominant Dolichoderinae, Generalised Myrmicinae and Opportunists and accounted for 93.9% of all ants in the 2004 collection. In this 2004 survey, there was a significant difference in the abundance of the functional group, Opportunists ($F=7.79$; d.f. 1,6; $p=0.032$). There were 7.0 ± 1.2 (mean $\pm$ s.e.) Opportunists per plot in bridal creeper areas and 2.8 ± 0.9 per plot in reference areas. There was however, no difference in Dominant Dolichoderinae (after log10 transformation, $F=0.15$; d.f. 1,6; $p=0.708$) or Generalised Myrmicinae (after log10 transformation, $F=2.20$; d.f. 1,6; $p=0.189$). Dominant Dolichoderinae averaged 158.5 ± 130.7 per plot in bridal creeper areas and 44.1 ± 26.2 in reference areas. Generalised Myrmicinae averaged 4.5 ± 1.7 per plot in bridal creeper areas and 24.6 ± 18.2 in reference areas.

In October 2004, there was no relationship between native plant species richness and ant genus richness ($F=0.891$; d.f. 1,18; $p=0.358$, Figure 9.4a). There was also no relationship between native plant cover and the abundance of ants ($F=1.073$; d.f. 1,18; $p=0.314$, Figure 9.4b). At GC, in a plot in the bridal creeper area, only one ant was trapped in 2004. Even if this plot was removed from the analysis, there was still no

relationship between native plant cover and the abundance of ants (after log10 transformation, F=2.72; d.f. 1,17; p=0.117).

IMPACT OF THE BIOLOGICAL CONTROL OF BRIDAL CREEPER

In September 2006, ant genus richness was significantly different between sites (F=6.82; d.f. 3,12; p=0.006), but there was no difference between bridal creeper areas that had been biologically controlled and reference areas (F=0.67; d.f. 1,12; p=0.429, Figure 9.2b). When analysing ant abundance, there was a significant interaction between site and area (F=4.35; d.f. 3,12; p=0.027, Figure 9.3b).

Multivariate analysis indicated there were no significant differences between invaded areas and reference areas following the initial stage of biological control, when comparing ant genera (R=0; p=0.543) or ant functional groups (R=0.031; p=0.343). The three functional groups Dominant Dolichoderinae, Generalised Myrmicinae and Opportunists accounted for 79.4% of all ants in the 2006 collection. Unlike the 2004 survey, in 2006 there was no significant difference in the abundance of the functional group, Opportunists (F=0.00; d.f. 1,6; p=0.974). There were 18.3 $\pm$ 12.7 Opportunists per plot in bridal creeper areas and 17.8 $\pm$ 10.1 per plot in reference areas. There was also no difference in Dominant Dolichoderinae (F=1.22; d.f. 1,6; p=0.311) or Generalised Myrmicinae (F=3.47; d.f. 1,6; p=0.112). Dominant Dolichoderinae averaged 31.4 $\pm$ 17.1 per plot in bridal creeper areas and 11.8 $\pm$ 4.7 in reference areas. Generalised Myrmicinae averaged 3.3 $\pm$ 1.1 per plot in bridal creeper areas and 7.1 $\pm$ 1.8 in reference areas.

Discussion

This study did not detect any impact by either bridal creeper invasion or the biological control of bridal creeper on ant assemblages. Holt (2005) also investigated the impact of bridal creeper on ants between August 2001 and February 2002 at a site in South Australia. The result from this study is in agreement with mine, with the mean number of ant species and overall abundance not significantly different between their bridal creeper area and their native reference area (Holt, 2005). In addition, there were no overall differences in ant assemblages between *Asparagus aethiopicus* L. dominated sites and control sites in urban areas in Sydney (Hochuli and Robinson, 2008).

The only difference between bridal creeper areas and reference areas in my study was in the functional group, Opportunists, although their abundance was only 7.0 $\pm$ 1.2 per plot in bridal creeper areas and 2.8 $\pm$ 0.9 per plot in reference areas. However, this result was also evident in South Australia, with three out of four sampling periods, the Opportunists were higher in bridal creeper plots compared to the reference plots (Holt, 2005). The functional group, Opportunists, have been described as a 'weedy' species which increase in abundance following habitat disturbance (Andersen, 1991; Hoffmann and Andersen, 2003). Grimbacher and Hughes (2002) also compared a weed-infested zone to a bush regeneration zone and a reference zone in remnant bushland near Sydney and found no significant difference in ant abundance or genera. However, like my study, they also established that Opportunists were more dominant in the weed-infested zone.

The functional group Dominant Dolichoderinae, which includes the genus *Iridomyrmex* (Table 9.1), is described as being highly abundant and favouring hot open habitats (Hoffmann and Andersen, 2003). They are usually the first ants to colonise and dominate mine sites that are undergoing restoration in Australia (Schnell et al., 2003). This functional group decreases in shaded areas with a thick layer of litter (Hoffmann and Andersen, 2003). Given that my study sites were located within native woodland, and plots positioned in shady areas (see Chapter 3 - Turner et al., 2008c, especially on the selection of plots below trees, as bridal creeper is usually clumped within these shady areas) it is not surprising that no differences were found in the functional group Dominant Dolichoderinae. The similarity in ant assemblages between bridal creeper areas and reference areas could also be related to the lack of difference in the readily germinable seed-bank between bridal creeper areas and reference areas (Chapter 3) and that there was no difference in the litter biomass between areas (Figure 5.5).

There is little known about the impact of weeds on invertebrate assemblages (French and Major, 2001). Studies that have included invertebrate responses include that undertaken by French and Major (2001), who established that weed infestations of *Acacia saligna* (Labill.) H.L. Wendl. in South Africa supported fewer ants, but there was no significant change in species richness. French and Eardley (1997) while studying bitou bush (*Chrysanthemoides monilifera* (L.) Norl. ssp. *rotundata* (DC.) Norl.) infestations and their effects on litter invertebrates within Australia also observed

no differences in overall species richness or overall abundance of invertebrates and in particular, ants. Similarly, Lindsay and French (2006) established that invertebrates appeared resilient to the invasion of bitou bush, with infestations supporting large number of leaf litter invertebrates with the abundance not significantly reduced in the weedy habitats when compared to native habitats. Yeates and Williams (2001) investigated the influence of three invasive weeds on soil microfauna in New Zealand. They found differing responses to the weeds at paired sites, with species and site characteristics interacting to determine the impact of weeds on soil fauna. Unfortunately, their study therefore found no consistent response of soil fauna to the presence of a particular weed.

Given the above, it appears that no clear patterns have yet emerged when investigating impacts of environmental weeds on invertebrate communities. Focusing in on ant communities in Australia, it also appears that no overall trends are apparent, with no changes in richness or abundance in my study or reported in the studies of French and Eardley (1997), Grimbacher and Hughes (2002) or Holt (2005), however French and Eardley (1997) did establish differences in seed dispersing ants. Clay and Schneider (2000) also reported that coastal wattle (*Acacia sophorae* (Labill.) R.Br.) invasion was accompanied by changes in the associated ant communities and that at some sites following weed control, by mechanically slashing and/or burning, ant communities were recovering. Vegetation structure is well known to influence ant composition (Majer et al., 1984). Yet, the differences in vegetation structure reported in Chapter 3 did not appear to influence the overall ant assemblages at my sites (Figure 9.4).

As mentioned earlier, Majer et al. (1984) established a positive association of ant species richness and diversity with plant richness and diversity, and percentage litter cover. This is in contrast to Lassau and Hochuli (2004) who established that ant richness was negatively associated with herb cover, tree canopy cover, soil moisture and leaf litter, with ant richness higher within habitats with low complexity. The study by Majer et al. (1984) was undertaken in rehabilitated bauxite mines, while the study by Lassau and Hochuli (2004) was undertaken in woodland within three National Parks. These contrasting results; the lack of clear trends of ant assemblages to environmental weed invasion; and that ant assemblages in my study did not respond to changes caused by

bridal creeper to the native vegetation structure diminishes the worth of ants as bioindicators of change caused by weed invasion into native ecosystems.

As ant communities had a very limited response to bridal creeper, a more comprehensive sampling programme, across different invertebrate groups, would have been advantageous in detecting the impacts of a weed invasion (Douglas and O'Connor, 2004). However, Holt (2005) investigated the impacts of bridal creeper on Coleptera, Collembola as well as Formicidae and established there was no significant difference in the mean number of beetle species (Coleoptera) in a bridal creeper habitat versus a native habitat and reported that the collembolan diversity was also not different in her study. In addition, Stephens et al. (2003) reported an increase in the number of Phoridae (Diptera – a probable pollinator of an endangered orchid) with increasing cover of bridal creeper. Therefore, this would suggest that the impacts of bridal creeper invasion on invertebrates can be positive and are either limited to individual groups of invertebrates or are difficult to detect.

The only difference between bridal creeper areas and reference areas in my study was in the functional group, Opportunists. Following the biological control of bridal creeper at my four sites, there was no longer a significant difference in the abundance of this functional group, with 18.3 $\pm$ 12.7 (mean $\pm$ s.e.) Opportunists per plot in bridal creeper areas and 17.8 $\pm$ 10.1 per plot in reference areas. As there were no other significant differences in ant assemblages between bridal creeper areas and reference areas following biological control, it appears that ants will continue to play an important role in these bridal creeper areas. Biological control of bridal creeper has not impacted on these functionally important fauna and they will assist in the recovery of native vegetation at these sites. As mentioned above, some ant species are important dispersal agents of Australian native plants and therefore would play an important role in ecosystem restoration. Although only dispersing seeds short distances, some native plants rely on ants for seed burial which protects their seeds from fire and predators (French and Eardley, 1997).

Acknowledgments

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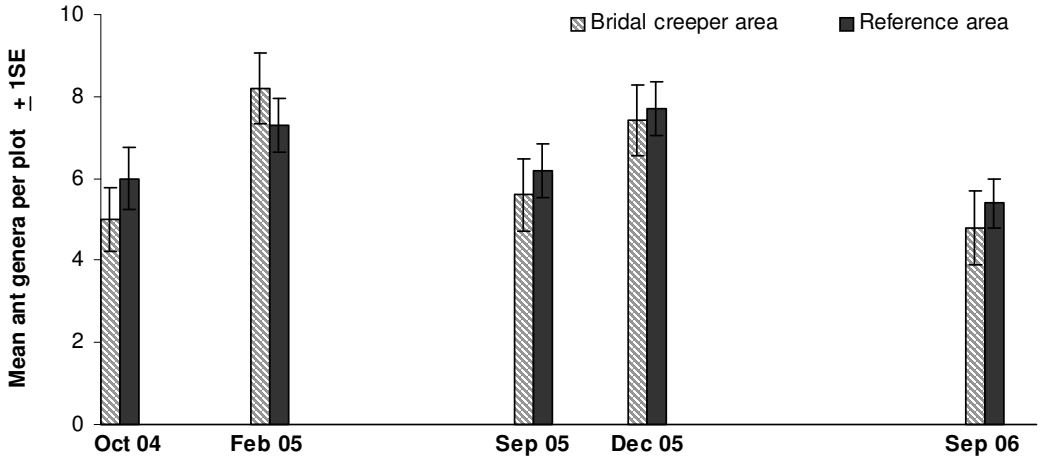
a) genera



b) abundance

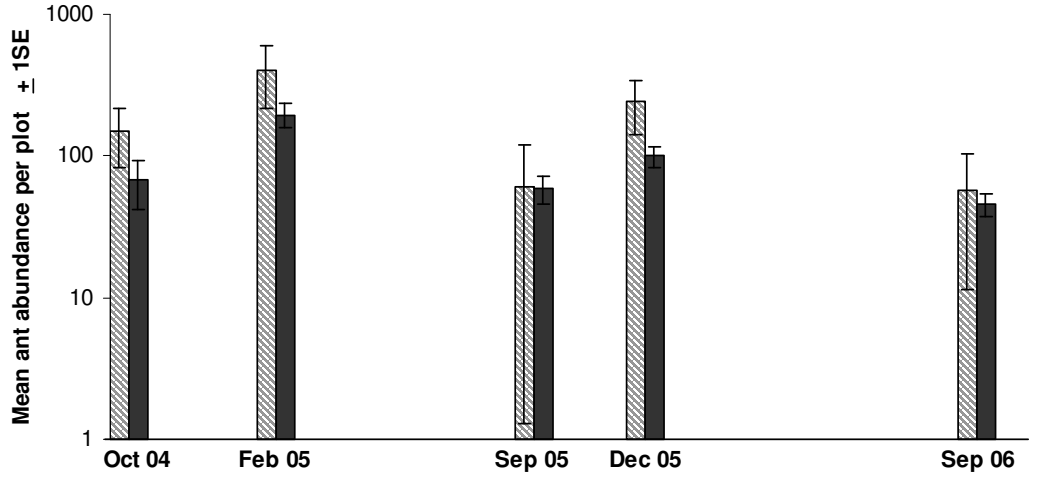
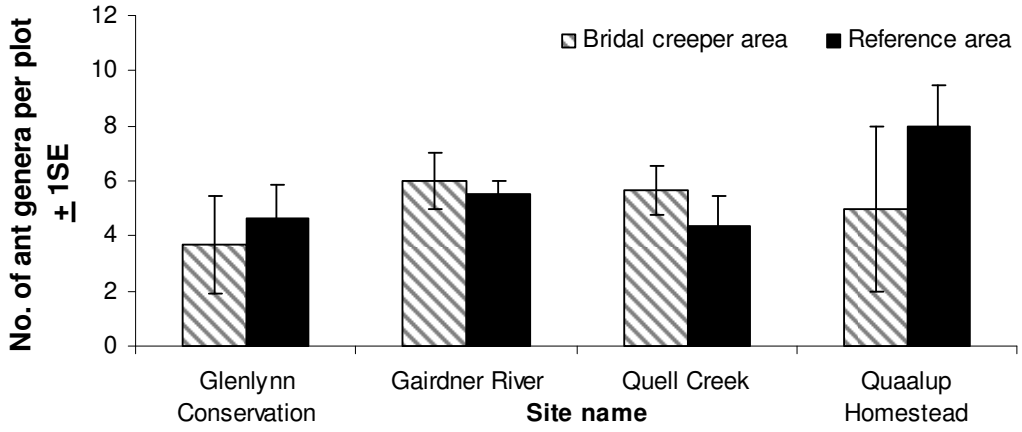


Figure 9.1. a) Mean (± s.e.) number of ant genera and b) mean ant abundance per plot (10 pitfall traps) across four sites and five sampling periods comparing bridal creeper invaded areas and native reference areas.

The biological control agent, the bridal creeper rust, was released at these sites in June 2005. In October 2004 within the bridal creeper areas, average bridal creeper cover was 49.9% + 4.4 (mean + s.e.) and in September 2006, cover was 10.2% + 2.7. In the reference areas, bridal creeper cover was 2.3% + 0.9 in October 2004 and 0.6% + 0.1 in September 2006.

a) 2004



b) 2006

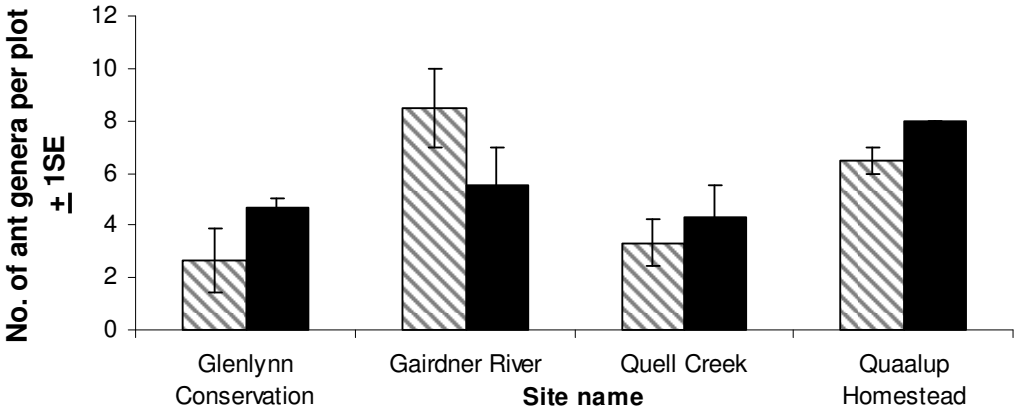
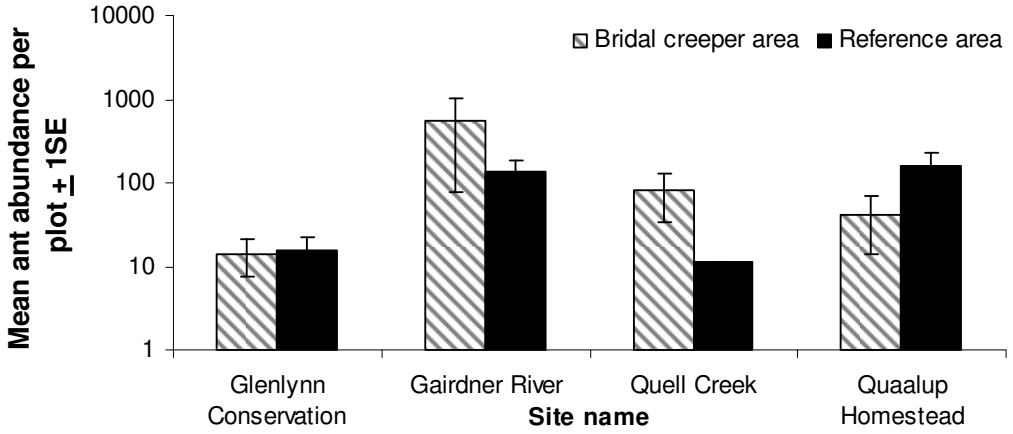


Figure 9.2. a) Mean (± s.e.) number of ant genera per plot (10 pitfall traps) in 2004 before the biological control of bridal creeper across the four sites. b) Mean number of ant genera per plot in 2006, following the biological control of bridal creeper.

There was no variation between plots in the reference area at Quaalup Homestead in 2006.

a) 2004



b) 2006

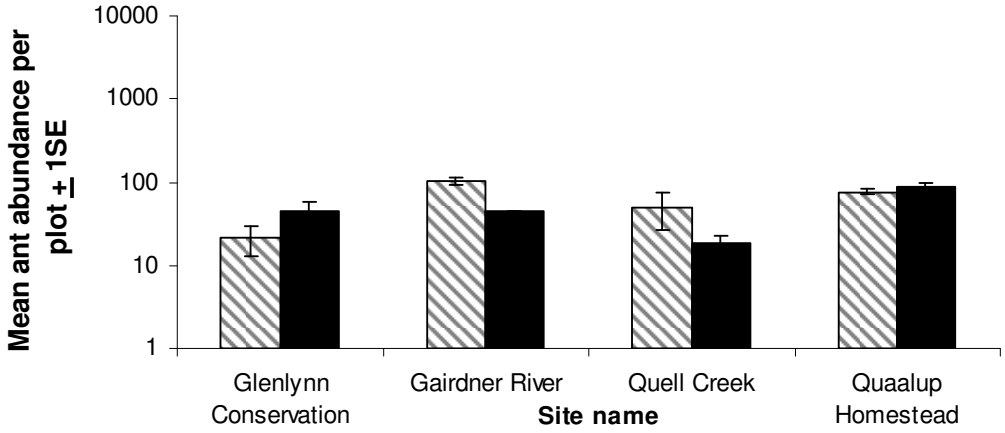
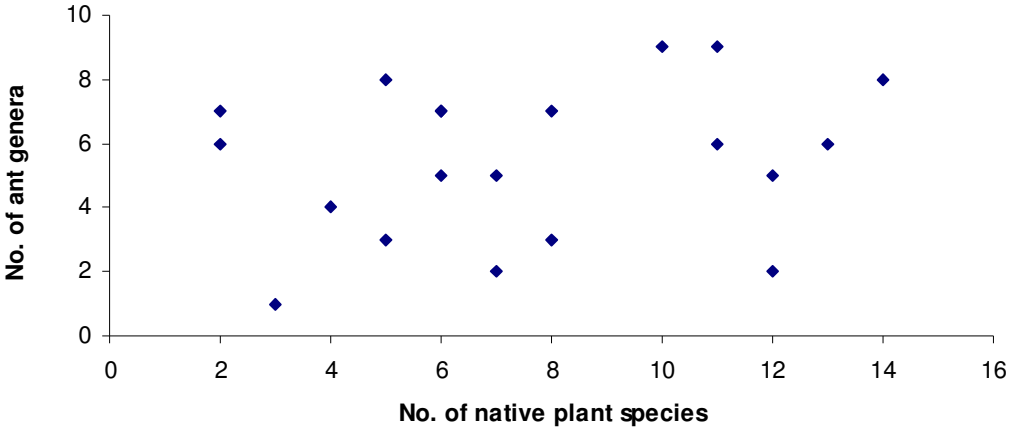


Figure 9.3. a) Mean (± s.e.) ant abundance per plot (10 pitfall traps) in 2004 before the biological control of bridal creeper across the four sites. b) Mean ant abundance in 2006, following the biological control of bridal creeper.

There were variations between plots in 2004 in the reference area at Quell Creek (s.e.=0.33) and in 2006 in the reference area at Gairdner River (s.e.=1.00), however these standard errors were too small to be visually shown on the above figures.

a)



b)

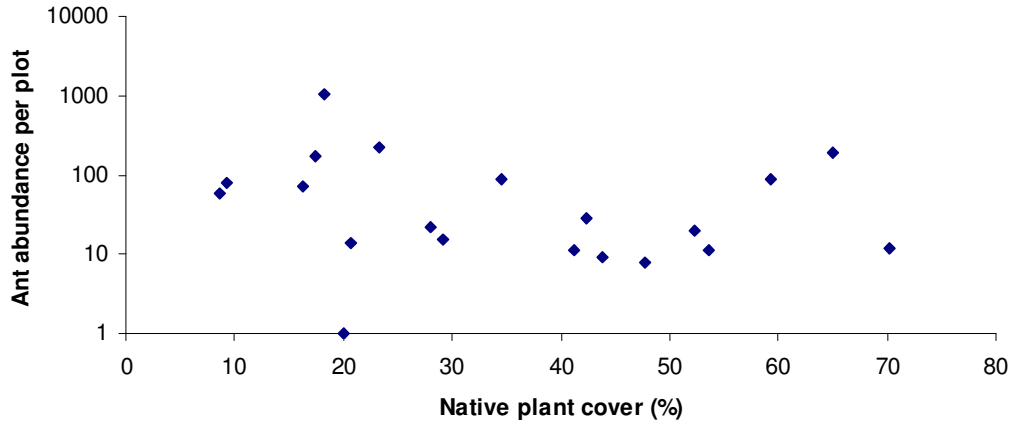


Figure 9.4. a) The number of native plant species present compared to the number of ant genera present per plot, in 2004. b) The percentage cover of native plant species compared to the total abundance of ants per plot, in 2004.

At GC, within a plot in the bridal creeper area, only one ant was trapped. Even if this plot was removed from the analysis, there was still no relationship between native plant cover and the abundance of ants (after log10 transformation, $F=2.72$; d.f. 1,17; $p=0.117$).

Table 9.1. List of Australian ant functional groups (see Andersen, 1995; Schnell et al., 2003) and genera identified in this study.

Functional group	**Ant genera**
Dominant Dolichoderinae	*Anonychomyrma, Iridomyrmex* and *Papyrius*
Generalised Myrmicinae	*Crematogaster, Monomorium,* and *Pheidole*
Opportunists	*Doleromyrma, Ochetellus, Paratrechina, Rhytidoponera* and *Technomyrmex*
Subordinate Camponotini	*Calomyrmex, Camponotus, Opisthopsis* and *Polyrhachis*
Specialist Predators	*Cerapachys, Colobostruma, Epopostruma, Myrmecia, Pachycondyla* and *Platythyrea*
Cold Climate Specialists	*Dolichoderus, Heteroponera, Myrmecorhynchus, Notoncus, Podomyrma* and *Stigmacros*
Cryptic Species	*Amblyopone* and *Sphinctomyrmex*
Hot Climate Specialists	*Adlerzia* and *Melophorus*

CHAPTER TEN

SYNTHESIS AND GENERAL DISCUSSION

The impacts of the environmental weed bridal creeper and the mechanisms underlying these impacts

Plant invasions that are of the greatest concern are those that dramatically change the rate and direction of succession within native ecosystems, which in turn causes a corresponding decrease in native species richness (Luken, 1997). The invasion of the southern African geophyte *Asparagus asparagoides* (L.) Druce (bridal creeper) into southern Australia is one such example. Understorey native shrubs and trees are most affected and soil phosphorus availability has been increased due to changes in nutrient cycling. Many impacts from bridal creeper may be indirect. When bridal creeper modifies the soil through changes in nutrient cycling, this would also negatively impact on a suite of native species, while positively impacting on the growth of bridal creeper (see Chapter 4). Therefore the increase in soil fertility would have been a major contributing factor to the formation of the monocultures of bridal creeper found within Australian native ecosystems. Sites that have been heavily invaded by bridal creeper, over a long period of time, will have a legacy of this high available soil phosphorus, long after bridal creeper control.

Because of the normally low soil fertility of the ancient Australian environment, many Australian plant communities were thought to be protected against weed invasion (Beadle, 1953; Beadle, 1966). Nutrient enrichment of these low fertility soils was seen as a prerequisite for a successful invasion (Lake and Leishman, 2004). The ability of bridal creeper to change the soil conditions is an important characteristic that has enabled bridal creeper to invade and then dominate Australian native ecosystems without this prerequisite of nutrient enrichment. Bridal creeper can invade undisturbed native ecosystems (Hobbs, 1991; Raymond, 1995; Siderov and Ainsworth, 2004) and can persist in nutrient poor soil (see Chapters 4 and 7). Transforming species, such as bridal creeper, which invade these undisturbed nutrient poor environments, would then change the soil conditions which would aid in the increase of their own abundance or would open up these communities to invasion by other weeds.

From a successional perspective, the events of primary importance in the invasion of environmental weeds are the i) entry into an established plant community; ii) performance of the weed and competition with surrounding native plant species; and iii) long-term persistence (Luken, 1997). Bridal creeper usually invades undisturbed communities (Hobbs, 1991; Raymond, 1995; Siderov and Ainsworth, 2004) through the dispersal of its seed by native birds (Raymond, 1996; Thomas and Miller, 2000). The long term dominance of the understorey by bridal creeper has then modified the nutrient cycling processes (Chapter 5). Over time, bridal creeper has also dominated the top-soil profile with a thick tuberous root mat which has also contributed to the corresponding change in the native understorey (Chapter 6).

Bridal creeper impacts mostly on the understorey shrubs and trees it climbs over (Turner et al., 2008c) as well as ground-cover plants (Stephens et al., 2008). Competition can explain some of bridal creeper's dominance, but it appears several mechanisms are involved and may be interdependent. Bridal creeper seedlings (see Chapter 4) and adult plants growing in low nutrient soil (see Chapter 7) appear to lack superior competitive ability with other plants. Most environmental weeds do not have superior growth rates or competitive abilities when compared to co-occurring natives (Daehler, 2003). However, when faced with strong competition, bridal creeper seedlings allocate more resources to belowground growth (see Chapter 4). The belowground biomass of bridal creeper would accumulate over time and the tuberous mats would impact on other plants.

Allelopathy could partially explain bridal creeper's dominance (see Chapter 6), but its competitive dominance is mainly related to the large volume of space that the tuberous mats, of long established plants, occupy. This competition for space may explain why it is the native understorey shrubs and trees that are the most impacted (see Chapters 2 & 3). Jackson et al. (1996) established that for sclerophyllous shrubs, 67% of their total root biomass was also found in the upper 30 cm of the soil and this amount of biomass was approximately 3.2 kg m^{-2}. Also, Low and Lamont (1990) established that root biomass in *Banksia* scrub-heath in south west Australia was 2.27 kg m^{-2} in the upper 30 cm of the soil profile. Therefore, given the tight packing of the bridal creeper tuberous mat within the upper part of the soil profile, this biomass may have replaced or

displaced the area previously occupied by the roots of native shrubs. This issue with space was also evident in Chapters 2 and 6, with even the dead tuberous mats impacting on other plants.

RECOMMENDATIONS FOR MANAGEMENT AND FUTURE RESEARCH

Although this thesis highlights the mechanisms and the broad impacts of bridal creeper, it does not identify those rare and threatened species that are listed under threatened species legislation which are also threatened by bridal creeper. To date only four listed threatened species are acknowledged as being at risk from bridal creeper. Downey (2006) identified two species in southern New South Wales. In addition, the small endangered shrub *Pimelea spicata* R. Br. was also identified as being threatened by bridal creeper, in south-eastern New South Wales (Willis et al., 2003) as well as a vulnerable listed ground orchid in South Australia, *Pterostylis arenicola* M.A.Clem. & J.Stewart (Sorensen and Jusaitis, 1995). Given the widespread distribution of bridal creeper and the impacts discussed in this thesis, it can be assumed that the threat from bridal creeper extends to more than four listed species and therefore this still needs to be quantified.

Additional studies are also recommended, especially on the ability of bridal creeper to invade intact, undisturbed communities and then on its ability to transform the community through changes in soil fertility. For successful invasion to take place in nutrient poor soil within Australian native communities, nutrient enrichment was thought to be required (Hobbs and Atkins, 1988; Lake and Leishman, 2004). Davis et al. (2000) also postulated a general theory of invasibility based on resource enrichment. It would be expected that an environmental weed like bridal creeper, that has displaced native woody shrubs and trees and changed the nutrient cycling, would cause a gradual shift in nutrient pools from aboveground plant biomass to the soil. However, of greater concern would be if an environmental weed could invade intact native communities with nutrient poor soil and access additional nutrients that would not normally be available to the resident vegetation. These species would be able to transform a community at a greater rate than a gradual shift in the nutrient pools.

As discussed in Chapter 5, within low nutrient soils, roots of some plants exude organic acids, such as caffeic, citric and malic acid, which is an important function in their

acquisition of nutrients such as phosphorus (P) and iron (Attiwill and Weston, 2003; Dakora and Phillips, 2002). These exudates convert the fixed P (normally unavailable for plant use) into soluble forms that can be used by plants (Grierson et al., 2004). These three organic acids mentioned above are all found in the roots of a species in the same genus as bridal creeper, *Asparagus officinalis* L. (Hartung et al., 1990). Further research is needed on the ability of bridal creeper to access the additional source of P. This area of research should also be extended to other environmental weeds, with Thorpe (2006) suggesting that root exudates produced by the environmental weed *Centaurea maculosa* Lam. enabled this species to acquire more P compared to that of the native species. The ability of some plants to access additional nutrients may explain why some invaders of intact communities are more successful than others. These weeds should be identified and be the highest priority for control, given the speed in which they could transform a community.

The allelopathic impacts of bridal creeper also requires more in-depth research, given that many of the organic compounds found in *A. officinalis* have also been previously reported to be important in allelopathic interactions (see Hartung et al., 1990). If bridal creeper does exude similar chemicals as *A. officinalis*, it could have a double effect, with allelopathic impacts on other plant species while bridal creeper increases its own growth rate through additional phosphorus acquisition.

Recovery of native biodiversity and ecosystem function following the control of bridal creeper

With the goal of gradually producing a dynamic system dominated by native species, environmental weed management should involve both the manipulation of the invader as well as the native species that management is hoping to protect (Luken, 1997). The control of bridal creeper will minimise the weed's impact. However, control will not result in the restoration of invaded sites, even though bridal creeper at my study sites was under the initial stages of biological control. Invaded sites respond differently to weed management and to the management technique employed (for example see Denslow and D'Antonio, 2005; Harms and Hiebert, 2006; Lesica and Hanna, 2004; Marrs et al., 2004; and Mason and French, 2007). This is supported within this thesis (see Chapter 8). The speed of the response of the plant communities to control also

varied across sites. The Quell Creek site had plants responding faster to biological control when compared to the other three sites. However, my research has demonstrated that bridal creeper removal can have a positive influence on native communities. Native plants responded to bridal creeper removal (Chapter 2) and control led to lower soil nutrients (Chapter 7).

At the beginning of an invasion, when the environmental weed is rare or sparsely distributed, the weed probably has little effect on ecosystem functions (Ehrenfeld, 2003). Therefore, it is suggested that the longer a site has been invaded by bridal creeper and the greater the dominance of bridal creeper at a site, the stronger the impacts will be on nutrient cycling, due to increases in the amount of bridal creeper litterfall. Given this, at the sites where bridal creeper has dominated, it would be more difficult to reduce the elevated levels of soil available phosphorus. Methods for reducing available phosphorus are not well established (Marrs, 2002) and phosphorus can remain in the soil for many years (Heddle and Specht, 1975). In most instances increases in phosphorus availability will be irreversible, except through plant biomass or soil removal, which would be a large disturbance to the invaded community.

Control of bridal creeper at the Owen site in South Australia (see Chapter 2) did not lower the soil phosphorus levels even after eight years. However where bridal creeper was controlled at this site, it was replaced with another southern African geophyte, *Oxalis pes-caprae* L. This plant also senesces over summer and has also been associated with increases in phosphorus availability (Sala et al., 2007), which could explain why no difference in soil phosphorus was recorded at the site (Table 4.2). However, as reported in Chapter 7 at the Meningie site, bridal creeper control led to an associated decrease in soil nutrients, although phosphorus was not different across this site. At Meningie, individual bridal creeper shoots were shorter compared to all of my other study sites, with bridal creeper rarely having tall ‘curtains’ of bridal creeper shoots.

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Environmental weeds are normally described as a symptom of a degraded native community (Erskine Ogden and Rejmanek, 2005). This is not always correct as discussed above, especially for bridal creeper which can be the cause of the degradation. It has been suggested by Williams and West (2000) that environmental weeds should be

treated as a symptom of the ecological problem, not just the cause. In some cases bridal creeper would invade disturbed communities, such as roadsides, therefore the impacts of the disturbance need to be managed also. Therefore, site evaluations before bridal creeper control would be equally or more important to determining the impact of the target weed. This will assist in determining site conditions and help to determine the speed or likelihood of achieving the restoration goals at a particular site.

Successful restoration of many bridal creeper invaded sites will require the management of secondary invaders and may also require the manipulation of the native plant community. At the Quell Creek site which had bridal creeper biologically controlled (see Chapter 8) and the Owen site which had bridal creeper controlled with herbicide (see Chapter 2), both had increases in the cover of other exotic species following the control. Thus both sites will require additional restoration in the form of further weed control of secondary invaders. This follow-up control may have to be undertaken for many years into the future.

Environmental weeds that alter soil nutrients may facilitate the invasion of other exotic species (Simberloff and Von Holle, 1999). However, bridal creeper invasion did not facilitate the invasion of other exotics species (see Chapter 3) even though bridal creeper increased the availability of phosphorus and exotic species like veldt grass responded positively to these higher nutrients (see Chapter 4). This increase in available phosphorus and dominance of a site by bridal creeper has allowed for a positive feedback to develop, through increased nutrient cycling (see Chapter 5). Facilitation of the invasion of other exotic species will only occur once the dominance of bridal creeper is reduced, that is through targeted weed control of bridal creeper. Important restoration goals of bridal creeper invaded areas will therefore include breaking this positive feedback between bridal creeper and nutrient cycling and reducing the elevated nutrient levels. Long-term experiments of the impacts of the changes in soil status on the native plant communities are also required.

Tighter integration of weed management and with other restoration techniques should be pursued (Beater et al., 2008; Witkowski and Garner, 2008). For example, it may not be possible for a site, where bridal creeper has been controlled, to reach its full potential of natural regeneration without the use of fire (McLoughlin, 1997). Fire has an

important role in the regeneration of Australian native communities (Fisher, 1999). Fire may be one of the best management tools as exotic seeds in the soil are more likely to be killed by fire (Fisher, 1999; Smith et al., 1999), while in contrast fire could promote the germination of native plants. Fire can be an important restoration tool that can be used to stimulate the regeneration of native plants to speed up the recovery of bridal creeper invaded sites. Bridal creeper and other weeds must be kept at a low post-fire density, which will involve additional follow-up weed control (see Chapter 7). However, more research into this area is needed, especially on the combined use of fire and weed biological control in Australian native ecosystems, given that fire is a natural occurrence in most Australian ecosystems and weeds that have invaded these native ecosystems are increasingly becoming targets for biological control (McFadyen, 1998).

The biological control of bridal creeper

In this thesis, I have incorporated bridal creeper biological control into a broader restoration and conservation context. My research indicates that bridal creeper cover can be successfully reduced with biological control (see Chapter 8); however other exotic species as well as a suite of native species appear to benefit from this control in heavily invaded areas. This is mainly due to changes in soil nutrient status below bridal creeper infestations.

The decision to target bridal creeper for biological control in Australia, made some twenty years previously, and the subsequent success of the biological control agents (particularly the rust) in reducing bridal creeper's density will be potentially very beneficial for conserving Australia's biodiversity. There are areas in southern Australia that are still free of bridal creeper or have sparse populations (ARMCANZ, 2000). They are mainly in New South Wales and Tasmania, but also there are such areas in the other southern states. As the bridal creeper rust reduces and in most cases prevents flowering and fruiting of bridal creeper (Morin et al., 2006b), it is highly likely that the biological control programme has led to the protection of these areas (see Chapter 8). Therefore, sites that are at an early stage of bridal creeper invasion and sites where bridal creeper could potentially invade, but has yet to do so, would most likely be protected from the impacts of bridal creeper due to the biological control programme. This protection

would not have been possible if other control measures were chosen over biological control.

As mentioned earlier, biological control of an environmental weed has a number of advantages over other control options, with self-dispersing agents able to give continuous control (Adair, 1995). This means that weed biological control in conservation areas can be very effective and is really the only economically viable option for the control of widespread environmental weeds such as bridal creeper. An additional benefit of the biological control of bridal creeper, over chemical control, is the ability of the bridal creeper rust to draw down the tubers during control (Morin et al., 2002; Turner et al., 2004). Therefore, unlike at the Owen site (see Chapter 2 and 6) where dead tuberous mats remained after herbicide control, the biological control agent, the bridal creeper rust, should reduce this residual impact over time.

Unfortunately, the post-release monitoring on the impacts of the biological control agents on the target weed and the changes in associated plant communities are rarely completed (Blossey, 2004; Blossey and Skinner, 2000; Thomas and Reid, 2007). This monitoring and evaluation has been undertaken for the biological control programme for bridal creeper, with the impact of biological control agents on the target weed reasonably well understood. For example in a caged shade house experiment in South Africa, *Zygina* sp. was shown to reduce the vegetative and reproductive output of the widespread form of *A. asparagoides* (Kleinjan et al., 2004a). In Australia, Morin et al. (2002) established that the bridal creeper rust (*Puccinia myrsiphylli* (Thuem.) Wint.) could reduce bridal creeper's root and shoot biomass. Also in Australia, Batchelor and Woodburn (2002) demonstrated that *Zygina* sp. could reduce the rate of tuber production. Even the interactions between the biological control agents have been investigated in glasshouse and field exclusion experiments (Spafford Jacob et al., 2007; Turner et al., 2004).

In collaboration with other researchers across southern Australia, Morin et al. (2002) also established permanent trellis sites to gather field data on the before and after impacts of the biological control agents on bridal creeper populations. Morin et al. (2002) reported that they had collected three years pre-release data from this trellis work and therefore the results from this study should become available in the near future,

given it was in 1999 that *Zygina* sp. was released in Australia and the rust in 2000. In addition, as the bridal creeper rust is currently the most effective agent in Australia, a fully controlled, three year exclusion experiment is being undertaken in the field at six sites across New South Wales and Western Australia (Morin et al., 2006b). The results from this study when published should complement the results reported in this thesis.

However, what is evident from my thesis is the value of reference sites in evaluating environmental weed biological control, and that these reference sites may be more useful than, or at least complement, before and after comparisons. With before and after comparisons, each sampling period would experience different climatic events; this would confound any before and after comparisons. As discussed in Chapter 8, when comparing bridal creeper plots in south west Australia, in 2004 the exotic cover was 4.4% and following control it had increased to 13.8%. It could be argued that there has been a three-fold increase in exotic cover. However, the exotic cover in 2006 in the reference areas was comparable to the 2006 measurements in the bridal creeper plots. Similarly, it could be shown that the number of native species in the bridal creeper plots had nearly doubled during the two years of biocontrol, yet a higher number of native species were still found in the reference areas compared to bridal creeper areas in 2006.

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Although control is often viewed as an applied issue, research and monitoring of impacts of biological control agents and the removal (control) of environmental weeds contribute to our understanding of ecology (Byers et al., 2002). Restoration can also be seen as an acid test for ecological theories (Bradshaw, 1987). Therefore, it is essential that all environmental weed biological control programmes measure the responses of the agents on the target as well as the response of the native communities to control. Successes in environmental weed biological control can then be documented and assist in changing the negative perception of biological control (see McFadyen, 2000). However, all programmes, successful or not, when monitored will contribute to our understanding of ecology.

The biological control of bridal creeper needs to be incorporated in the larger restoration framework. As bridal creeper is listed as a Weed of National Significance (WONS) in Australia (Thorp and Lynch, 2000), a national strategic plan was released to assist with

its management. The need for additional restoration beyond the control of bridal creeper was acknowledged within the strategic plan (ARMCANZ, 2000) and was reinforced as the highest priority following the National Asparagus Weeds Management Workshop in November 2005 (Gannaway and Virtue, 2006). The research undertaken in this thesis supports this, acknowledging that some sites will require additional assistance for recovery of native species. It was suggested in the National Asparagus Weeds Management Workshop that this restoration could be applied within high priority biodiversity areas that were invaded by this weed. However to date, these areas have not been identified as it is not known which rare and threatened species are at risk from bridal creeper. The biological control of bridal creeper in southern Australia has been very successful. Failure to identify these high priority areas as well as the additional restoration that may be required at each site, may see many sites change from bridal creeper dominance to dominance by secondary, exotic invaders.

A method for identifying the high priority areas is available and has been demonstrated for two other WONS (DEC, 2006; Turner et al., 2008a). Therefore, it is recommended that this approach also be followed for bridal creeper, given that the biological control of bridal creeper can not guarantee the protection of native species in all instances or reduce the impacts caused to ecosystem processes in heavily invaded areas in the short term.

Conclusion

The quantification of impacts of environmental weeds on other plant species, both exotic and native, are urgently needed (Simberloff and Von Holle, 1999). Ten years ago it was recommended that there was a need to better understand and document the impacts of environmental weeds on native species and ecosystems, so that it could be demonstrated to policy-makers the importance of controlling and prohibiting new invasive exotic plants (Parker and Reichard, 1998). Also ten years ago, Adair and Groves (1998) documented a number of approaches that could be undertaken to determine weed impacts. Yet such studies to determine impacts are still rare (Grice et al., 2004). This study has provided an important first step in determining the impacts of a dominant invader as well as the impacts of removing it so that conservation goals can be met for bridal creeper invaded sites.

One of the goals of the national strategic plan for bridal creeper management in Australia was the eradication and prevention of spread of bridal creeper into new areas (ARMCANZ, 2000). My research indicates that the biological control programme for bridal creeper will assist with meeting this goal. Another goal for this strategic plan was to reduce the existing impacts of bridal creeper through the reduction of bridal creeper density (ARMCANZ, 2000). This goal can not be met in some areas without additional restoration and in most cases it was always unlikely to be met by simply reducing the weed's density. It has been acknowledged previously that reducing the density of an environmental weed does not necessarily lead to a reduction in impacts and a re-establishment of native species (for example see Beater et al., 2008; Downey, 2008; Humphries et al., 1993; Lesica and Hanna, 2004; Luken, 1997). This is supported by the research within this thesis, with a legacy of past impacts of increased soil fertility and a large tuberous mat, coupled with invasion by secondary invaders all suggesting that the impacts will remain long after bridal creeper control. It has been suggested that management of environmental weeds is central to the conservation of Australia's native plant diversity (Coutts-Smith and Downey, 2006; Willis et al., 2003), however weed management in isolation may not conserve these species. More emphasis therefore, should be placed on protecting and promoting desirable species and less on simple weed control (Lesica and Hanna, 2004; Luken, 1997).

There were four main objectives of this thesis:

1. to determine the impacts of bridal creeper on native community composition, structure and ecosystem function,
2. to determine the mechanisms behind the impacts caused by bridal creeper invasion and to determine if the residual impacts or legacies from bridal creeper invasions remained after control,
3. to assess the condition of the sites where bridal creeper was to be managed and to determine if other restoration techniques will be needed, in addition to bridal creeper control, and
4. to determine the likely successional changes on native community composition following weed suppression, via biological control.

This thesis has addressed these objectives:

1. Bridal creeper reduces plant diversity, with its main impacts on the understorey shrubs and trees that bridal creeper climbs over. Bridal creeper has a limited impact on ant communities; however the biggest impact of bridal creeper is on an ecosystem process. Bridal creeper has transformed the community by increasing the availability of soil phosphorus through changes to nutrient cycling.

2. Although bridal creeper appears to be a poor competitor at the seedling stage, bridal creeper can invade intact native vegetation. It allocates more resources to its tubers in the first year if faced with high competition. Once bridal creeper has produced a large tuberous mat, bridal creeper occupies a large area of space in the top-soil, which would exclude other plants. This tuberous mat is a legacy that will remain and still impact on plants, even after weed control. The changes to the soil nutrients and the possible allelopathic impacts of bridal creeper are all likely to contribute to bridal creeper monocultures within Australia.

3. Some sites invaded by bridal creeper will require additional restoration, given that they now contain elevated available phosphorus in the soil. These sites also have a large exotic seed bank that will readily germinate. As it is the native understorey shrubs and trees that are most impacted, and that many of these require heat shock or smoke for germination, without the use of fire, native plants may not establish after bridal creeper control. This area however does require further research. The main restoration technique at bridal creeper sites will be just additional control of other weed species, to ensure that secondary invaders do not dominate after bridal creeper control. However, the main concern is how to restore sites back to a lower soil fertility level. This issue remains un-resolved.

4. Following biological control and subsequent decrease in bridal creeper, there will be a suite of native and exotic plants that will benefit from this control. Without additional restoration, we will see those species that readily germinate and that respond positively to increases in soil nutrients dominate these sites. This would most likely be native climbers and exotic herbs. Biological control had no impact on ant communities; however the plant communities that

establish after control will not resemble that of the native reference areas, as the residual impacts of bridal creeper will remain, especially at sites where bridal creeper has dominated over the long-term.

Clearly when managing an environmental weed, efforts need to move beyond targeting a single weed species to one where a whole community is managed. This would involve targeting all undesirable exotic species and encouraging the native species that these control programmes are hoping to protect.

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