

Factors affecting the re-establishment of native plant species on abandoned pastures

Matthew W. A. Appleby B.Sc. (Hons)

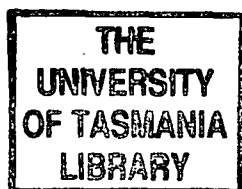
Submitted in fulfilment of the requirements of the degree of
Doctor of Philosophy

School of Geography and Environmental Studies

University of Tasmania

Hobart

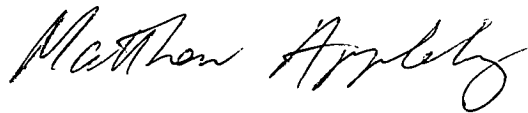
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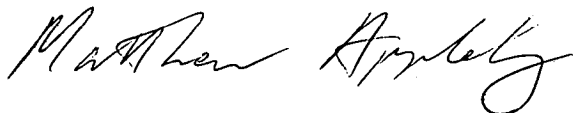
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Matthew Appleby

12 October 1998

Abstract

This thesis examines the re-establishment of native plant species on abandoned pastures in Tasmania adjacent to undisturbed native forest. The rate of native species re-establishment on these sites is typically very slow and limited to a small subset of species present in the adjacent forest. The aim of this study was to investigate the factors that limit or facilitate this re-establishment. With the continuing decline of remnant native vegetation in rural Australia, research in this area is required to promote the process of re-establishment.

Re-establishment on improved pastures was restricted to the edge of the pasture, whereas on unimproved (native) pastures re-establishment extended further into the pasture. In both cases, native trees and shrubs were relatively infrequent compared with herbaceous species.

The effects of fire, soil disturbance and grazing were examined. The exotic pasture species resprouted quickly following disturbance, but there was typically a reduction in the dominance of exotic grasses. However, very little germination or growth of native species occurred following disturbance of the pasture.

Significant inputs of seed were detected for native tree and shrub species (*Eucalyptus* spp., *Leptospermum scoparium* and *Epacris* spp.). However, relatively few seeds of native species were found in the soil seed bank in the pastures. Rates of seed predation were high in all seasons except winter. For some native species, the rate of predation may be sufficiently high to counter the large quantity of seed-fall.

Seedlings of native trees and shrubs (*Eucalyptus pulchella*, *Leptospermum scoparium* and *Bedfordia salicina*) were planted in the pasture with different levels of competition from the pasture grasses. Seedlings were more likely to survive or grow faster if grass root competition was reduced. Frost and herbivory contributed to the mortality of seedlings.

The soil nutrient status of the pasture was not significantly different from the adjacent forest soil, except for available and total phosphorus which were higher in the pasture. Under glasshouse conditions, the growth rates of the three selected native species (see above) were better on the soil collected from the pasture than forest soil. However, the formation of mycorrhizal associations was poor on seedlings grown in pasture soil, except for soils collected from the pasture edge and from beneath isolated native trees in the pasture.

In conclusion, the opportunities for the establishment of native seedlings are likely to be rare. This seems to be mainly due to the presence of exotic grasses that were highly resilient to disturbance and highly competitive.

Acknowledgments

I am indebted to my supervisor Prof. Jamie Kirkpatrick for his encouragement, wisdom and energy! Plan B worked!!

I acknowledge the assistance of an APA scholarship in supporting this project. Without the scholarship I would probably never have started a PhD or moved to Tasmania(so they're to blame!).

John Hamilton and Jean Taylor for allowing me to work on their land at Kettering. Hobart City Council allowed me to conduct surveys and experiments at the Ridgeway site. The Parks and Wildlife Service allowed me to work at the Meehan State Recreation Reserve.

Advice on statistics and some of the analyses was provided by David Ratkowsky, Andrew Zacharek and Adrian Pyrke.

The proof-reading was carried out by Mona Loofs, Jamie Kirkpatrick, Adrian Pyrke & Kerry Bridle. They're criticisms and advice were invaluable in making this thesis what it is.

Thanks to all the people that helped with fieldwork, especially the tedious bits. In particular I would like to thank Mick Ilowski, Jon Marsden-Smedley, Rachel Leary and Michelle Stewart.

I thank Nadia Marsh and James Bulinski for keeping me sane and happy, especially during the early years of the PhD.

A big thanks to all the students and staff in Geography and Environmental Studies who provided help, advice, fun and made the project more enjoyable.

Dennis Charlesworth carried out the chemical analysis on the soil samples.

Michael Harlow and David Sommerville assisted with putting recalcitrant computers and printers back in their place (*i.e.* helping me!).

Kate Charlesworth helped with aerial photographs and maps in the Resource Centre.

Michael Russell prepared the map of the sites.

To PK for the best music bar none.

To my family, thank you for your support and encouragement

Last but not least, Kerry Bridle. I thank her for putting up with me during the worst part of the PhD. What would I have done without the love and patience from the girl 'next door'? But how come she got Plan A?? Moral support came from the 'children', Horace, Tessa and John.

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Chapter One

Introduction

Land Degradation

In the relatively short period of time since European colonisation in 1788, well over half of Australia's native temperate forests and woodlands have been cleared or severely degraded (AUSLIG 1990; Kirkpatrick 1991). In Tasmania, more than a third of the native vegetation has been cleared since European settlement in 1803 (AUSLIG 1990). This situation is not unique to Australia. In countries with a longer history of agriculture, such as Europe, Central America and the USA, land clearance has removed most of the native vegetation.

In Australia and elsewhere, inappropriate agricultural practices have resulted in problems such as soil erosion and salinisation. At present an estimated 45% of agricultural land in Australia requires some form of reparation (Conacher & Conacher 1995). Restoration of native vegetation on agricultural land may help curb or prevent further degradation. For example, planting trees to reduce the water table can help reduce or prevent soil salinisation problems and reduce wind and water erosion.

Remnant Vegetation

Clearance and modification of native forests, woodlands and grasslands for pasture has been a major cause of habitat loss in Australia and eastern Tasmania in particular (Kirkpatrick & Dickinson 1982; DEST

1995). For example, in Tasmania between 1972 and 1980, at least 74,000 ha of native vegetation, mainly dry eucalypt forest, was converted to pasture (Kirkpatrick & Dickinson 1982). In sub-humid Tasmania the natural vegetation has been reduced to remnants of vegetation types which are poorly reserved and have high concentrations of rare and threatened species (Kirkpatrick *et al.* 1988; Gilfedder & Kirkpatrick 1995). In the central lowland region of Tasmania there are 8,781 remnants of forest and woodland vegetation, however the majority (87%) are less than five hectares in size, with only 4% between 25 and 200 hectares (Gilfedder & Kirkpatrick 1995). The degradation of these remnants continues as a result of unsuitable management techniques, such as overstocking of domestic cattle or sheep and further clearing of forest for pastures (Kirkpatrick 1991).

In the agricultural regions of Australia, remnants are often the only examples of particular native vegetation types left (Prober & Thiele 1995; Kirkpatrick & Gilfedder 1995; Yates & Hobbs 1997b). A further decrease of biodiversity can be expected if these remnants remain small and fragmented, poorly managed, and if remnants continue to be cleared for agriculture (Fensham & Kirkpatrick 1989; Saunders *et al.* 1987). Restoration of native vegetation can help buffer the effects of edges (Haila *et al.* 1993) and can be used to create corridors to connect fragmented remnants (Merriam & Saunders 1993). The protection and enlargement of these fragmented remnants is a priority if we are to manage and conserve biodiversity (see Saunders *et al.* 1993; Prober & Thiele 1995).

Strategy for Recovery

Restoration ecology examines the methods and practicality of restoring native ecosystems which have, in most cases, been degraded as a result of human activities. The definition of 'restoration' is broad

(McLoughlin 1997). There is a continuum from natural regeneration to more interventionist methods, such as reconstruction or fabrication of a native community (Perkins 1993). While restoration of the former composition and structure are the obvious aims, restoration of the function is also essential (Armstrong 1993). Ecosystem function includes nutrient cycling, hydrological cycles and soil development.

Once the composition, structure and function are restored, the former ecosystem processes—competition, regeneration, resource utilisation—should re-develop. However, the complete reconstruction of ecosystems from a highly degraded state is unlikely given the complexity of such systems (Cairns 1993).

The challenge is to devise strategies for restoration when some components are already lost or declining (Recher 1993). The most appropriate approach differs depending on the degree of modification of the land, the species involved and the level of restoration we wish to achieve (Fry & Main 1993; Yates & Hobbs 1997a). There is no single approach to restore native vegetation on farmland (Fry & Main 1993), though broad strategies have been developed (Fry & Main 1993; Yates & Hobbs 1997a, b). These strategies are currently a guide which require local knowledge and ongoing refinement.

Restoration of Agricultural Land

Resilience

The ability of the natural ecosystem to recover from disturbance is referred to as the 'resilience' of the system (Holling 1973; Westman 1986). Resilience is affected by the degree of disturbance and species' recovery mechanisms. For example, recovery from natural disturbance

can be relatively swift and complete in some ecosystems, such as eucalypt forests burnt by fire (Gill 1981). If severely disturbed, recovery may be slow and the end result may not resemble the original community without assistance, such as the re-introduction of species, weed control and soil remediation.

Resilience would be expected to be low following pasture improvement¹ or cropping due to the massive changes to the soil and species composition. The number of years since the native vegetation was cleared would also affect the resilience. Resilience would be expected to depend on migration from outside of the disturbed area, rather than from propagules *in situ* (Grubb & Hopkins 1986). There are exceptions, for example, the soil seed bank of particular hard-seeded species (*e.g. Acacia* spp.) may persist for decades, even following ploughing (Onans & Parsons 1980).

The degree of resilience of the native vegetation will determine whether or not a more interventionist (and therefore costly) approach to restoration is needed. If the rate of natural re-establishment is proceeding at a fast rate following the cessation of farming, then there is little need for intervention. However, if the rate is slow or restricted to a small number of native species, then site amelioration and/or the re-introduction of biota maybe necessary (Lamb 1994). In Australia, natural re-establishment on areas of abandoned farmland has produced meta-stable communities which have a mixture of exotic and native species (Onans & Parsons 1980; Zeng & Whelan 1993; Yates & Hobbs 1997a). Yates & Hobbs (1997b) suggested that further re-establishment by additional native species is prevented by the poor dispersal of seed and the inability of seedlings to compete with the established vegetation.

¹ 'Improved' pastures have had fertilizers applied and seeds of pasture species sown.

Succession and Natural Re-establishment

The successional pathway following particular types of disturbance is moderately predictable for individual natural communities. The regeneration of eucalypt communities after disturbance such as fire typically follows the initial floristics model of Egler (1954) (Purdie 1977a, b; Ashton 1981). After a pasture is abandoned, it is unlikely that a normal pathway of regeneration would resume. For example, even native grasslands can inhibit the establishment of the dominant *Eucalyptus* species (Fensham & Kirkpatrick 1992; Ellis & Pennington 1992). It is also likely that many other native eucalypt forest species will be unable to establish in a closed grass sward. In addition, the propagules of native species may be less abundant if the soil seed bank is depleted and the dispersal of native seeds is poor (Onans & Parsons 1980). Therefore restoration may require an interventionist approach to facilitate the re-establishment of the native community.

Abandoned pastures provide an opportunity to study the process of succession, that is, the natural re-establishment² of native species. In turn, such studies can provide evidence of the factors affecting the rate and/or degree of natural re-establishment of native species. With a better understanding of how these factors adversely affect or facilitate re-establishment, we can apply this knowledge to develop better methods of restoration (Ashby 1987; Nepstad *et al.* 1991). Due to economic changes and environmental degradation, large areas of land cleared for agriculture are now abandoned, both in Australia and overseas (Dennington & Chadwick 1982; Fry & Main 1993; Aide & Cavelier 1994; Motzkin *et al.* 1996).

² The term 're-establishment' will be used in conjunction with improved pastures because almost all native species are displaced when these pastures are created. 'Regeneration' will generally be used in relation to native (*i.e.* unimproved) pastures.

Factors Affecting Natural Re-establishment

In Australia, the documented rate of regeneration following abandonment of pasture is typically slow and limited to a few species from the adjacent native vegetation (Onans & Parsons 1980; Zeng & Whelan 1993). A number of factors may account for the apparent resistance of exotic pastures to the invasion of native species. These factors include; the degree of disturbance, the availability of native plant propagules, competition and the alteration of soil conditions.

Degree of Disturbance

The rate of succession of native species following the cessation of agricultural practices appears to depend, at least partially, on the degree to which the site was disturbed prior to abandonment (Onans & Parsons 1980; Uhl *et al.* 1988; Nepstad *et al.* 1991; Motzkin *et al.* 1996). In general, abandoned pastures (native and improved) can regenerate back to relatively natural forest quite rapidly if the pasture was lightly grazed, not frequently burnt, and the time since the original forest was cleared was minimal (Uhl *et al.* 1988; Aide & Cavelier 1994; Motzkin *et al.* 1996).

Availability of Propagules

Preparation of sites for pasture typically involves severe disturbance to reduce the possibility of regeneration of native species from seed or root stock. Techniques that reduce regeneration include deep and repeated ploughing, repeated burning or removal of the topsoil (Uhl *et al.* 1988; Tatoni & Roche 1994; Nepstad *et al.* 1991, 1996). In these circumstances, replenishment of propagules of native species is likely to depend on dispersal from adjacent, undisturbed native vegetation.

The dispersal of native seed from surrounding remnants of native vegetation can be expected to decrease with distance from the seed source (Cremer 1977; Onans & Parsons 1980; da Silva *et al.* 1996; Hutchings & Booth 1996). Seeds transmitted by animals—either ingested or on the fur of the animal—are not as frequently dispersed into the pasture habitat (McDonnell & Stiles 1983; Nepstad *et al.* 1996; da Silva *et al.* 1996). For example, a lack of perches (due to the absence of trees) reduces the dispersal of bird-dispersed seeds, and the more open habitat discourages many small ground-dwelling mammals from utilising pastures (McDonnell & Stiles 1983; Hobbs & Mooney 1986; Uhl *et al.* 1988; da Silva *et al.* 1996; Nepstad *et al.* 1996).

Competition

The dense sward and thick root mat produced by grasses in improved pastures, and other grassland vegetation, can prevent the germination and/or establishment of other species (Nepstad *et al.* 1991; Reader & Buck 1991; Fensham & Kirkpatrick 1992; Zeng & Whelan 1993). Disturbances which create gaps in the sward are likely to facilitate germination by reducing competition between the grasses and the germinating seedlings (Noble 1980; van Vegten 1983; Nepstad *et al.* 1991; Fensham & Kirkpatrick 1992).

The minimum gap size to facilitate successful establishment of native species is variable. It is likely to depend on factors such as the level of competition from the surrounding vegetation, and the environmental stresses imposed on the seedlings (Noble 1980; Goldberg & Gross 1988). In general, germination in the larger gap sizes is more successful than in small gaps (McConnaughay & Bazzaz 1987; Reader & Buck 1991; Morgan 1997), though these large gaps tend to occur less frequently in pastures (Reader & Buck 1991). However, seedlings that do establish

may still suffer high mortality rates within the first two years following disturbance (Reader & Buck 1991).

Alteration of Soil Conditions

Pasture improvement is likely to affect the soil conditions which, in turn, may affect the ability of native species to re-establish. For example, increased soil fertility can assist exotic species to compete with native species, especially in naturally low nutrient soils (Hedde & Specht 1975; Clements 1983; Hobbs & Atkins 1988; Hobbs *et al.* 1988). Zeng & Whelan (1993) found that the fertility of abandoned pastures may decrease with time to the same level as the adjacent, uncleared land. However, in that particular study, native species re-establishment was mostly restricted to pastures with the naturally less fertile soil types.

Soil fertility is not the only factor affected by the development of pastures. For example, soil micro-organisms and soil pH can be affected by the vegetation type (Ellis & Pennington 1992). The establishment of pastures can often lead to an increase in soil pH (Buschbacher *et al.* 1988; Pywell *et al.* 1995).

Pasture species may not support the particular soil microbes that are associated with many native species, such as particular mycorrhizal fungi (Theodorou & Bowen 1971; Ellis & Pennington 1992). In addition, ploughing the pasture is likely to reduce the amount of inoculum of mycorrhizal fungal species (Moorman & Reeves 1979; Allen & Allen 1980; Bellgard 1993), which may affect the competitive ability of the native species relying on mycorrhizae for improved nutrient uptake (Allen & Allen 1984; Marks *et al.* 1991).

Thesis Aims and Structure

The main aims of this thesis are:

- to examine the factors that inhibit or facilitate the natural re-establishment of native species on abandoned pastures;
- to determine the relative impacts of these factors on the rate of re-establishment and the extent of re-invasion.

Abandoned pastures were surveyed to determine the pattern and extent of native species re-establishment (chapter 3). Differences in the ability of species to re-establish in these pastures were examined with respect to seed dispersal mechanisms, life-form characteristics of native species, environmental variables, pasture type, and time since the native vegetation was cleared.

As a result of these surveys, several research hypotheses were tested:

1. The pattern of re-establishment of native species is a function of distance from the native forest.
2. Disturbance of the grass sward will facilitate the establishment of native species.

The effects of disturbance of the pasture vegetation on native species re-establishment were examined (chapter 4). Disturbance treatments were examined for their ability to adversely affect exotic pasture species and promote the establishment of native species.

3. Native seed availability decreases with distance from the native forest.

The availability of native seeds for re-establishment in the abandoned pastures was examined (chapter 5). The input and predation of native seeds were estimated and compared with the soil seed bank in the pastures.

4. Competition from exotic pasture species and conditions in the pasture prevents successful establishment of native species.

Three common native species were used to test the suitability of the soil and other factors in the pasture for seedling establishment (chapter 6). The effects of competition with pasture species were also investigated.

In the final chapter the relative impacts of the factors examined in this thesis will be discussed. Recommendations will also be made on ways to facilitate the restoration of native vegetation on improved pastures.

Chapter Two

Site Descriptions

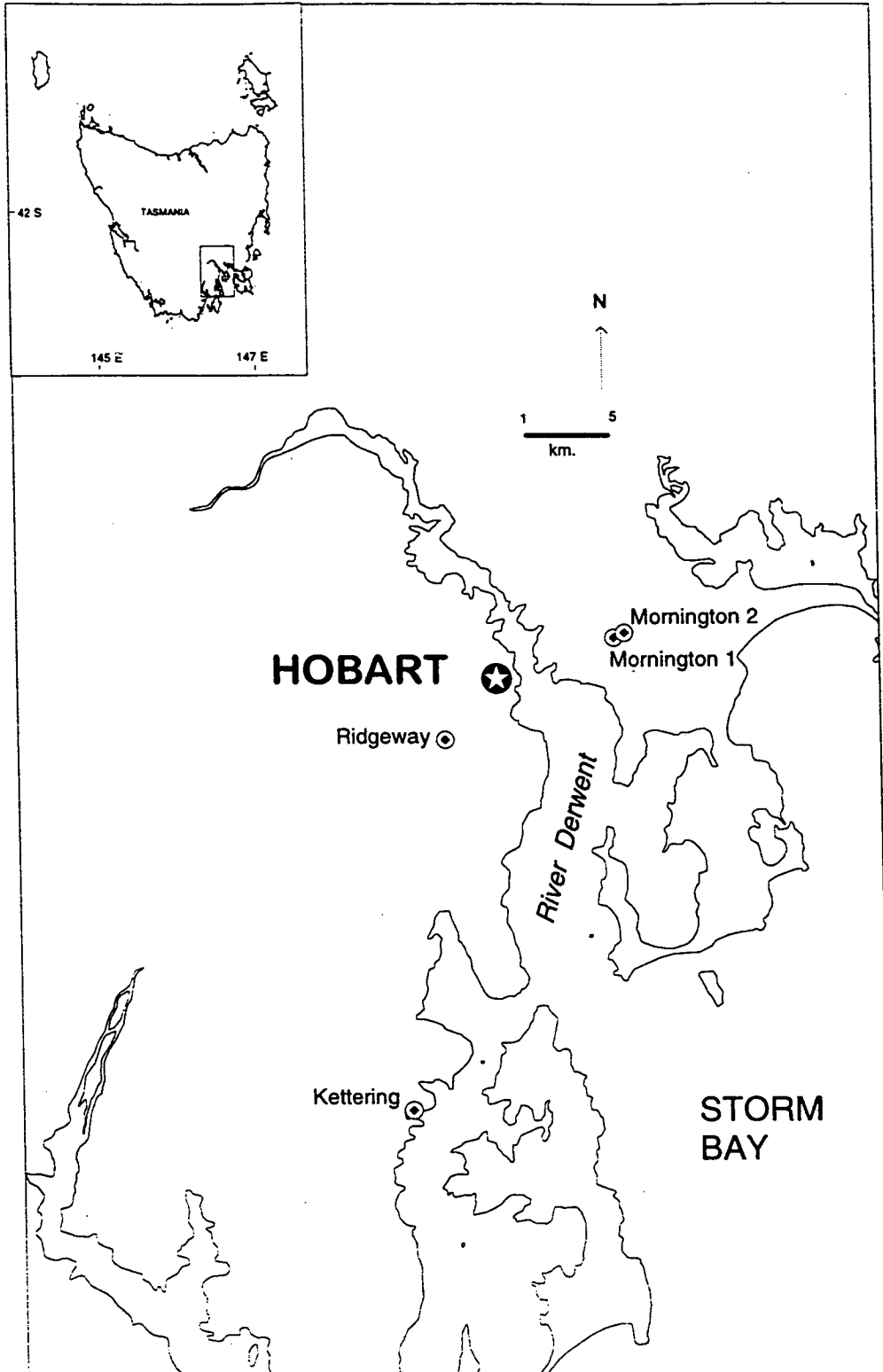
Four abandoned pastures were selected in order to examine the natural re-establishment of native species. Sites were selected on the basis that they were located adjacent to relatively undisturbed native forest. This ensured that there was a source of native species for re-establishment. Sites were selected if there was sufficient historical information about the site. All the pastures were grazed by cattle prior to being abandoned. Rabbits and native mammals such as wallabies (*Macropus rufogriseus*) currently lightly graze these sites, judging by the low abundance and variety of scats.

Site Histories

Ridgeway

The site at Ridgeway (figure 2.1; 2.2a) was resumed by the Hobart City Council in 1967 and incorporated into the water supply catchment reserve, Ridgeway Park. This site was cleared in around 1903 and had been grazed for 64 years. The pastures were the only cleared area in the vicinity. The surrounding forest shows few signs of being cleared in the past, though it is likely the understorey had been grazed. An aerial photograph of this site taken in 1965 shows that there were no native trees or shrubs present in the pastures close to the time it was abandoned. There have been no fires at the site since it was abandoned in 1967, except for January 1998.

Figure 2.1 Site locations in relation to Hobart, Tasmania.



Kettering

The site at Kettering (figure 2.1; 2.2b) was cleared in 1911 and had been grazed for 75 years. In 1986, a portion of this farm was sub-divided into blocks of between one to four hectares. The block selected for use in this study was left by the current owners to naturally revegetate with native species from an adjacent block of native forest. An aerial photograph taken in 1974 shows no native tree or shrubs present in the area of pasture surveyed. No fires have been recorded at this site since it was abandoned.

Mornington 1 & 2

Two sites were located at Mornington (figure 2.1; 2.2c, d). Both sites were abandoned when the paddocks were divided in two by the construction of a section of freeway connecting Hobart to the airport. The land was cleared in about 1954 and grazing ceased about 1970. The sections of pasture cut off by the freeway were both located next to native forest in the Meehan State Recreation Reserve. An aerial photograph taken in 1965 shows several isolated trees in each pasture around the time it was abandoned. At Mornington 1, there were seven isolated trees in the centre of the pasture. At Mornington 2, there was a single grove of trees close to the centre of the pasture.

Figure 2.2 Photographs of the sites taken in 1997

a) Ridgeway, taken from the forest / pasture boundary.



b) Kettering,
looking towards the
forest / pasture
boundary.

c) Mornington 1, the abandoned pasture is the low forest on the far side of the road barrier (centre of photograph).



d) Mornington 2, looking towards the forest / pasture boundary.



Pasture Improvement

The pastures at Ridgeway and Kettering were both 'improved' pasture. The native vegetation was cleared and the soil was ploughed to prevent regrowth of native species. The soil was then improved by the addition of fertilisers and exotic pasture species were sown.

The pastures at Mornington were not improved, and are referred to as 'native' pastures. These sites were cleared of native trees and shrubs to encourage the growth of native grasses. Any subsequent regrowth of woody species would have been suppressed.

In Australia, the establishment of exotic pasture species is favoured by the application of fertilisers because the soils are typically low in available phosphorus (Attiwill & Leeper 1987). The application of phosphorus at sowing is generally between five to ten kg per hectare (Thompson 1995) and other limiting nutrients such as nitrogen and potassium are also applied. The application of fertilisers in subsequent years varies according to the needs of the pasture species. The addition of 10 kg P per ha to the pasture soil over a period of 20–30 years can raise total soil phosphorus from 380 ppm to 670 ppm (Skinner & Attiwill 1981).

The creation of improved pastures in Tasmania generally leads to the displacement of all or most native vascular plant species. The species sown include exotic grasses such as *Dactylis glomerata* (Cocksfoot), *Lolium perenne* (Perennial Ryegrass) and nitrogen-fixing species such *Trifolium repens* (White Clover) and *T. subterraneum* (Subterranean Clover) (Thompson 1995). Many exotic species associated with improved pastures, though not deliberately sown, also establish. These include species such as the grasses *Holcus lanatus* (Yorkshire Fog-grass), *Agrostis stolonifera* (Creeping Bent-grass) and forbs such as

Ranunculus repens (Buttercup), *Hypochoeris radicata* (Flat Weed) and *Plantago lanceolata* (Plantain).

Vegetation of the Adjacent Native Forests

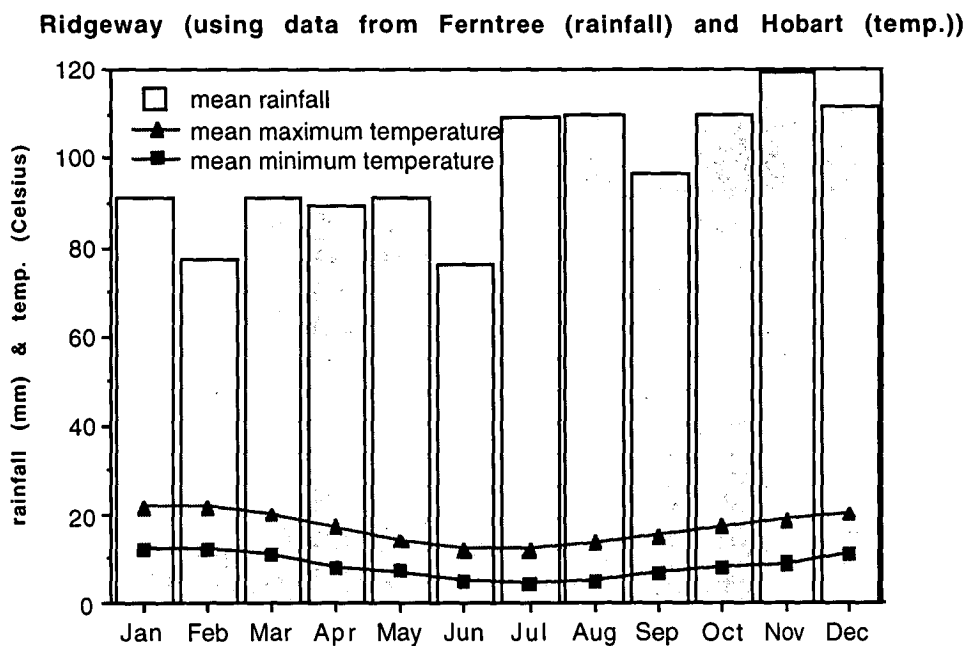
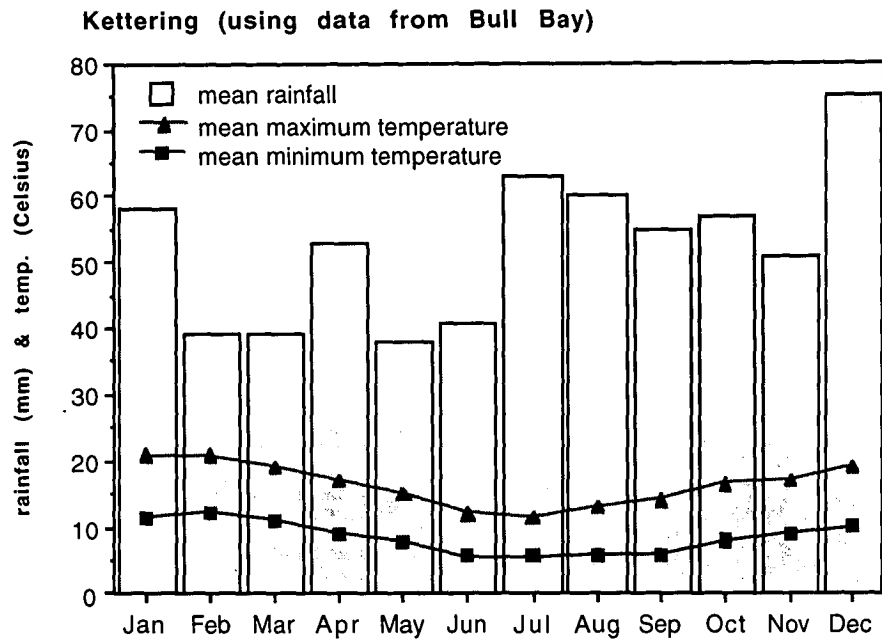
The native vegetation³ surrounding these abandoned pasture sites was similar in terms of structure and species composition. At each site, the native vegetation is open forest dominated by *Eucalyptus* species. The understorey is relatively open, with scleromorphic shrubs and a ground cover of grasses, graminoid species and bracken. There are a number of plant genera and families common to all the sites, for example, *Leptospermum* and *Eucalyptus* (Myrtaceae), *Cassinia* and *Helichrysum* (Asteraceae), *Lomandra* (Xanthorrhoeaceae), *Poa* and *Stipa* (Poaceae), *Epacris* and *Astroloma* (Epacridaceae), *Pultenaea* (Fabaceae) and *Acacia* (Mimosaceae) and Santalaceae. The species composition of each site is presented in more detail in the following chapter.

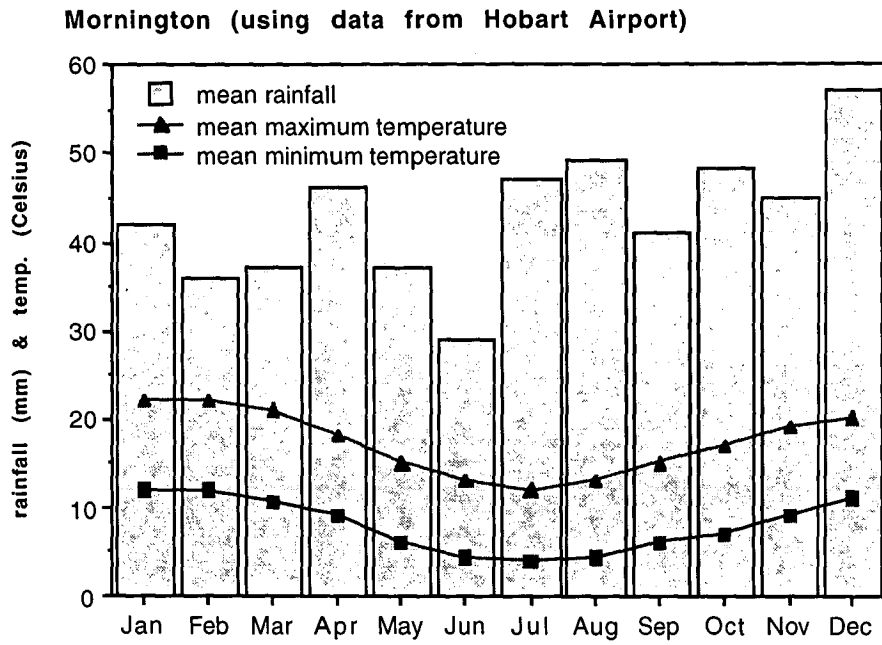
Climate and Soil Types

Data from the closest Bureau of Meteorology weather station was used to describe the climate of each site (figure 2.3). The temperature data from the Hobart station is likely to overestimate the temperature at Ridgeway by approximately 2° C (Nunez & Colhoun 1986). The rainfall data from the station at Ferntree will overestimate the rainfall at Ridgeway though the seasonality should be similar (figure 2.3). For the other two sites, the data from the weather stations should be more similar.

³ Nomenclature for vascular plant species follows Buchanan (1995).

Figure 2.3 Climate information for the three study sites (source: Bureau of Meteorology, 1997)





At Mornington and Kettering, the mean maximum temperature varies from around 22°C in summer to 15°C in winter. The mean minimum temperature varies from around 12°C in summer to 5°C in winter.

Ridgeway has slightly lower minimum and maximum temperatures than the other two sites because it is located at a higher altitude (290 m above sea level). Kettering is around 15 m above sea level and the Mornington sites are about 125 m.

Rainfall is generally uniform throughout the year, with a slight peak towards November/December. February and June are generally the driest months. Hobart Airport (near Mornington) is the driest site.

Rainfall at Ridgeway is likely to be lower than at Ferntree since Ridgeway is located on the lee side of Mount Wellington (1266 m above sea level).

The soils at Ridgeway and Kettering are both brown soils derived from Jurassic dolerite. The surface layer is brown friable loam or clay loam over a subsoil of brown or red-brown friable soil (Loveday 1955). The soil pH of the A1 horizon (0–10 cm) is 5.9 and total phosphorus is approximately 176 ppm (Grant *et al.* 1995). Sites with this soil type are generally capable of pasture improvement (Loveday 1955).

The soils at Mornington are podzols derived from Permian mudstone. The surface soil is typically grey in colour with a sandy loam texture (Loveday 1955). The soil depth is often shallow and unsuitable for development, though pastures are present where the soils are deeper. The soils derived from mudstone are slightly more acidic than those derived from dolerite (Hogg & Kirkpatrick 1974). Those soils formed on mudstone are less fertile than those formed on dolerite which also makes it less suitable for pasture improvement (Loveday 1955).

Chapter Three

The Pattern of Re-establishment in Abandoned Pastures

Introduction

A knowledge of the key factors facilitating or inhibiting re-establishment on pastures is necessary to provide a sound basis for developing techniques to restore the function and composition of the native ecosystem (Gross 1987; Nepstad *et al.* 1991; Armstrong 1993). The patterns of re-establishment of native species in previously cleared areas may indicate some of the factors that are likely to be affecting the incidence and rate of re-establishment.

Studies on the recovery of abandoned pastures have generally found that the pattern of re-establishment, and the speed of recovery, generally depend on the degree of disturbance used to create and maintain the pasture (Uhl *et al.* 1988; Nepstad *et al.* 1991, 1996; Motzkin *et al.* 1996). The results of these disturbances affect the ability of native species to regenerate within the pasture vegetation. For example, pastures created by slash-and-burn agriculture recover rapidly because native propagules are still present *in situ* and the area is farmed for only a short period (Uhl *et al.* 1988). In contrast, pasture establishment that results in a closed grassland vegetation tends to prevent other species from establishing, in particular, trees and shrubs (Nepstad *et al.* 1991; Zeng & Whelan 1993; Pywell *et al.* 1995; Ashton *et al.* 1997)

Following abandonment of agricultural land, re-establishment is likely to follow one of two patterns which relate to the resilience of the native ecosystem (Holling 1973). Firstly, if native species are able to recover from

propagules on site, such as from the soil seed bank and/or resprouting from buried root stock, this is defined as '*in situ* resilience' (Grubb & Hopkins 1986). In this case, we might expect native species to regenerate across the entire site. Secondly, if native species rely on the dispersal of propagules from outside the site, this is defined as 'resilience by migration' (Grubb & Hopkins 1986). In this case, regeneration would tend to develop from the edge(s) of the site closest to the source of propagules. However, the pattern of re-establishment will also be affected by the ability of species to establish, not simply the availability of propagules.

Resilience also depends on the duration of disturbance and the extent to which the vegetation and the site has been modified. For example, the addition of fertilisers and/or sowing seeds of exotic species can change the direction of recovery such that the original species composition may not be restored without intervention or assisted regeneration (Heddle & Specht 1975; Marrs 1985; Lambert & Turner 1987; Hobbs & Atkins 1988; Gough & Marrs 1990). Therefore, the rate of recovery is likely to be more rapid on areas of abandoned native pasture than on improved pasture. Recovery of native pastures will also be more rapid because fewer native species would have been displaced, unlike improved pastures where few or no native species persist.

Aims

The aim of this chapter is to determine whether the pattern of re-establishment is a function of the distance from the forest.

The pastures were surveyed to determine the pattern and the extent of native species re-establishment on abandoned improved pastures and regeneration on native pastures. The ability of species to establish was examined in terms of the type of seed dispersal mechanisms, species life-

form, environmental variables, the pasture type (native or improved), the number of years that the site was farmed, and the number of years since the pasture was abandoned.

We might expect that any differences in the rate of regeneration between the sites will be influenced by the age of the abandoned pasture (the number of years since abandoned) and the degree of modification to the vegetation and soil. The lower the degree of modification and the longer the pasture has been abandoned, the greater the extent of regeneration that would be expected.

Methods

Site Selection

The sites selected were Ridgeway, Kettering—improved pastures—and the two sites near Mornington—both native pastures (see chapter 2).

The original fences between the forest and the pasture were located in order to determine the line between the re-established native vegetation and the undisturbed forest. Wooden fence-posts were still relatively intact which made it easy to re-locate the fence-line. Aerial photographs showing the sites before they were abandoned were used to confirm the position of the fences and the condition of both the pastures and the adjacent forest.

Vegetation Surveys

Floristic surveys of the pasture vegetation were designed to show the pattern of re-establishment by native species. The vegetation of the pasture and the forest was surveyed along transects that ran

perpendicular to the fence. The transects started 10 metres inside the forest and ran out towards the centre of the pasture. Only the sides of the paddock adjoining undisturbed native forest were surveyed. The transects were located at least 30 metres from any other fence-line and the transects were at least 15 metres apart. Nine transects were used to survey Ridgeway; six transects at Mornington 2 and three at each of Kettering and Mornington 1. Fewer transects were used to survey Kettering and Mornington 1 due to the lack of suitable boundaries with undisturbed forest.

The size of the pastures varied between the sites. At Kettering, the pasture was 100 m by 175 m. At Ridgeway, the three pastures were each approximately 125 m by 75 m. At Mornington 1, the abandoned pasture was 175 m by 75 m, whereas the pasture at Mornington 2 was 225 m by 125m. Transects were never more than half the shortest length of the pasture.

Two metre by two metre quadrats were arranged contiguously along the length of each transect. The vascular plant species present in each quadrat were recorded and their projective cover estimated using the following scale:

1 = <1%; 2 = 1–5%; 3 = >5–25%; 4 = >25–50%; 5 = >50–75%; 6 = >75–100%.

The projective cover for the following groups of plants were also estimated in each quadrat: native shrubs; native grasses; exotic shrubs; and exotic grasses. The size of the quadrat used was determined from a species versus area curve of the pasture vegetation. A two metre by two metre square quadrat (4 m²) was sufficient to include around 90% of the vascular plant species richness at these sites.

Environmental measurements were also recorded for each quadrat. These included aspect, litter cover and bare ground cover.

Extent of Re-establishment

The maximum distance from the forest that each native species was present was determined at each site. The median distance was calculated for each species using the combined data from all the transects in the pasture at each site. If a species was not present in a transect then the value of zero was used in calculating the median distance.

Vegetation Classification

The quadrats used to survey the forest and pasture vegetation were classified into floristic groups using the program TWINSpan (Hill 1979). This program uses a polythetic divisive technique to sort the quadrats. Presence/absence data were used.

The sites were analysed separately, except for the two sites at Mornington which were in close proximity, and have a similar history and vegetation type. In all cases, the classification was taken to two divisions (*i.e.* four floristic groups). The frequencies of species present in each floristic group were calculated.

Ordination and Vector Fitting

The floristic data were ordinated using global non-metric multi-dimensional scaling (GNMDS) using the program MDS developed by ANUTECH Pty Ltd (Australian National University). The input file for MDS was created in DECODA (Minchin 1990) using the database created for the TWINSpan analysis. The measure of dissimilarity was calculated using the Czekanowski (Bray-Curtis) co-efficient. The co-efficient was calculated using the species composition (presence/absence) data. The

analyses were performed with one to four scaling dimensions, with 10 random starts.

The plots of the number of dimensions and the stress values were used to determine the most appropriate number of dimensions in which to display the results of the GNMDS ordination. The point at which the slope decreases (the 'elbow') indicates the most suitable number of dimensions. In this case, if a higher number of dimensions was selected there would not be a significant reduction in the stress level from the previous increase in number of dimensions (Kruskal & Wish 1978). The two dimensional solution was satisfactory in all three cases.

Correlations between the floristic trends produced by GNMDS and sample variables were explored using the vector-fitting algorithm in DECODA. The level of significance of the correlation was tested using a Monte-Carlo correlation test with 99 random permutations. The variables fitted were distance along the transect, aspect of the quadrat, the amount of exposed mineral soil (bare ground), and the cover of litter and grasses in the quadrat.

The vegetation at Mornington 1 (transects M1–3) was very similar to the vegetation at the southern end of the Mornington 2 site (transects M4–6). Therefore, the data for Mornington 1 and 2 were combined for the ordination and vector fitting analysis.

Vegetation Profiles

Vegetation profiles of the re-established trees and shrubs were produced along transects which ran from the edge of the forest out into the pasture. The heights of shrubs and trees were measured at every metre mark on the

transect. The plants measured were the tallest example of every shrub and tree species within 25 cm of the line transect. The transects were 50 metres long, which more than covered the area in which native shrubs and trees were found.

The heights of shrubs and trees were also measured along transects leading from isolated, mature trees in the pasture. Four transects were arranged radially around the mature tree (north, south, east, west). The heights of the tallest example of every tree and shrub species were measured using the same method as described above. The transect length was 50 metres unless other factors may have been influencing the regeneration of native species (for example, the proximity of the undisturbed forest).

Results

Change in the Number of Species

The average number of native species in the adjacent undisturbed forest communities varied between 8 and 11 per quadrat (figure 3.1). The exotic species were poorly represented in the forests; usually less than one exotic species per quadrat.

At the sites with improved pasture (Kettering and Ridgeway), the number of native species steadily declined with increasing distance from the forest boundary (figure 3.1a, b). In general, the number of native species decreased from around ten species per quadrat to only two species in the pasture at the end of the transects. There was a corresponding increase in the number of exotic species from the forest out into the pasture. The number of exotic species per quadrat was close to zero in the forest and quickly rose to about six species in the pasture. The point at which the

number of exotic species was greater than the number of native species (the 'cross-over' point) varied between five and 27 metres from the forest, with an average at 11 metres (table 3.1).

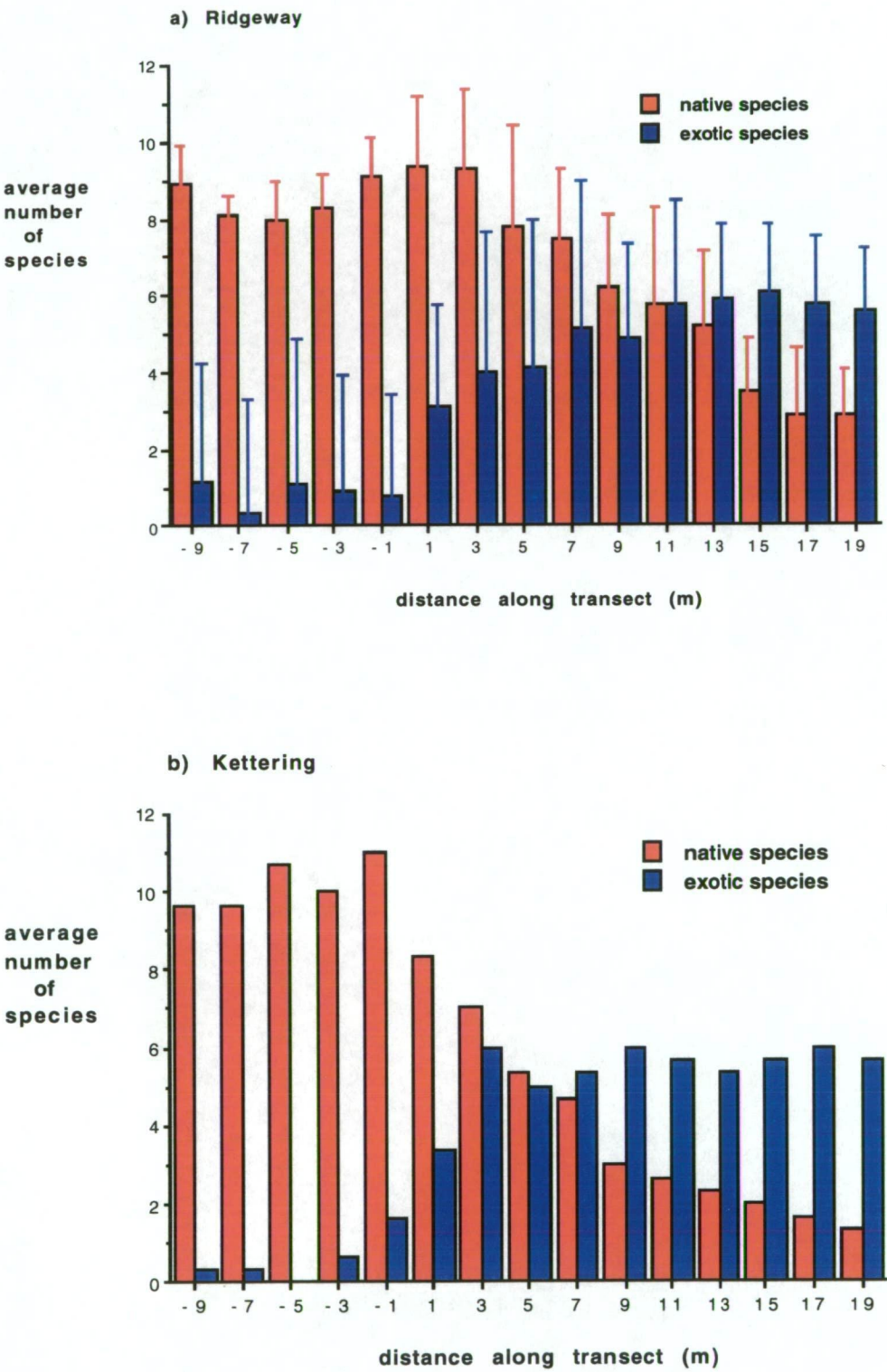
Table 3.1 The 'cross-over' point on each transect at the improved pasture sites.*

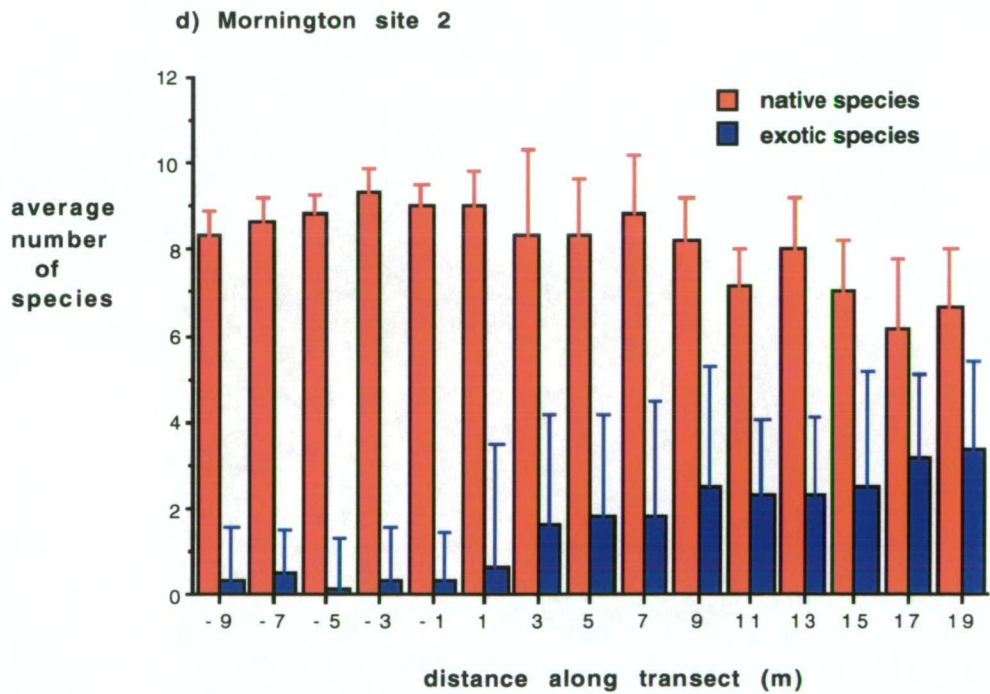
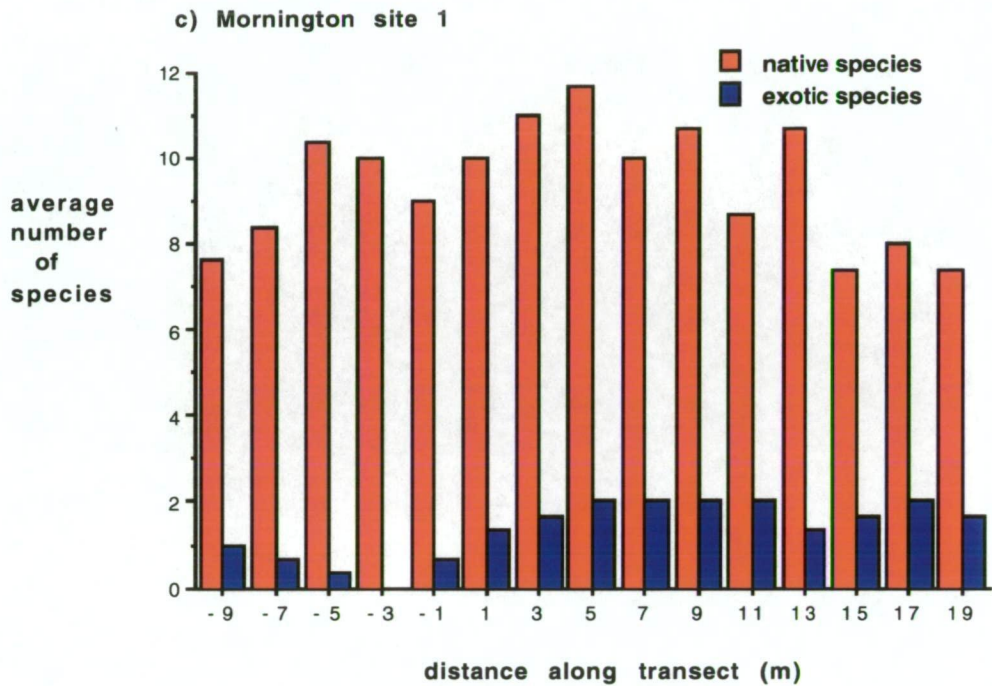
Site and Transect Number	'Cross-over' point (metres)
Ridgeway	
R 1	27
R 2	21
R 3	13
R 4	15
R 5	11
R 6	7
R 7	7
R 8	5
R 9	9
R 10	5
Kettering	
K 1	9
K 2	7
K 3	5

* The distance from the forest where the number of exotic species is greater than the number of native species

The native pastures at Mornington 1 & 2 showed a different pattern of regeneration compared with the improved pastures. The number of native species was always greater than the number of exotic species (figure 3.1c, d). The number of native species varied between seven and eleven per quadrat along the length of the transects. There were typically two or three more exotic species per quadrat in the pasture compared with the forest.

Figure 3.1 The average number of native and exotic species along the transects at each site. (Negative distance = distance from fence into the forest. Positive distance = distance from fence into the pasture. Error bars = standard deviation.)





Change in Vegetation Cover

At the two improved pastures, Kettering and Ridgeway, the median cover of exotic grasses was very low in the forest but increased dramatically at five metres from the forest (figure 3.2a, b). At ten metres from the forest, exotic grasses dominated the vegetation in the pasture with between 60 and 80% cover. The median cover of native shrubs declined from the forest out into the pasture. At approximately 15 m from the fence, the native shrub cover was zero. At Kettering, native grass cover increased from the forest to the pasture. At Ridgeway, the cover of native grasses peaked at the edge of the pasture.

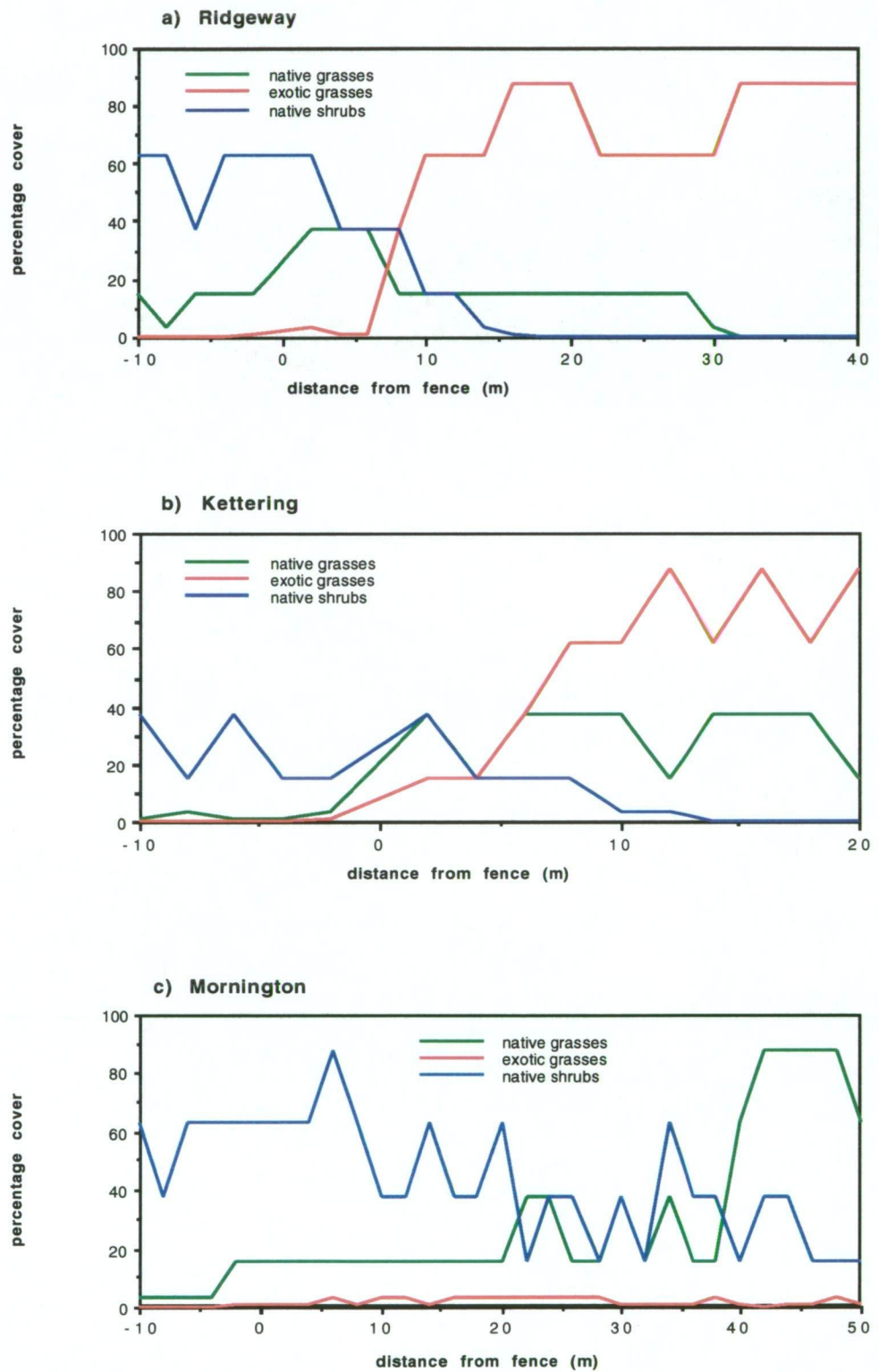
At the native pastures at Mornington, the median cover of both native grasses and shrubs remained high in both the pasture and the forest (figure 3.2c). Native grass cover peaked towards the end of the transects (40–50 m from the forest), whereas native shrub cover was greater in the forest and the edge of the pasture. The median cover of exotic grasses did not rise above 10%.

Types of Native Species that Re-establish

Kettering:

The native species that had re-established in the pasture at Kettering represented most lifeforms (woody plants, forbs, grasses and tussock graminoids). All these species are perennials and none were considered ruderal species.

Figure 3.2 The median cover of native shrubs and grasses and exotic grasses along transects at each site (Negative distance = distance from fence into forest. Positive distance = distance from fence into pasture.)



The most common species were the native grasses, *Poa rodwayi* and *Danthonia* spp., one forb, *Acaena novae-zelandiae*, and one shrub, *Epacris tasmanica* (table 3.2). The most common native species in the pasture were not as well represented in the forest community. *Leptomeria drupacea* and *Cassytha pubescens* were only found in the forest (table 3.2). *Lomatia tinctoria* and *Wahlenbergia* spp. were not present in the transect surveys of the pasture but were found elsewhere in the pasture.

Table 3.2 The re-establishment of native species at Kettering.

Species present in the pasture (frequency >10%)	Species that were more common in the pasture than the forest	Species that had not re-established in the pasture
TREES		
<i>Eucalyptus ovata</i>		
SHRUBS		
<i>Cassinia aculeata</i>	<i>Cassinia aculeata</i>	<i>Leptomeria drupacea</i>
<i>Epacris impressa</i>	<i>Epacris tasmanica</i>	
<i>Epacris tasmanica</i>		
<i>Leptospermum scoparium</i>		
<i>Pultenaea juniperina</i>		
FORBS		
* <i>Acaena novae-zelandiae</i>	<i>Acaena novae-zelandiae</i>	<i>Cassytha pubescens</i>
<i>Geranium</i> spp.	<i>Geranium</i> spp.	
<i>Gonocarpus tetragynus</i>		
<i>Viola hederacea</i>		
TUSSOCK		
GRAMINOIDS		
<i>Lepidosperma laterale</i>		
GRASSES		
* <i>Danthonia</i> spp.	<i>Danthonia</i> spp.	
<i>Ehrharta stipoides</i>		
* <i>Poa rodwayi</i>		

* The most common native species in the pasture

Ridgeway:

The native species that had re-established at Ridgeway also represented most lifeforms and were perennial species (table 3.3). The most common native plants to re-establish were two shrubs, *Leptospermum scoparium* and *Pultenaea juniperina*, a grass, *Poa rodwayi* and a forb, *Acaena novae-zelandiae*. These four species were also common in the forest. Seven native species were more common in the pasture than the forest. *Hypericum gramineum* and *Diplarrena moraea* were only found in the forest and appear to be unable to re-establish in the pasture (table 3.3).

Table 3.3 The re-establishment of native species at Ridgeway.

Species present in the pasture (frequency >10%)	Species that were more common in the pasture than the forest	Species that had not re-established in the pasture
TREES		
<i>Acacia dealbata</i>	<i>Eucalyptus globulus</i>	
<i>Eucalyptus pulchella</i>		
SHRUBS		
<i>Epacris impressa</i>		
* <i>Leptospermum scoparium</i>		
* <i>Pultenaea juniperina</i>		
MAT SHRUBS		
<i>Astroloma humifusum</i>	<i>Bossiaea prostrata</i>	
<i>Bossiaea prostrata</i>		
FERNS		
<i>Pteridium esculentum</i>		
FORBS		
* <i>Acaena novae-zelandiae</i>	<i>Geranium solanderi</i>	<i>Hypericum gramineum</i>
<i>Geranium potentilloides</i>	<i>Schoenus apogon</i>	
<i>Gonocarpus tetragynus</i>		
TUSSOCK GRAMINOIDS		
		<i>Diplarrena moraea</i>
GRASSES		
* <i>Poa rodwayi</i>	<i>Danthonia</i> sp.	
<i>Stipa</i> spp.	<i>Stipa</i> spp.	
<i>Themeda triandra</i>	<i>Themeda triandra</i>	

* The most common native species in the pasture

Table 3.4 The regeneration of native species at Mornington.

Species present in the pasture (frequency >10%)	Species that were more common in the pasture than the forest	Species that have not re-established in the pasture
TREES		
<i>Acacia dealbata</i>	# <i>Acacia genistifolia</i>	none
* <i>Eucalyptus amygdalina</i>	<i>Eucalyptus globulus</i>	
<i>Eucalyptus globulus</i>		
<i>Eucalyptus viminalis</i>		
SHRUBS		
<i>Bursaria spinosa</i>	<i>Bursaria spinosa</i>	
* <i>Cassinia aculeata</i>	# <i>Dodonaea viscosa</i>	
<i>Epacris impressa</i>		
<i>Exocarpos cupressiformis</i>		
* <i>Pultenaea daphnoides</i>		
<i>Pultenaea juniperina</i>		
FERNS		
* <i>Pteridium esculentum</i>		
MAT SHRUB		
<i>Astroloma humifusum</i>		
<i>Bossiaea prostrata</i>		
FORBS		
<i>Acianthus</i> sp.	<i>Acaena novae-zelandiae</i>	
<i>Clematis aristata</i>	# <i>Acianthus</i> sp.	
* <i>Gonocarpus tetragynus</i>	# <i>Clematis aristata</i>	
* <i>Goodenia elongata</i>	# <i>Geranium solanderi</i>	
<i>Helichrysum scorpioides</i>	# <i>Luzula flaccida</i>	
<i>Senecio</i> spp.	<i>Senecio</i> spp.	
<i>Stylidium graminifolium</i>	<i>Stylidium graminifolium</i>	
<i>Veronica gracilis</i>	# <i>Veronica gracilis</i>	
* <i>Viola hederacea</i>		
GRASSES		
<i>Danthonia</i> spp.	# <i>Deyeuxia</i> sp.	
<i>Deyeuxia</i> sp.		
<i>Dichelachne rara</i>		
* <i>Poa</i> sp.		

* The most common native species in the pasture

Native species that are apparently absent in the forest but present in the pasture

Mornington:

A larger number of native species was found in the native pastures of the Mornington sites compared with the improved pastures (table 3.4).

Woody species were the most common native species present in the pasture (12 species), followed by forbs, grasses and one fern. The most common species in the pasture were also common in the forest. Five species were more common in the pasture. Nine species were only found in the pasture, though some of these species may have been missed in the forest surveys (table 3.4).

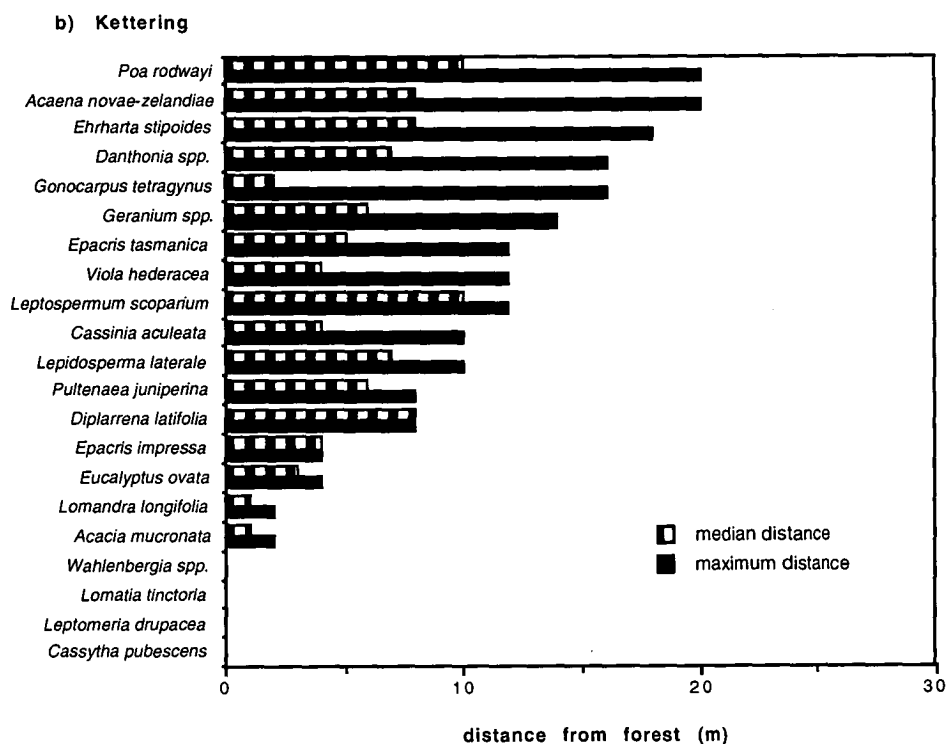
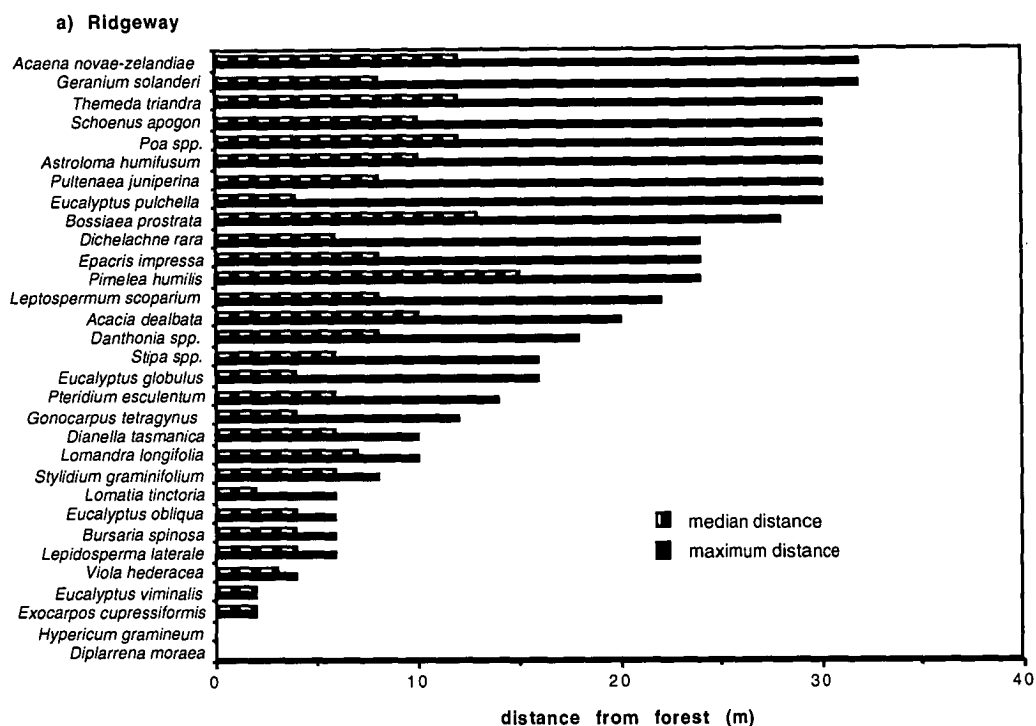
Extent of Re-establishment

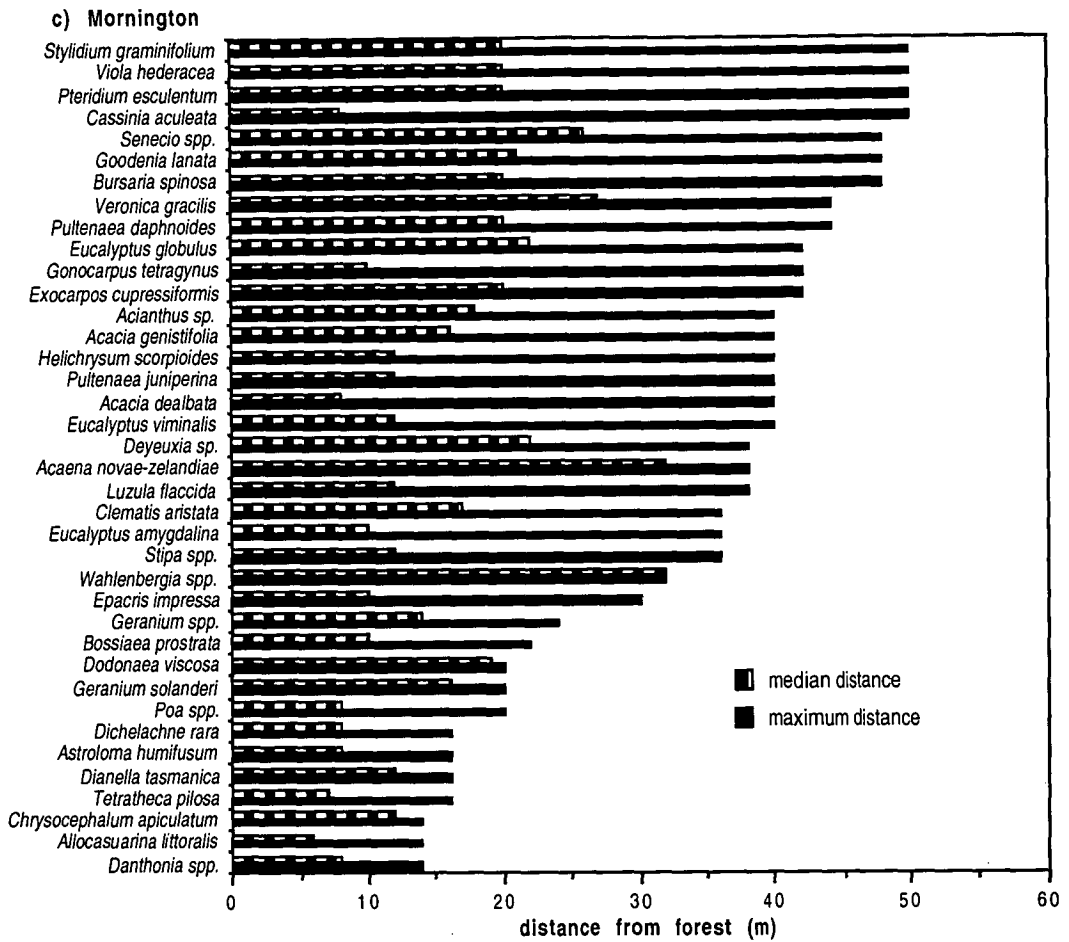
The maximum distance that native species had established into the pasture varied greatly at all sites (figure 3.3; appendix 3.1–3.3). The median distance for most species at the improved pasture sites tended to be within 10 metres of the forest (figure 3.3a, b), whereas the distance ranged between 10 and 20 metres on the native pastures (figure 3.3c). At all sites, the maximum distances were typically double the median distance.

In the improved pasture sites, the extent of re-establishment was greater at Ridgeway, the site which has been abandoned for a longer period.

However, the extent of re-establishment on the native pastures (Mornington) was far greater than at Ridgeway, even though these sites were abandoned at around the same time.

Figure 3.3 The extent of re-establishment of native species at each site.





The native species that had re-established far into the improved pastures tended to be herbaceous species (grasses and forbs) (figure 3.3a, b). The majority of native trees and shrubs were closer to the forest, though some were able to establish far into the pasture (e.g. *Pultenaea juniperina*, *Epacris* spp. and *Astroloma humifusum*). Tussock graminoid species, such as *Lepidosperma laterale*, *Lomandra longifolia* and *Diplarrena moraea*, only established close to the forest, or not at all.

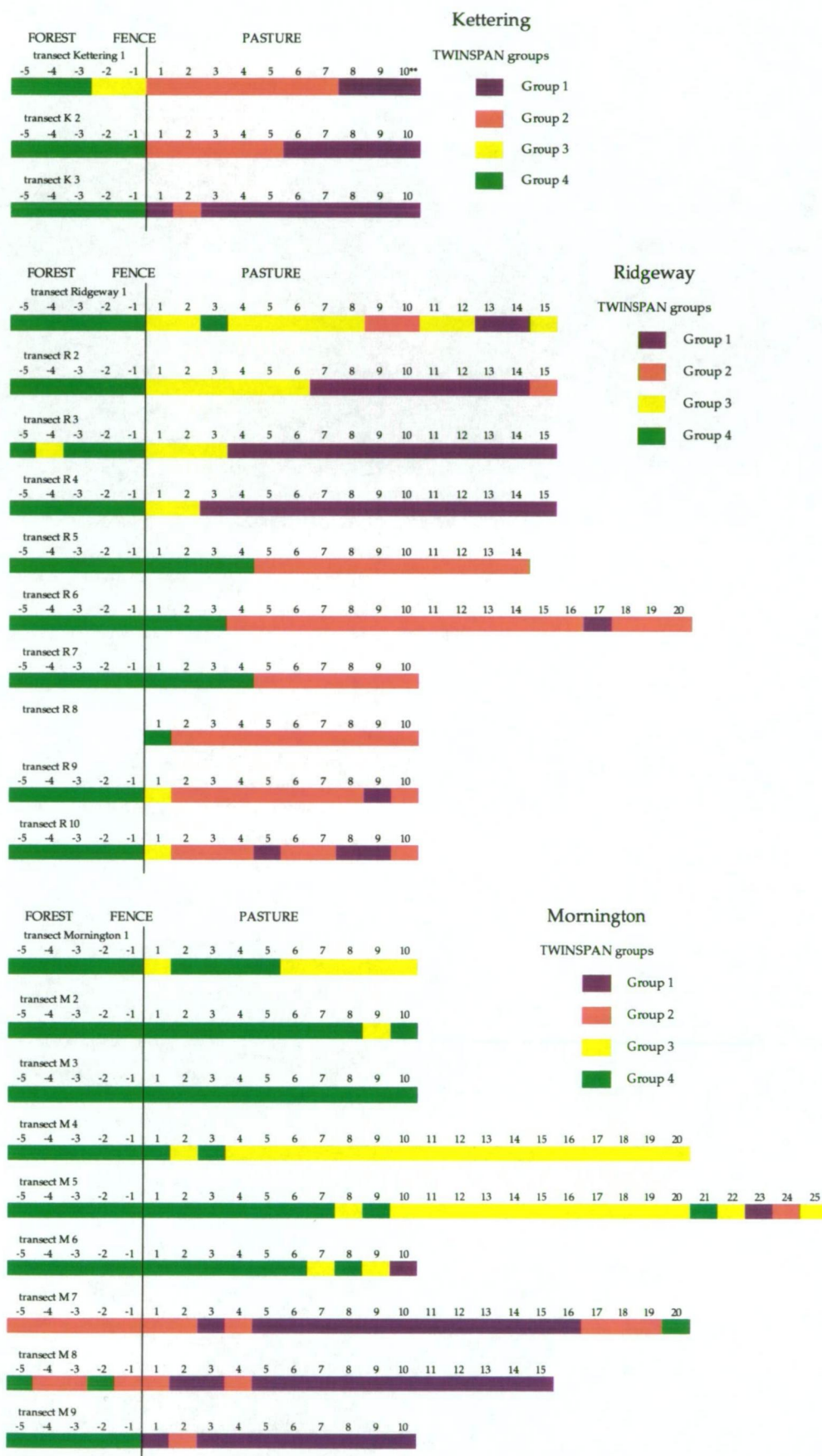
In the native pastures, there were no obvious trends with respect to the different life-forms. Species that tended to be close to the forest in the improved pastures, such as *Exocarpos cupressiformis*, *Stylidium graminifolium* and *Viola hederacea*, were present far into the native pastures (figure 3.3c).

Classification of Vegetation Data

Kettering:

The quadrats at this site were primarily divided into those with mostly native species and those with a larger proportion of exotics and few native species (appendix 3.4). This division separated the forest quadrats from those in the pasture (figure 3.4). The forest quadrats were separated into one large group (4) composed of purely native species and another group (3) composed of native species with a few exotic species. The pasture quadrats were divided into one group with predominantly exotic species (1) and another group with a mixture of native and exotic species (2). Along all three transects, quadrats in group 2 tended to be closer to the forest than those in group 1.

Figure 3.4 The change in vegetation type (represented by TWINSpan groups) across each transect.
(**negative numbers = forest quadrats; positive distances = pasture quadrats)



Ridgeway:

The quadrats were separated primarily into those with predominantly native species (groups 3 and 4) and those with a high proportion of exotic species and few natives (groups 1 and 2) (appendix 3.5). This separated the quadrats in the forest and near the fence from those further out in the pasture (figure 3.4). In the majority of the transects, quadrats in the forest were represented in group 4 and the quadrats adjacent to the forest were in group 3. The quadrats further out into the pasture tended to be either group 1 or group 2.

Mornington:

At the Mornington sites, the primary division of the quadrats did not separate those with native species from those with predominantly exotic species, as had occurred at the other sites. The primary division related to the particular combination of native species. The second division tended to separate quadrats on the basis of the number of exotic species (appendix 3.6). The transects were generally divided into two groups; groups 4 (forest) and 3 (pasture) or groups 2 (forest) and 1 (pasture) (figure 3.4). The transition from the forest vegetation to the pasture was not as well defined as at the other sites, for example, there was no significant change in vegetation across transect 3 (figure 3.4).

Ordination and Vector Fitting

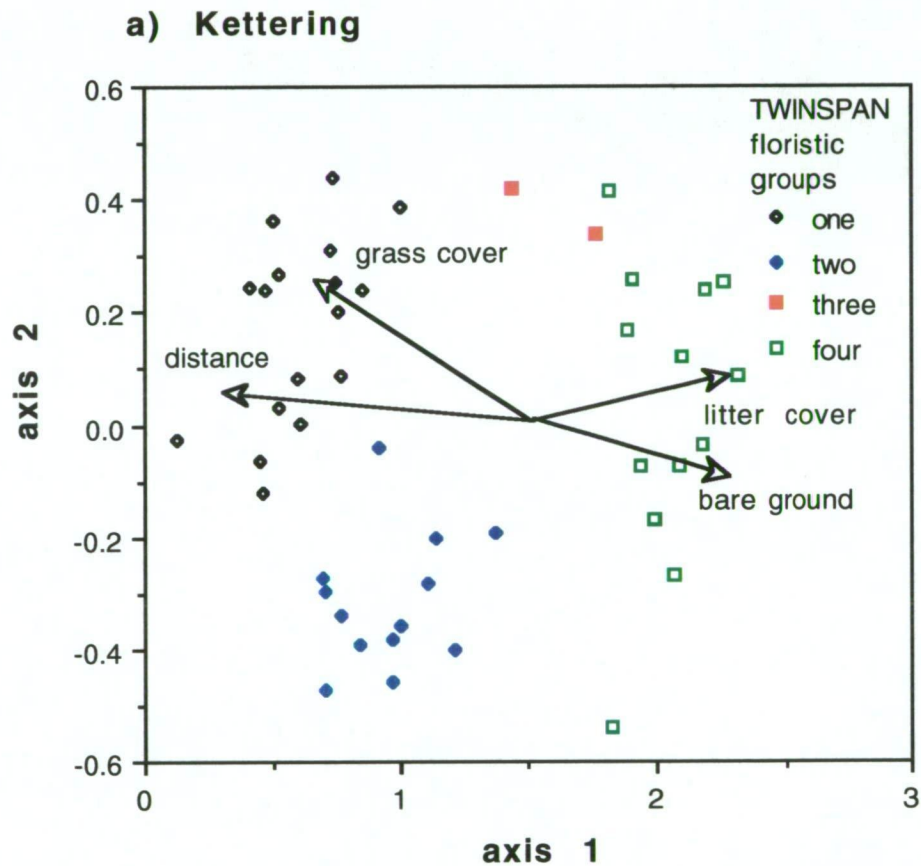
The two dimensional ordination of the quadrats at all sites tended to separate the quadrats according to the groupings defined by the classification of the floristic data—the TWINSpan groups (figure 3.5). The overlap between these groupings was minor at the improved pasture sites

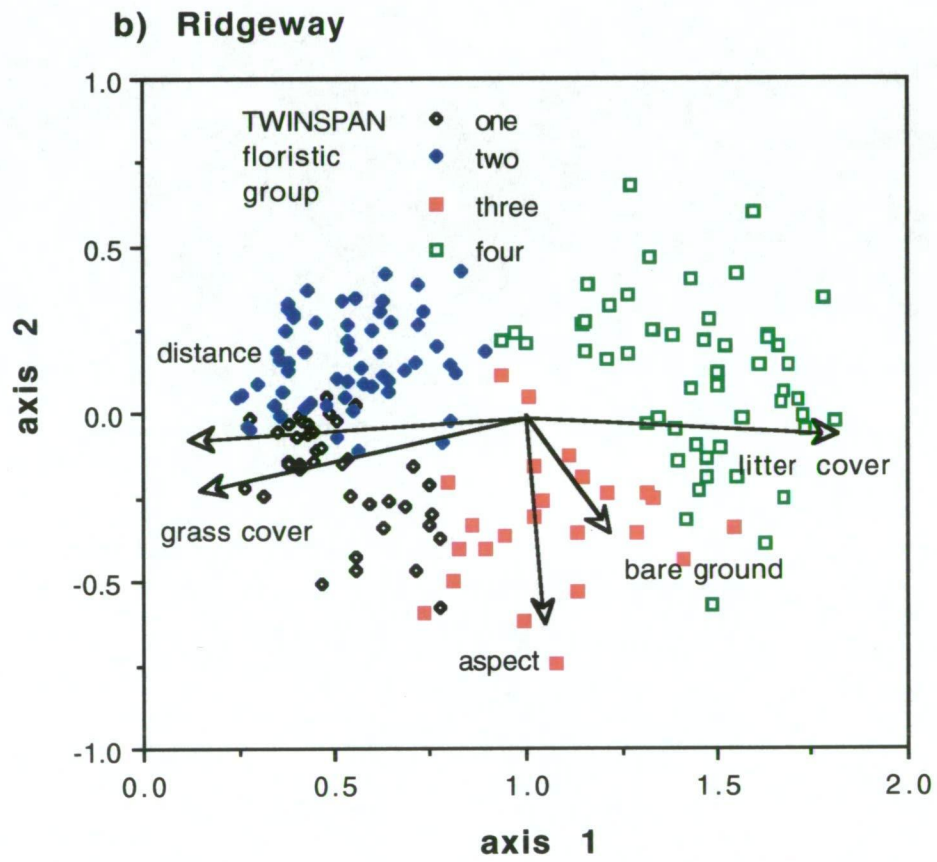
(Kettering and Ridgeway) but greater at the native pasture sites (Mornington).

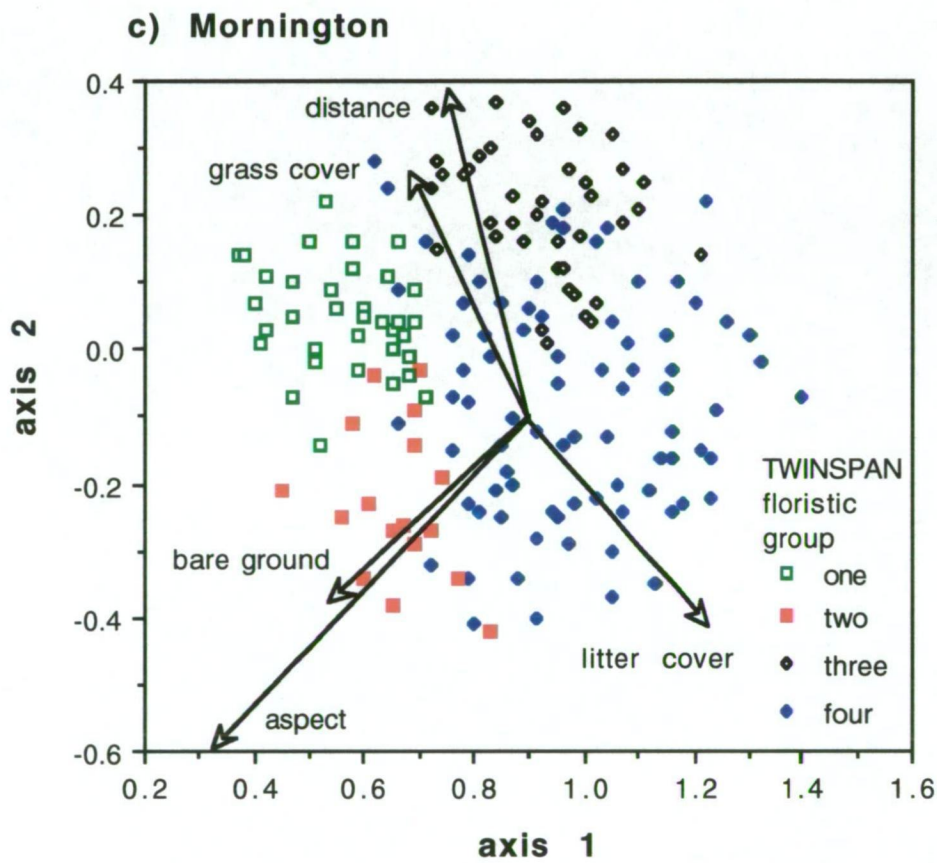
Distance along the transect, bare ground, grass cover, aspect and litter cover were significantly correlated with the trends apparent in the floristic composition (TWINSPAN groups) at each of the sites (table 3.5; figure 3.5). The angle between the vector for litter cover and the vectors for the distance along the transect and grass cover approaches 180° . This indicates that these vectors are related to the same trend in the floristic composition at each of the sites but litter cover decreases from the forest to the pasture. Grass cover increases from the forest to the pasture edge, and increases further from the edge towards the centre of the pasture. At the edge of the pasture, litter and grass cover were intermediate between the levels in the forest and the pasture.

At the two sites where the aspect varied (Mornington and Ridgeway), the vectors for aspect and bare ground were very similar, but perpendicular to the vectors for distance from the forest, grass cover and litter cover (figure 3.5b, c). This indicates that the trend in species composition relating to aspect or bare ground is distinct from the trend in species composition relating to distance, grass cover or litter cover. At Kettering, the vectors for bare ground and litter cover were almost 180° to the vector for distance along the transect.

Figure 3.5 Ordination diagrams with vectors of the sample variables. Quadrats are represented by their floristic groups, as determined by the TWINSpan classification. (The direction the vector points indicates increasing values of bare ground, grass cover and litter cover. The vector for distance indicates increasing distance along the transect from the forest out into the pasture. The vector for aspect indicates a change from southerly aspects to northerly aspects. The length of each vector is proportional to the maximum correlation co-efficient (see table 3.5))







Kettering:

In the ordination diagram, the forest quadrats (TWINSPAN floristic groups 3 and 4) and pasture quadrats (Group 1 and 2) were separated along all four vectors (figure 3.4; 3.5a). Both litter and bare ground were higher in the forest. Pasture quadrats closer to the forest tended to have greater bare ground and less grass cover than those closer to the centre of the pasture. There was less difference between pasture quadrats with respect to litter cover.

Ridgeway:

The pasture quadrats (groups 1 and 2) were separated from group 4 (mostly forest quadrats) along the vectors for distance, grass cover and litter cover (figure 3.5b). Quadrats from the pasture edge (group 3) overlapped all three other groups along these three vectors. Litter cover in the pasture quadrats (primarily groups 1, 2 and 3) increased with decreasing distance to the forest, whereas grass cover decreased towards the forest. Quadrats in groups 1 and 3 had higher bare ground and were located on northern aspects of the pastures, whereas group 2 quadrats had less bare ground and were found on southern aspects.

Mornington:

The floristic groups composed of pasture quadrats (1 and 3) usually had lower litter cover and higher grass cover than groups associated with mainly forest quadrats (2 and 4) (figure 3.5c). The two groups of pasture quadrats were separated along the vectors for bare ground and aspect. Quadrats from group 1 were found on northern aspects and had more bare ground. The same relationship appears to separate the two forest

groups (2 and 4). Both groups 3 and 4 are found on southern aspects and have less bare ground.

Table 3.5 The maximum correlation co-efficients (R_{\max}) and the angles between fitted vectors for sample variables and the configuration axes for the two dimensional ordination of the floristic data at each site.

Site / Variable	Number of quadrats	*R _{max}	Angle to axis	
			axis 1	axis 2
Kettering				
<i>distance along transect</i>	45	0.93***	176	86
<i>grass cover</i>	45	0.79***	156	66
<i>bare ground</i>	45	0.56***	19	109
<i>litter cover</i>	45	0.46**	17	73
<i>aspect</i>		n/a		
Ridgeway				
<i>distance along transect</i>	174	0.85***	168	101
<i>grass cover</i>	174	0.85***	161	110
<i>bare ground</i>	174	0.24***	68	158
<i>litter cover</i>	174	0.78***	6	96
<i>aspect</i>	174	0.48***	86	176
Mornington				
<i>distance along transect</i>	175	0.71***	101	11
<i>grass cover</i>	175	0.56***	114	24
<i>bare ground</i>	175	0.46***	152	118
<i>litter cover</i>	175	0.57***	55	145
<i>aspect</i>	175	0.81***	151	119

Monte-Carlo correlation test *** Probability < 0.001 ** 0.001 < P < 0.01

n/a = not applicable

Vegetation profiles of native and exotic shrubs and trees

The vegetation profiles of the pastures at Kettering and Ridgeway show that the native shrubs and trees were taller close to the boundary with the forest (figure 3.6a; 3.7a). The extent of the re-establishment was around 20 metres from the forest at Ridgeway and 13 metres at Kettering.

Occasionally there were single trees or shrubs established far into the pasture, away from the main group. The height of the native trees and shrubs decreased with distance from the forest.

The distribution of the exotic shrubs, mostly *Erica lusitanica*, was less constrained (figure 3.6b; 3.7b). The exotic shrubs spread along the length of the transect with only a few gaps. However, not all paddocks were affected by the exotic shrubs. The height of these plants did not usually exceed one metre.

Around isolated eucalypt trees, the number of seedlings/saplings increased dramatically at around 5 m from the trunk of the adult tree (figure 3.8; figure 3.10). The number and height of seedlings/saplings was greatest on the north side of the adult tree and lowest on the west. Litter cover tended to decrease with distance from the trunk, whereas bare ground increased. Beyond the canopy of the adult tree, grass cover increased dramatically.

Around isolated *Acacia dealbata* trees, there was a dense grove of younger individuals close to the trunk of the adult tree (figure 3.9; 3.11). These young individuals were clones, connected to the adult tree by its roots. The greatest density of clones was on the east side of the adult and lowest on the west and south.

Figure 3.6 Vegetation profiles of shrubs and trees along transects leading from the fence into the pasture at Kettering. (Height = average maximum height. Error bars = standard deviation).

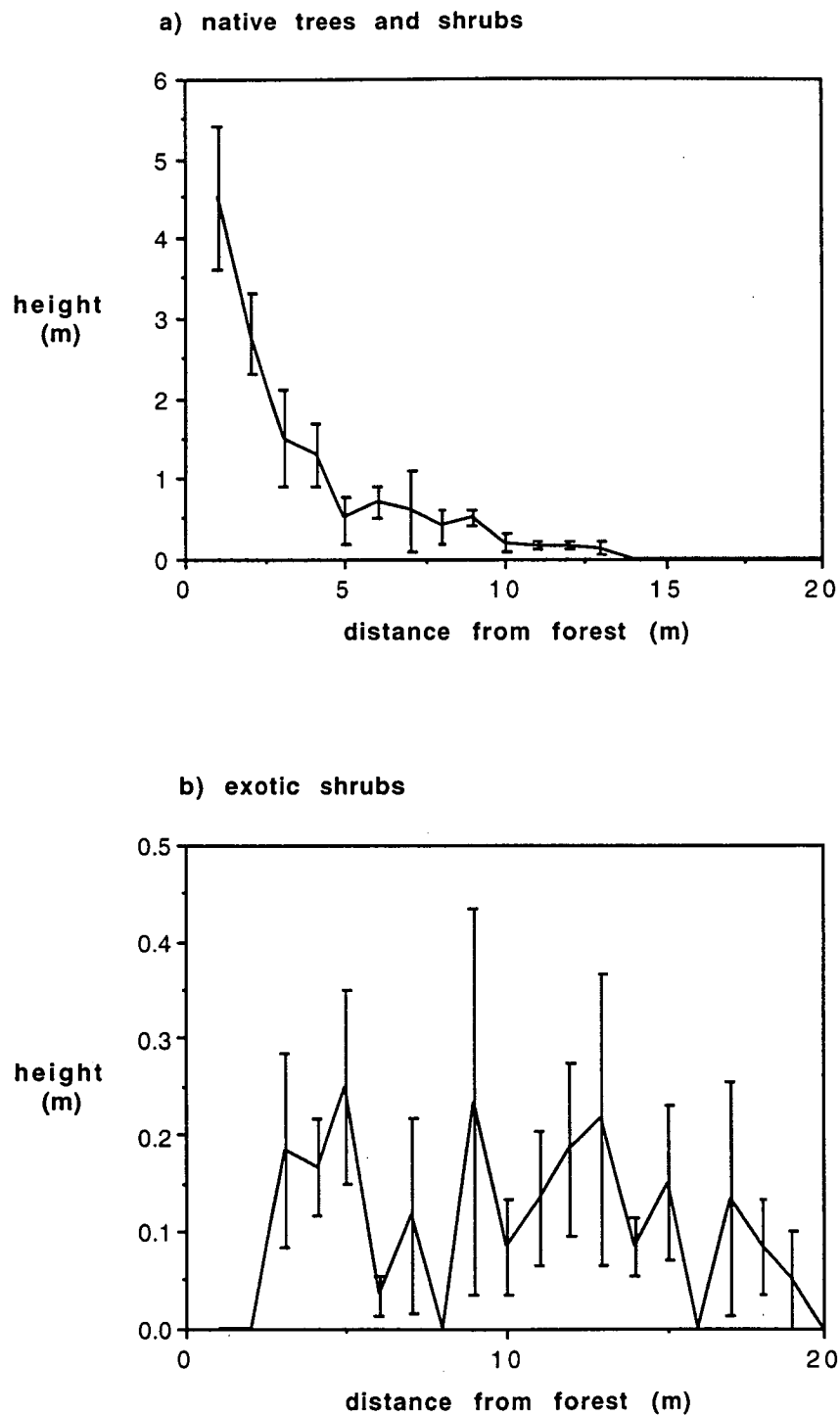


Figure 3.7 Vegetation profiles of shrubs and trees along transects leading from the fence into the pasture at Ridgeway. (Height = average maximum height. Error bars = standard deviation).

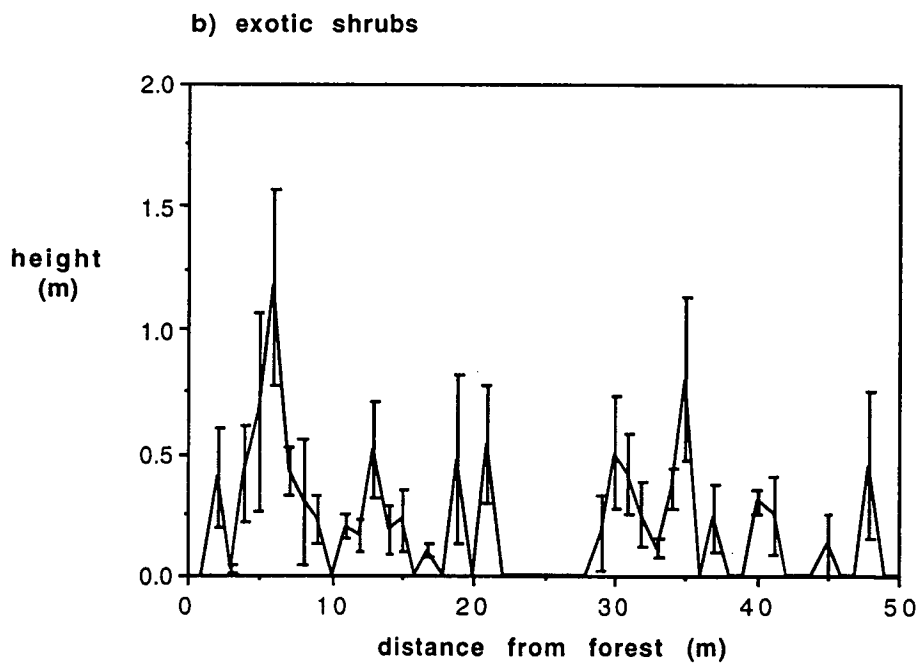
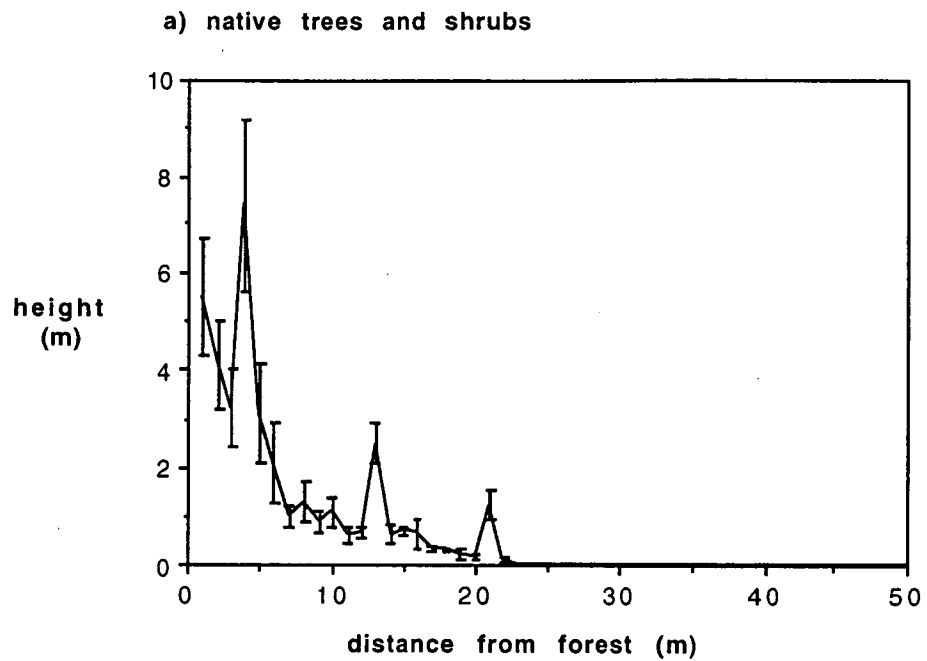


Figure 3.8 Vegetation profiles of *Eucalyptus amygdalina* seedlings / saplings growing beneath isolated adult trees in the pasture. Transects were placed in a north / south and east / west direction beneath the adult tree. (Height = average maximum height. Error bars = standard deviation).

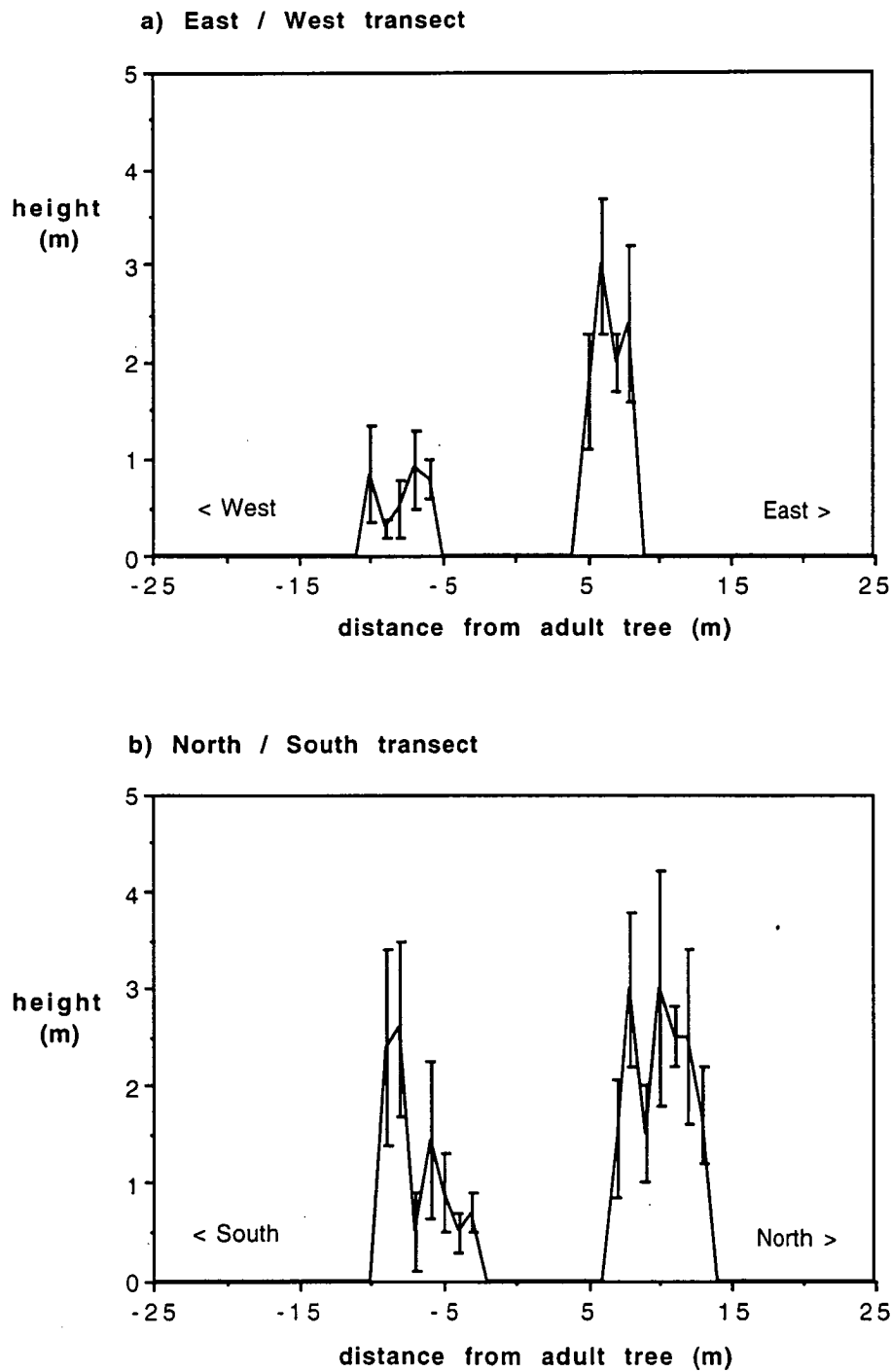


Figure 3.9 Vegetation profiles of *Acacia dealbata* seedlings / saplings growing beneath isolated adult trees in the pasture. Transects were placed in a north / south and east / west direction beneath the adult tree. (Height = average maximum height. Error bars = standard deviation).

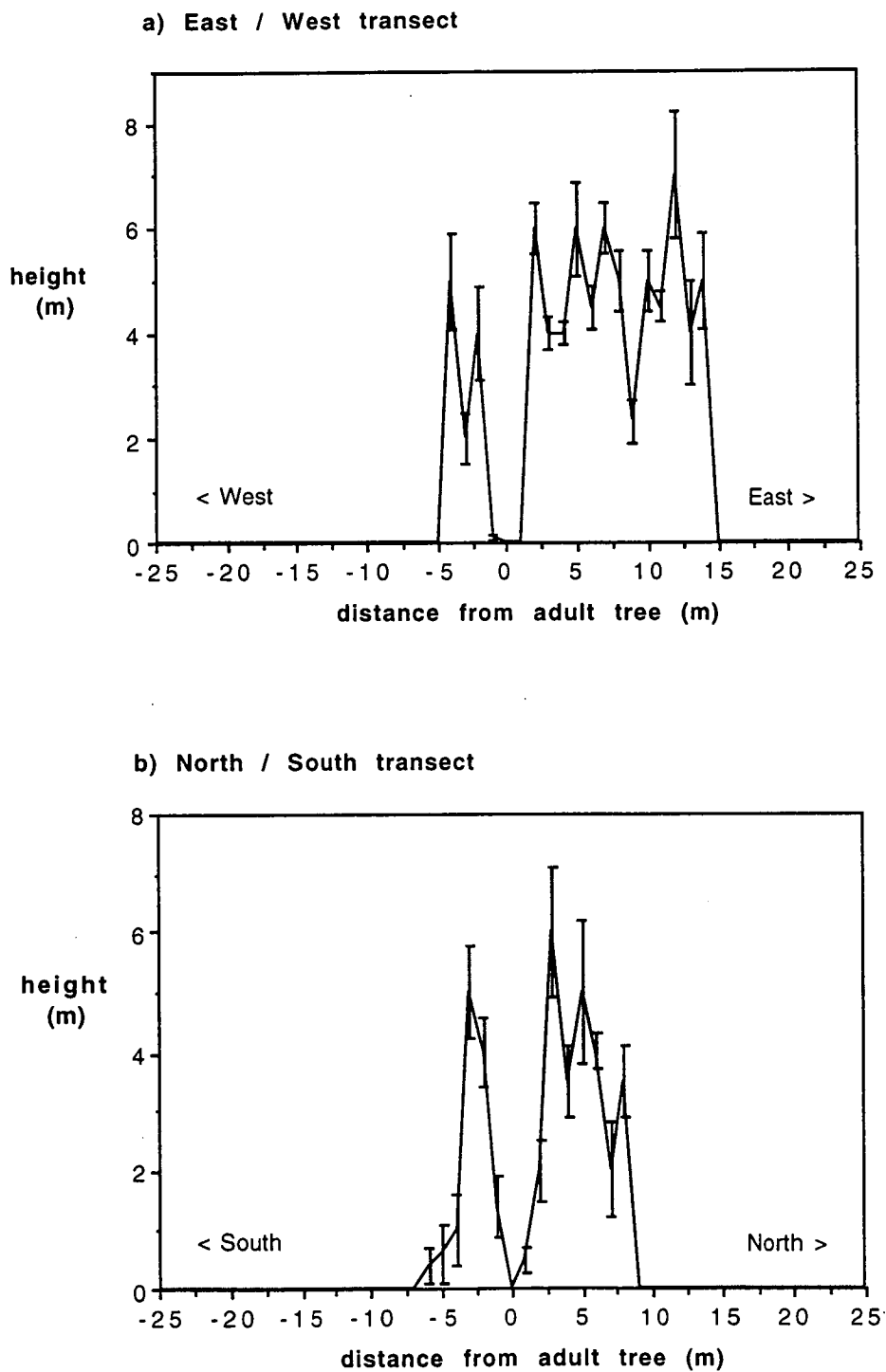


Figure 3.10 Seedlings and saplings of Eucalyptus amygdalina around the base of an adult tree, Mornington 2.



Figure 3.11 Root-suckers of Acacia dealbata around the base of an adult tree, Mornington 2.



Discussion

Resilience of Native Species

The recovery of the abandoned pastures is progressing slowly, especially on improved pastures. It appears that almost all native species in the forest are able to re-establish, though with varying degrees of success (table 3.2–3.4). The composition of the pastures close to the forest at each site is similar to the forest vegetation, except for the persistence of a small proportion of exotic species (figure 3.4; appendix 3.4–3.6). The pasture edge also resembles the forest in structure with the development of a canopy of native shrubs and trees (figure 3.6a; 3.7a). Very few exotic species have managed to invade the forest from the pasture. Therefore, it seems likely that the number of exotic species in the pasture may continue to decline as the vegetation in the pastures resembles the forest in both composition and structure (see Nepstad *et al.* 1991).

Re-establishment on improved pastures was generally restricted to the strip of the pasture adjacent to undisturbed native forest (figure 3.1; 3.2). Towards the centre of the paddock there were usually only one or two native species, such as *Poa rodwayi* and other native grasses. This pattern of re-establishment suggests there is no *in situ* resilience (Grubb & Hopkins 1986). The recovery of the native community therefore depends on migration of propagules (resilience by migration) from the adjacent forests (Grubb & Hopkins 1986). In abandoned improved pastures generally, the availability of propagules *in situ* is not common and re-establishment depends on seed dispersal (Nepstad *et al.* 1991; Aide & Cavelier 1994; da Silva *et al.* 1996). However, the seeds of some species may persist in the soil, particularly those with hard seeds, such as some Fabaceae and Mimosaceae (Onans & Parsons 1980).

Many of the species present far into the improved pastures have adaptations that would assist dispersal over long-distances. These adaptations include: seeds that attach to the fur of animals (e.g. *Acaena novae-zelandiae*, *Stipa*, *Danthonia*), small seeds or those with features to assist with wind dispersal (e.g. *Epacris* spp., *Cassinia aculeata*); and seeds which are collected by seed harvesting ants (e.g. *Bossiaea prostrata* and *Pultenaea juniperina* (Berg 1974)).

On native pastures, native species richness did not decrease significantly from the forest out into the pasture (figure 3.1c, d; 3.3c). The types of native species present far from the forest were not restricted to grass species as was found in the improved pastures. This pattern of re-establishment at the native pastures is perhaps more indicative of *in situ* resilience (Grubb & Hopkins 1986). Some native species were probably retained following clearing since the soil was not disturbed by ploughing, and exotic pasture species were not actively promoted to replace native species. A similar pattern was observed in the studies by Nepstad *et al.* 1991, Taton & Roche 1994 and Motzkin *et al.* 1996.

However, for some species, especially *Eucalyptus* spp., *in situ* resilience would be negligible if individuals from these species were cleared, even in native pastures. The soil seed banks of *Eucalyptus* spp. are short-lived and regeneration from seed usually only follows the mass release of seed stored in the canopy (Ashton 1979; Vlahos & Bell 1986; Cremer 1965a, b).

Some differences in the extent of re-establishment between the sites may relate to the dispersal capabilities of the native species present in the adjacent forest. The relative lack of perches in improved pastures may account for the poor regeneration of the species with seeds typically dispersed by birds, such as *Exocarpos cupressiformis*, *Cassytha pubescens* and

Leptomeria drupacea (see Nepstad *et al.* 1991, 1996; Vieira *et al.* 1994; da Silva *et al.* 1996). Comparisons of dispersal between the native and improved pastures are difficult since there was possibly a residual seed bank in the native pastures. However, comparisons of the extent of eucalypt regeneration indicates that re-establishment maybe inhibited on improved pasture compared with native pastures (figure 3.3a–c).

Even if we accept that recovery in improved pastures is a gradual process dependent on dispersal, there still appear to be other barriers that inhibit re-establishment by native species.

Regeneration Niche

The resilience of the native community will depend not only on the availability of seeds and other propagules but also the ability of native species to compete with the pasture species. At the improved pastures, ploughing and the application of fertilizers (to relatively fertile soil) promoted a dense and vigorous sward of the sown exotic species. The less fertile soils at Mornington did not produce a dense grass sward.

At the Mornington sites, the range of native species able to re-establish away from the edge of the pasture was far greater. For example, shrubs (*Cassinia aculeata*, *Pultenaea daphnoides*) and trees (*Eucalyptus globulus*, *Exocarpos cupressiformis*) were present up to 45 m from the forest at Mornington (figure 3.3c). Aerial photographs taken in 1965 confirm that these species had not coppiced from cut stumps following clearing of the site. At Ridgeway and Kettering, native grasses were typically the only native species invading the dense swards of exotic grasses (figure 3.3a, b). This suggests that only native grasses can invade where the sward is dense. This could be due to the similarities in growth form, competitive ability and the regeneration niche of the native and exotic grasses.

There is a considerable difference in the process of regeneration between forests and closed grasslands, such as these improved pastures (Grubb 1977). The regeneration of forest communities generally involves seeds germinating following disturbance which creates clearings (*e.g.* fire or falling trees). The forest communities in the study area mostly regenerate following fire which leaves large areas of bare mineral soil free of vegetation.

In closed grasslands, such as the improved pastures, vegetative regeneration is probably more important than seed regeneration (Grubb 1977; McConnaughay & Bazzaz 1990; Williams 1992). Gaps in the sward are typically only 1–5 cm in diameter. Seed regeneration is usually only successful in large gaps in the dense sward, like those created by burrowing animals (Watt 1974; Platt 1975; Fensham & Kirkpatrick 1992; Morgan 1997). In larger gaps, competition is less intense due to the greater distance to the established plants that surround the gap. Away from the edge of the pasture, gaps were small and resulted from bandicoots digging into the soil in search of fungal fruiting bodies, invertebrates and grass roots (see Pyrke 1994).

These differences in the regeneration niches between forests and improved pastures are likely to affect the ability of species from each vegetation type to invade the other. As expected, native grasses were more able than other lifeforms to invade further into the improved pastures where the sward is dense.

In open grasslands, such as the native pastures, Grubb (1977) proposed that regeneration would generally be from seed rather than from vegetative means. In this situation, forest species could be expected to invade since the gaps are larger than in closed grasslands and, therefore,

provide a more suitable regeneration niche. This may partially explain the greater extent of re-establishment of native trees and shrubs on native pastures compared with improved pastures.

In this study, there was also evidence to suggest that the established trees and shrubs in the pasture and at the edge of the forest play an important role in the creation of large gaps in the grass sward. The cover of grasses typically decreased close to the edge of the pasture beneath the developing canopy of native trees and shrubs (figure 3.2; 3.5). The resulting larger gaps in the sward and the increase in litter cover were correlated with an increase in the number of native species (figure 3.4; 3.5 appendix 3.4–3.6).

Facilitation

The facilitation model of succession proposed by Connell & Slatyer (1977) best describes the process of re-establishment on the improved pastures. In this model, each new stage is dependent on the previous one creating a 'favourable' environment through, for example, modification of the physical environment.

Dominance of exotic pasture species

For this facilitation process to take place there needs to be a reduction in the dominance of the exotic sward. A dense perennial grass sward tends to inhibit the re-establishment of forest species, including the dominant tree species (Nepstad *et al.* 1991; Fensham & Kirkpatrick 1992). For example, the primary reason why eucalypt seedlings fail to establish in dense native grassland vegetation in central Tasmania was due to competition for moisture and root space caused by the grass sward (Fensham & Kirkpatrick 1992). Seedlings of eucalypts established better in grasslands when the grass sward was short or in gaps in the sward that

were greater than 4 cm in diameter (Noble 1980; Fensham & Kirkpatrick 1992).

In this study, gaps in the grass sward were frequent in the pasture close to the edge of the forest. The presence of adult shrubs and trees may help reduce exotic grass cover by limiting resources (*e.g.* moisture, light and nutrients) and possibly through other interactions (*e.g.* allelopathy).

Available moisture:

Around 20% of rainfall is intercepted by the canopy of *Eucalyptus* woodland/forest in S-E Tasmania (Russell 1994). Losses due to transpiration from *Eucalyptus* species can also substantially reduce soil water availability (*e.g.* around 45% of annual rainfall in *Eucalyptus salmonophloia* / *E. wandoo* woodlands in Western Australia) (Farrington *et al.* 1994; Stoneman *et al.* 1994). These two factors will substantially reduce moisture availability for species growing beneath the tree canopy, especially shallow-rooted species such as grasses.

Nutrient availability:

The success of most exotic pasture species in maintaining a dense sward partially depends on the availability of soil nutrients, in particular nitrogen and phosphorus. Pastures with less fertile soils tend to be more patchy and native species are able to invade (Nepstad *et al.* 1991; Robinson *et al.* 1993; Zacharek 1997). As eucalypts at the edge and within the pasture grow, these plants may deplete available nutrients in the soil beneath (accumulating them in plant tissues) as well as increasing soil acidity (Attiwill 1980; Bargali *et al.* 1993; Kirkpatrick 1997).

Light penetration:

The canopy of Eucalypt forests is typically more open than other tree genera, although the litter does tend to persist, creating a thick layer on the soil surface (Kirkpatrick 1997). A thick litter layer is likely to reduce the cover of shade-intolerant understorey species and inhibit further germination of many species. In the present study, the litter layer was typically thinner around the edge of the pasture than within the adjacent forest. However, the presence of litter was correlated with the re-establishment of native species and a decrease in the cover of grasses (figure 3.2; 3.5).

Allelopathy:

The release of allelopathic compounds from eucalypt species has the potential to inhibit exotic grasses. In an experiment by May & Ash (1990), stem-flow collected from eucalypt species reduced the growth of an exotic grasses, *Lolium perenne*.

Herbivory:

In California, small herbivores tended to congregate near the edge of open grasslands vegetation with shrublands (Hobbs & Mooney 1986). This probably reduced the chance of predation of rabbits, mice and voles. However, this concentrated browsing at the edge of the grassland and contributed significantly to the reduction in grass cover. In the present study, rabbits and wallabies were present at all the sites and their scats tended to be more plentiful at the edge of the pasture.

Establishment of native species

It is almost certainly the combination of all the factors discussed above that plays a role in the suppression of exotic grasses. These conditions probably adversely affect many native grasses too, although there are species which achieve greater cover beneath the canopy of eucalypts, for example *Ehrharta stipoides* (Magcale-Macandog & Whalley 1991). While the litter layer and other factors relating to the presence of the taller species may suppress pasture species, do these conditions also prevent the establishment of native species? Even if the litter layer was thick enough to block out light, there are many native species that can also germinate in the absence of light (Bell *et al.* 1993; Bell 1994) and, presumably, emerge through the litter layer. For example, studies on *Eucalyptus marginata* have found that shading and the presence of litter did not affect germination (Abbott & Loneragan 1986).

Interestingly, there was no correlation between the amount of bare ground and the number of native species in the pasture. However, soil in large gaps free of litter can be subject to alternating cycles of wetting and drying which can be detrimental to young seedlings (Fowler 1986; Battaglia & Reid 1993). In the pasture, the litter layer beneath established trees and tall shrubs was typically thin with bare ground beneath it rather than grasses. This thin litter layer may create “safe sites” for germination by acting as a mulch to prevent the soil around a seedling from drying out (Battaglia & Reid 1993). In addition, Kirkpatrick (1997) described how the tangle of small branches in the litter may provide a ‘cage’ that protects seedlings from herbivores during critical stages such as establishment.

Other conditions created below the canopy are not necessarily suitable or ideal for the establishment of native species. For example, in central Tasmania, seedlings of *Eucalyptus delegatensis* are suppressed beneath the canopy of the adult trees due to competition for soil moisture (Bowman &

Kirkpatrick 1986). Allelopathic compounds released by the canopy species may also prevent other native species (or juveniles of the same species) from re-establishing (del Moral *et al.* 1978; May & Ash 1990). In the present study, the native understorey species from the adjacent forest are presumably adapted to the conditions experienced beneath the canopy, at least to a greater extent than the exotic pasture species.

Further re-establishment

For establishment of native species to continue further away from the forest, the same type of conditions that occur at the edge of the pasture will need to be created. To create these conditions there will need to be suppression of the exotic pasture by the outer-most edge of the advancing native vegetation in the pasture (see Hobbs & Mooney 1986). This is likely to be a slow process if a canopy of native species must form in order to suppress the exotic grasses.

There were a few native trees and shrubs that had managed to establish since abandonment away from the edge of the pasture (isolated trees). How these isolated trees established is not clear. However, successful establishment almost certainly required the creation of large gaps in the grass sward.

These isolated trees have the same adverse effect on the grass sward as trees at the edge of the pasture. Beneath *Eucalyptus* species, the ground was typically bare or covered in litter, with a ring of eucalypt seedlings just beyond the reach of the adult tree canopy (figure 3.8). Beneath isolated *Acacia dealbata* trees, there were a mass of saplings produced by root suckering and very little grass cover, but high litter cover (figure 3.9).

Newly sprouted individuals of *Acacia dealbata* appear to overcome the stresses imposed by grasses through the supply of resources via the roots of the adult plant. The lack of vegetation beneath the isolated eucalypt trees was probably due to root competition from the adult plant which excludes even seedlings of the adult species (Bowman & Kirkpatrick 1986). The leaching of allelopathic compounds from the adult tree may also contribute to observed pattern (del Moral *et al.* 1978; May & Ash 1990). Beyond the canopy, the grass cover was also reduced presumably because the influence of the roots of the adult eucalypt extend beyond the canopy (Storey 1967). However, these conditions were not severe enough to prevent eucalypt seedlings from establishing (figure 3.8)

Given time, the areas beneath these isolated, dense stands of *Eucalyptus* and *Acacia* would probably start to open up, which could facilitate other native species to establish beneath them. These results suggest that the recovery of these pastures could be more rapid if these tree species are planted in the pasture—the problems associated with such planting are addressed in chapter 6.

Conclusion

The native species tend to advance as a front from the forest into the pasture. Both improved and native pastures exhibit resilience by migration, though there is some degree of *in situ* resilience in native pastures. The results indicate that there needs to be suppression of the grasses by tall shrubs and trees to facilitate native re-establishment. The rate of re-establishment is necessarily slow because there needs to be a period of growth before newly established trees and tall shrubs can suppress exotic pasture species. Therefore, re-establishment is primarily a function of distance from the forest because there was very little establishment of native trees and shrubs away from the edge of the pasture.

Appendix

Appendix 3.1 The cover and distribution of native species at the Kettering sites (numbers = vegetation cover values: 1–6).

Species	Distance along transect				
	<	FOREST	><	PASTURE EDGE	PASTURE >
<i>Acacia</i> spp.	1121	---	3	-----	2-----
<i>Cassytha pubescens</i>	-11	-1-11	-1	-----	-----
<i>Lomandra longifolia</i>	35314324233	-333	-1	-----	-----
<i>Leptomeria drupacea</i>	12	-1-213	-12	-11	-----
<i>Lomatia tinctoria</i>	1	-----	1	-1	-----
<i>Wahlenbergia</i> spp.	-11	-----	11	-----	-----
<i>Leptospermum scoparium</i>	1	-21-2112	-3--22	-----	2-----1-1-----
<i>Gonocarpus tetragynus</i>	111111	-1111	-111	-11	-----1-----
<i>Eucalyptus ovata</i>	12332222233244323	-12	-----	-----	-----
<i>Diplarrena latifolia</i>	1--1--2	-21-32	-2	-----	2-----
<i>Lepidosperma laterale</i>	--24--312113	-2--2	-----	1-1--1	-----
<i>Epacris impressa</i>	---11111	--11	-1-2--211	-----	-----
<i>Pultenaea juniperina</i>	----2-2--12	-1	-----	1-31-1	-----
<i>Viola hederacea</i>	11--11--1	-1-1--11	-1-111	-----	1-----
<i>Cassinia aculeata</i>	---1	-----	1-2-11	-1	-----
<i>Ehrharta stipoides</i>	1	-----	1	-----	2-----1---
<i>Geranium</i> spp.	-----	1--1--1	-----	1	-----1-----
<i>Epacris tasmanica</i>	1----	11--1	-----	32121222	-1----1-11-----
<i>Acaena novae-zelandiae</i>	-----	1--1--11111111	-111	---	1--11--1-1--1-
<i>Danthonia</i> spp.	----	1	-----	121--11	-111-11----1----1-----
<i>Poa rodwayi</i>	2--1--1--21	-12-21322423233233232332432432422			

3

	Distance along transect														
Species	<	FOREST					>	<	EDGE OF PASTURE					TOWARDS CENTRE OF PASTURE	>
<i>Exocarpos cupressiformis</i>	-2	-2	-2	-2	-3	-13	-2	-2	-3	-2	-2				
<i>Eucalyptus viminalis</i>	3	-2	-2	-1	-1	-3	-21	-2	-1	-2	-2				
<i>Diplazrea moraea</i>		-2	-13	-2	-22	-13	-3	-22	-12	-3	-32				
<i>Stylidium uraminifolium</i>		-1	-1	-11	-1	-1	-1	-1	-1	-1	-1				
<i>Lepidosperma laterale</i>	24	-2	-2	-1	-24	-1	-23	-42	-312	-112	-2				
<i>Lomandra longifolia</i>	1	-31	-2	-21	-2	-1	-222	-3	-33	-1	-1	-1	-1		
<i>Bursaria spinosa</i>	-3	-22	-3	-11	-11	-2	-1	-1	-2						
<i>Hypericum gramineum</i>		-1	-1	-11	-11	-11									
<i>Viola hederacea</i>		-11	-1	-1	-1	-1	-1	-1	-1	-1					
<i>Eucalyptus obliqua</i>	-43	-32	-31	-32	-224	-2	-3	-1	-1	-2	-1				
<i>Pimelea humilis</i>	1	-11	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	
<i>Gonocarpus tetragynus</i>	1	-1111	121111	111111	121111	1	-11	-111111	11111	-11111	1	-11	-111	-1	
<i>Eucalyptus pulchella</i>	2	-23243	222233	-2434443	-3222	-2	-23	-3444	-142323	42	-2	-3	-1	-1	
<i>Lomatia tinctoria</i>		-1	-1	-1	-1	-111	-11	-11	-1	-1	-1				
<i>Diarella tasmanica</i>	-21	-1	-1	-2	-1	-21	-1	-1	-1	-1					
<i>Acacia dealbata</i>	2	-1	-211	-1	-211	-1	-2	-2	-232	-31	-1	-1	-1	-1	
<i>Epacris impressa</i>	1	-1	-1111	-1	-1	-111	-1	-11	-1111	-1111	-11	-11	-1	-1	
<i>Pteridium esculentum</i>	-11	-21	-1	-1	-1	-12	-122	-1	-1	-2	-1	-1	-1	-1	
<i>Leptospermum scoparium</i>	2	-131323	-3	-23	-221132322332232	-233233	-2222212	-2222	-221	-222212221111	-21321	-11	-1221	-1	
<i>Dichelachne rara</i>	-1	-1	-1	-1	-1	-12	-2	-1	-211	-1	-1	-1	-1	-1	
<i>Eucalyptus globulus</i>		-14	-12	-12	-1	-1	-1	-1	-2	-1	-1	-1	-1	-1	
<i>Fultenaea juniperina</i>	23222	-1323	-22	-2	-2213	-221	-221	-211	-32	-32	-13232	4	-2	-222112	
<i>Stipa</i> spp.	3	-222	-1	-1	-1	-1	-1	-1	-211	-1	-1	-1	-1	-1	
<i>Astroloma humifusum</i>	-2	-111	-1	-111	-1	-2	-1	-1	-11	-3	-11	-2	-121	-1	
<i>Poa</i> spp.	-2	-23432	-1	-233	-2	-12333231	-12332321	13441214232222112332231	-2122112	-2231	-11212111	-213221211	-3221	-211	
<i>Danthonia</i> spp.		-2	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	
<i>Geranium solanderi</i>		-11	-11	-11	-11	-11	-11	-11	-11	-11	-11	-11	-11	-11	
<i>Schoenus apogon</i>		-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	
<i>Bossiaea prostrata</i>	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	
<i>Acaena novae-zelandiae</i>	-11	-1	-1	-1	-11	-1	-1	-1	-111111	-1	-1111	-1	-1	-11111	
<i>Thymochla triandra</i>		-2	-21	-3	-23	-1	-3	-2	-14	-1	-53	-54	-55	-31	

Appendix 3.3 The cover and distribution of native species at the Mornington sites (numbers = vegetation cover values: 1-6)

[illegible]

Appendix 3.4 The percentage occurrence of key species in each TWINSpan floristic group at Kettering.

(key species = species found in at least 20% of quadrats in at least one group.

* denotes exotic species)

Species	Percentage Occurrence			
	Group 1	Group 2	Group 3	Group 4
<i>Prunella vulgaris</i> *	29	-	-	-
<i>Arrhenatherum elatius</i> *	-	31	-	-
<i>Agrostis stolonifera</i> *	100	100	-	-
<i>Erica lusitanica</i> *	47	46	-	-
<i>Dactylis glomerata</i> *	35	85	-	-
<i>Anthoxanthum odoratum</i> *	53	46	-	-
<i>Hypochoeris radicata</i> *	65	15	-	-
<i>Trifolium</i> spp.*	29	8	-	-
<i>Holcus lanatus</i> *	71	69	50	-
<i>Acaena novae-zelandiae</i>	35	85	100	-
<i>Plantago lanceolata</i> *	82	100	50	8
<i>Epacris tasmanica</i>	24	62	50	23
<i>Rubus fruticosus</i> *	6	38	50	8
<i>Poa</i> sp.	100	8	100	23
<i>Gonocarpus tetragynus</i>	12	8	100	85
<i>Danthonia</i> spp.	18	69	-	8
<i>Geranium</i> spp.	6	23	-	8
<i>Leptospermum scoparium</i>	18	-	-	77
<i>Ehrharta stipoides</i>	18	-	50	8
<i>Diplarrena latifolia</i>	6	-	100	46
<i>Lomandra longifolia</i>	-	8	100	92
<i>Viola hederacea</i>	-	54	50	46
<i>Lepidosperma laterale</i>	-	31	50	62
<i>Eucalyptus ovata</i>	-	31	100	100
<i>Poa rodwayi</i>	-	92	-	15
<i>Cassinia aculeata</i>	-	38	-	23
<i>Pultenaea juniperina</i>	-	31	-	38
<i>Epacris impressa</i>	-	31	-	62
<i>Lomatia tinctoria</i>	-	-	100	15
<i>Cassytha pubescens</i>	-	-	50	46
<i>Sonchus oleraceus</i> *	-	-	50	-
<i>Astroloma humifusum</i>	-	-	50	-
<i>Acacia mucronata</i>	-	-	50	-
<i>Wahlenbergia</i> spp.	-	-	-	31
<i>Acacia verticillata</i>	-	-	-	31
<i>Leptomeria drupacea</i>	-	-	-	77

Appendix 3.5 The percentage occurrence of key species in each TWINSpan floristic group at Ridgeway.

(key species = species found in at least 20% of quadrats in at least one group.

* denotes exotic species)

Species	Percentage Occurrence			
	Group 1	Group 2	Group 3	Group 4
<i>Carex flacca</i> *	63	28	13	-
<i>Trifolium</i> spp.*	33	14	4	-
<i>Geranium solanderi</i>	3	30	17	-
<i>Poa</i> spp.	83	49	79	87
<i>Prunella vulgaris</i> *	28	47	4	6
<i>Pteridium esculentum</i>	18	4	29	21
<i>Acacia dealbata</i>	18	2	50	36
<i>Acaena novae-zelandiae</i>	23	70	67	38
<i>Agrostis stolonifera</i> *	98	98	67	9
<i>Anthoxanthum odoratum</i> *	3	44	8	19
<i>Arrhenatherum elatius</i> *	88	19	17	2
<i>Bossiaea prostrata</i>	25	2	46	9
<i>Centaureium erythraea</i> *	33	11	17	4
<i>Dactylis glomerata</i> *	85	68	75	2
<i>Holcus lanatus</i> *	68	93	13	13
<i>Hypochoeris radicata</i> *	23	32	4	11
<i>Leptospermum scoparium</i>	18	33	38	87
<i>Plantago lanceolata</i> *	98	100	88	62
<i>Themeda triandra</i>	30	4	75	4
<i>Vicia sativa</i> *	65	77	4	2
<i>Astroloma humifusum</i>	35	2	75	23
<i>Eucalyptus globulus</i>	3	-	25	-
<i>Pultenaea juniperina</i>	-	30	63	77
<i>Rubus fruticosus</i> *	-	14	25	6
<i>Pimelea humilis</i>	-	4	21	19
<i>Eucalyptus pulchella</i>	-	5	46	83
<i>Gonocarpus tetragynus</i>	-	2	38	91
<i>Erica lusitanica</i> *	-	25	-	9
<i>Stipa</i> spp.	20	-	42	11
<i>Epacris impressa</i>	10	-	54	66
<i>Eucalyptus viminalis</i>	-	-	4	21
<i>Lomatia tinctoria</i>	-	-	4	21
<i>Lomandra longifolia</i>	-	-	13	28
<i>Eucalyptus obliqua</i>	-	-	25	23
<i>Diplarrena morea</i>	-	-	-	30
<i>Lepidosperma laterale</i>	-	-	-	36

Appendix 3.6 The percentage occurrence of key species in each TWINSpan floristic group at the Mornington sites.

(key species = species found in at least 20% of quadrats in at least one group.

* denotes exotic species)

Species	Percentage Occurrence			
	Group 1	Group 2	Group 3	Group 4
<i>Eucalyptus globulus</i>	2	29	-	-
<i>Pteridium esculentum</i>	76	47	-	-
<i>Epacris impressa</i>	41	47	6	-
<i>Viola hederacea</i>	32	37	6	-
<i>Acacia dealbata</i>	22	66	11	-
<i>Eucalyptus viminalis</i>	17	20	6	22
<i>Exocarpos cupressiformis</i>	2	38	17	3
<i>Stipa</i> spp.	10	28	44	14
<i>Eucalyptus amygdalina</i>	51	70	67	35
<i>Astroloma humifusum</i>	51	53	50	73
<i>Bossiaea prostrata</i>	37	29	78	19
<i>Poa</i> sp.	100	90	56	65
<i>Pultenaea daphnoides</i>	24	35	28	11
<i>Pultenaea juniperina</i>	12	22	94	84
<i>Agrostis stolonifera</i> *	83	37	28	100
<i>Hypochoeris radicata</i> *	83	10	11	16
<i>Oxalis corniculata</i> *	7	9	39	51
<i>Gonocarpus tetragynus</i>	78	59	50	92
<i>Cassinia aculeata</i>	71	58	72	3
<i>Acaena novae-zelandiae</i>	22	6	-	3
<i>Centaureum erythraea</i> *	39	3	-	68
<i>Holcus lanatus</i> *	59	5	-	5
<i>Trifolium</i> spp.*	54	5	-	5
<i>Luzula flaccida</i>	44	9	-	3
<i>Geranium solanderi</i>	39	4	-	3
<i>Briza minor</i> *	46	13	-	49
<i>Chrysocephalum apiculatum</i>	2	-	6	38
<i>Acacia genistifolia</i>	2	-	39	5
<i>Danthonia</i> spp.	-	23	94	97
<i>Goodenia lanata</i>	-	19	44	14
<i>Allocasuarina littoralis</i>	-	-	22	16

Chapter Four

The Effect of Disturbance on the Composition of the Abandoned Pasture Community

Introduction

Grasslands with a closed sward appear to be particularly effective at preventing the invasion or establishment of shrub and tree seedlings (Pryor & Clarke 1964; Nepstad *et al.* 1991; Fensham & Kirkpatrick 1992; Zeng & Whelan 1993; Vieira *et al.* 1994). In a number of cases, this was due to intense competition for both moisture and root space close to the soil surface (McConnaughay & Bazzaz 1991; Fensham & Kirkpatrick 1992; Vieira *et al.* 1994; Nepstad *et al.* 1996). In grasslands, the establishment of trees and shrubs occurs primarily on patches of bare ground (Leigh *et al.* 1987; Williams & Ashton 1987; Nepstad *et al.* 1991; Vieira *et al.* 1994). Therefore, disturbances such as animal digging, grazing and fire may facilitate invasion by creating gaps in the vegetation (Reader & Buck 1991; Fensham & Kirkpatrick 1991; Vieira *et al.* 1994; Belsky & Blumenthal 1997).

It is generally accepted that disturbance is an important precursor to the invasion of existing plant communities by exotic species (Fox & Fox 1986; Kruger *et al.* 1986; Crawley 1987; Hobbs 1989). Disturbance reduces competition with the established species and can increase the availability of resources.

Gaps in the existing vegetation can stimulate germination by increasing temperatures or light at the soil surface. Particular types of disturbance may also stimulate germination more directly. For example, heat or

smoke produced from fire can promote the germination from the soil seed bank of a wide range of native species in Australia (Bell *et al.* 1993; Dixon *et al.* 1995; Marsden-Smedley *et al.* 1997).

The proximity of established grass roots surrounding a young seedling is considered to be an important factor determining the success of seedling establishment (Snaydon & Howe 1986; Reader & Buck 1991; Morgan 1997). However, even large gaps in grasslands can be rapidly recolonised by grasses (Reader & Buck 1991; Morgan 1997). The ability of the species present before disturbance to regenerate and possibly exclude any invading species will depend on the severity of disturbance and the life-histories of the species involved. For example, even after intense fires, geophytes and hemicryptophytes will regenerate rapidly from protected buds (Zacharek 1997). In these situations, competition for space and resources will increase rapidly after disturbance, and affect the success of the invading species (Hobbs & Huenneke 1992).

Small gaps in abandoned pastures and fields, such as those created by animal diggings, may not provide sufficient space for newly germinated species to escape competition from surrounding plants (Goldberg & Gross 1988; Reader & Buck 1991). Small gaps are often revegetated rapidly by clonal species, such as species with rhizomes (Goldberg & Gross 1988; Carson & Pickett 1990). Larger gaps created by more severe disturbance, such as fire or intense grazing, may provide more suitable conditions for invasion (Christensen & Burrows 1986; Noy-Meir *et al.* 1989).

Grazing can reduce competition from grasses and provide opportunities for other species, such as eucalypts, to establish (Noy-Meir 1989; Fensham & Kirkpatrick 1992). However, even light grazing

may prevent the establishment of seedlings of some species (Williams & Ashton 1987; Leigh *et al.* 1987; Wahren *et al.* 1994).

Aims

The aim of this chapter is to investigate the effects of different disturbance treatments on the rate of re-establishment of native species in an abandoned improved pasture. The resilience of the exotic species to these disturbances is also examined.

Treatments were selected that:

- reduced the severity of disturbance (fencing to exclude grazing mammals);
- increased the severity of disturbance (soil disturbance and burning).

The single and interactive effects of these treatments were determined.

These types of disturbance were examined because they occur naturally in these abandoned pastures. For example, the reason for the soil disturbance treatment was to mimic small diggings created by mammals such as bandicoots and rabbits. The pastures are also lightly grazed by rabbits and small native herbivores. Burning was selected because fires are a normal disturbance event in the type of environment found at the study sites. For example, fires at Ridgeway occurred in 1967 and 1998.

Methods

Experimental Design

This experiment was established at the Ridgeway site. The paddock selected was typical of the abandoned pastures. Native species were relatively well established only around the edge of the pasture.

The treatments selected were burning, small-scale disturbance of the soil, fencing the vegetation from grazing animals (*i.e.* rabbits, possums and wallabies) and some combinations of these treatments (table 4.1).

Table 4.1 The types of treatments applied to test the effects of disturbance.

(1) Control (c)	(lightly grazed, unburnt)
(2) Fenced (f)	(not grazed, unburnt)
(3) Soil disturbance (sd)	(lightly grazed, unburnt)
(4) Soil disturbance + fenced (sd/f)	(not grazed, unburnt)
(5) Burnt (b)	(lightly grazed)
(6) Burnt + fenced (b/f)	(not grazed)

The treatments were applied to 1 m x 1m plots. The corners of each plot were marked so that a quadrat frame could be relocated in exactly the same place at each survey time. The 1 m² quadrats were divided into a grid of one hundred 10 cm x 10 cm squares. The frame was placed around the plot and string threaded around the frame and through the vegetation to create the grid. This method reduced the compaction of the vegetation when the frame was placed over the quadrat.

The species present within each square were recorded and the dominant species was noted. Dominance was measured using projective foliage cover. Species frequency in a quadrat was measured as a percentage (*i.e.* the number of squares in which a particular species was present). Species dominance was also expressed as a percentage (*i.e.* the number of squares in which a particular species was dominant). Therefore, for each quadrat, the sum of the percentage dominance equals 100%, whereas the sum of the species frequencies may be greater than 100%.

The *fencing treatment* was constructed to exclude most grazing mammals present at this site (rabbits and wallabies) and those which create small holes in the grass sward (*e.g.* bandicoots). The fences were slightly larger than the plots and constructed of chicken wire (2.5 cm mesh). The bottom of the fence was pegged into the ground using 10 cm long staples to prevent animals from burrowing under the fence.

The *soil disturbance* treatment was designed to mimic the disturbance caused by the diggings of small mammals (especially rabbits and bandicoots) (Pyrke 1994). Holes were dug using a small trowel, creating a conical-shaped hole approximately 5 cm long, 3 cm wide, 3 cm deep with a small pile of soil in front of the hole. The whole quadrat was dug over in this manner so that there was one hole for each of the 100 squares in the quadrat. (During the course of the experiment, animals occasionally dug holes in the plots which were not fenced, including the control plots).

Attempts were made to keep the *burning treatment* as natural as possible whilst not compromising the experimental design. This resulted in the fires being very small (slightly larger than the plot itself)

to avoid problems with pseudoreplication. The fires were planned for spring. However, the sward was too green to burn during this period. The conditions for burning were suitable in autumn of the following year (1994). At this stage, the grasses were quite well cured (dried) which would allow the fire to carry on its own accord and the fuel to burn thoroughly.

The vegetation around each quadrat was cut and removed to form a firebreak 30 cm wide. A metal frame was placed around the quadrat to help prevent the fire from escaping. A gas flame was used to start the fires. The fires were lit on the upwind side so that the breeze would carry the flames over the quadrat. A section of grass in front of the quadrat was lit to allow some time for the fuel to catch and the fire to establish.

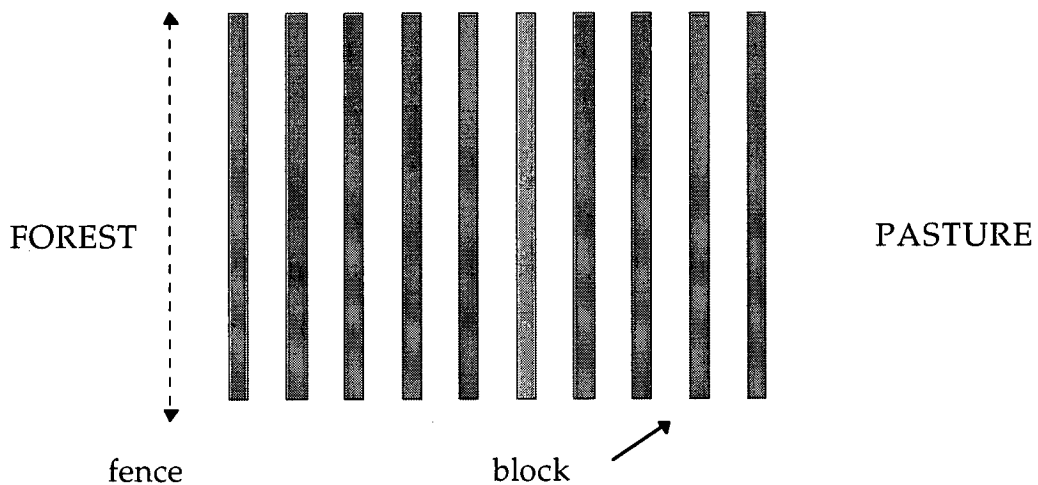
The fires did not need to be assisted after they were lit. Most of the vegetation and litter was thoroughly burnt, leaving just a thin layer of ash on the surface of the ground. However, some species were not completely burnt. Some *Plantago lanceolata* leaves were only burnt around the edges and the bases of *Dactylis glomerata* plants were usually unburnt because they were quite moist.

The fires varied in intensity from quadrat to quadrat, mostly because of the different levels of fuel available. Those quadrats closer to the forest tended to have less fuel. The intensity of the fires was recorded in five quadrats, representing the different fuel levels. To measure the change in temperature in each quadrat, two thermocouples were placed on the surface and another one was buried at approximately 1 cm below the surface. The thermocouples were linked to a datalogger which recorded the temperatures every 10 seconds.

The quadrats were arranged using a randomised block design (Neter *et al.* 1985). This design was used to determine if the effect of distance from the forest was important. There were 9 blocks, each containing two quadrats of each treatment and four quadrats of the control. Within a block, the location of each treatment was randomised. Each block was made up of fourteen quadrats placed in a line so that the block was parallel to the fence which divided the forest from the abandoned pasture (figure 4.1).

From the results of the line transect surveys, it would be expected that the distance from the forest would be a factor affecting the rate of re-establishment of native species. Soil moisture, nutrient status and/or dispersal distance could be expected to vary with distance from the forest.

Figure 4.1 The arrangement of blocks within the pasture at Ridgeway.



Each quadrat was surveyed in spring 1993, before the treatments were applied in late summer 1994. The quadrats were visited at three-

monthly intervals to check for any germination of native species, in particular, shrubs and eucalypts. The quadrats were re-surveyed in autumn 1995. No further surveys were made because there was almost negligible germination after the first year.

Analysis

Comparisons were made on the effects of the treatments on the change in species richness as well as the frequency and dominance of species and groups of species. The normality of the data was tested using plots of the standardized residuals versus fitted values and normal probability plots (McPherson 1990). It was necessary to log transform some of the data. The following equation was used to log transform the data (using frequency as an example):

$$\log_{10}(\text{frequency of species}) = \log_{10}(\% \text{ frequency} + 0.5).$$

Species richness was calculated as the number of species per quadrat (1m²). The mean change in species richness from 1993 to 1995 was calculated for both native and exotic species. Comparisons between the treatments were made using analysis of variance (ANOVA) with the statistical package SAS (SAS 1989).

The analyses of the differences between the treatments were made by one-way analysis of variance using the GLM procedure (SAS 1989). The significance of the difference in means between treatments was determined using an F-test in the GLM procedure. The level of significance was adjusted from $p < 0.05$ to $p < 0.01$. This was considered necessary because the large number of comparisons made using the same data set increases the chance of a type II error (Sokal & Rohlf 1995).

The effect of distance from the forest was also tested using treatment and block as co-variates. The analyses of the differences between the treatments and between the blocks were made by two-way analysis of variance using the GLM procedure (SAS 1989). This test would determine whether there was a significant interaction between treatment and distance from the forest.

Table 4.2 Species grouped together for the analysis of data.

Group	Species composition
Native trees & tall shrubs	<i>Acacia dealbata</i> , <i>Bursaria spinosa</i> , <i>Eucalyptus</i> spp.
Native shrubs	<i>Epacris impressa</i> , <i>Leptospermum scoparium</i> , <i>Pultenaea juniperina</i>
Native grasses	<i>Ehrharta stipoides</i> , <i>Stipa</i> spp., <i>Themeda triandra</i>
Exotic grasses	<i>Agrostis stolonifera</i> , <i>Arrhenatherum elatius</i> , <i>Dactylis glomerata</i> , <i>Holcus lanatus</i>
Exotic forbs	<i>Centaurium erythraea</i> , <i>Geranium dissectum</i> , <i>Linum</i> <i>trigynum</i> , <i>Prunella vulgaris</i> , <i>Veronica persica</i> , <i>Vicia sativa</i>

For many of the uncommon species there were too little data to analyse in the manner described above. To partially overcome this problem, the data for uncommon species were grouped together (table 4.2) and then analysed.

Results

Burning Intensity

The maximum temperature at the soil surface in the burning treatment varied considerably—from 150° to 350° C (see appendix 4.1). The increase in soil temperature at 1 cm below the surface varied from approximately 0° to 35° C. In general, areas with high fuel levels recorded high temperatures at 1 cm below the soil surface. There was likely to be variation in burning intensity and residence time both within and between quadrats.

Species Richness

Overall, there was a small, non-significant increase in native species richness ($F = 1.96$; $p = 0.09$) regardless of the treatment (including the control) (table 4.3). The only exception was a small drop in native species richness with the fenced treatment. Relative to the control, the application of the treatments lowered the increase in exotic species richness, but not significantly ($F = 0.83$; $p = 0.53$). In both cases, the effect of distance from the forest (the block effect) was not significant ($F = 0.54$; $p = 0.93$ and $F = 1.70$; $p = 0.06$).

The change in species richness was broken down into two zones (0–10m and 10–20m from the forest). The number of native species was always higher in the area closest to the forest (figure 4.2). However, in both zones there were only small changes over time in the number of species, regardless of the treatment.

Table 4.3 The mean change in the species richness of native and exotic species (number of species per $m^2 \pm$ standard deviation).

treatment	exotic species	native species
control	1.11 ± 1.21	0.25 ± 1.13
fenced	0.50 ± 1.25	-0.11 ± 0.90
soil disturbance	0.78 ± 1.11	0.89 ± 1.37
soil disturbance/fenced	0.67 ± 1.41	0.94 ± 1.21
burnt	1.00 ± 1.91	0.33 ± 1.71
burnt/fenced	0.56 ± 1.42	0.28 ± 0.83

Changes in the Vegetation of the Control Plots

Over the duration of this experiment, there was very little change in the composition of the vegetation of the control plots. Overall, there was a slight (non-significant) increase in the number of exotic species and an even smaller rise in the number of native species (table 4.3).

The dominance and frequency of both native and exotic species tended to vary with distance from the forest (figure 4.3; 4.4). From 1993 to 1995, there was little change in either the frequency or dominance of each species or group of species in the control plots. The only exception was the exotic grass *Arrhenatherum elatius*. The frequency and dominance of *Arrhenatherum* doubled from 1993 to 1995, both close to the fence and further into the pasture (figure 4.3; 4.4)

Figure 4.2 The change in native and exotic species richness at the pasture edge (0-10 m from the forest) and 10-20 m from the forest. Treatment code: c = Control sd = Soil disturbance f = Fenced sd/f = Soil disturbance & Fenced b = Burnt b/f = Burnt & Fenced

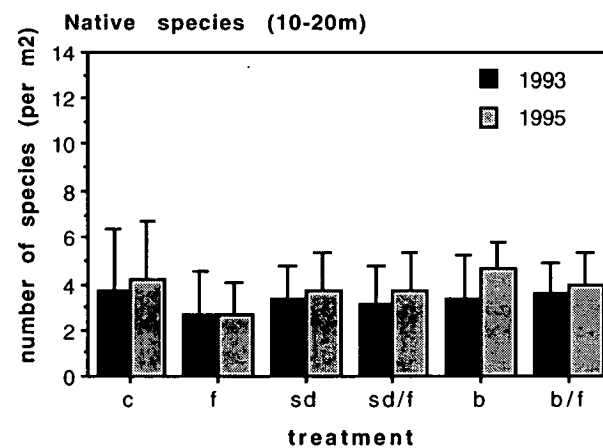
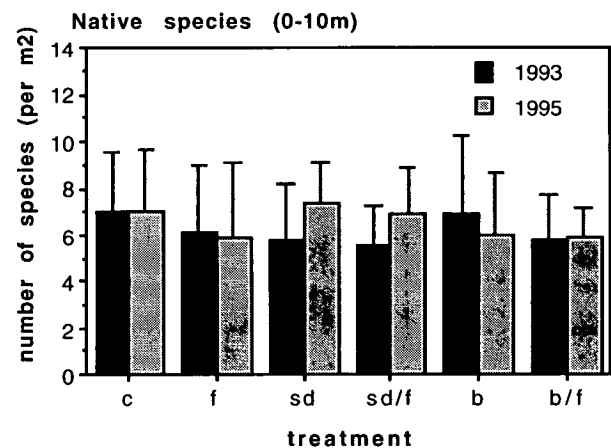
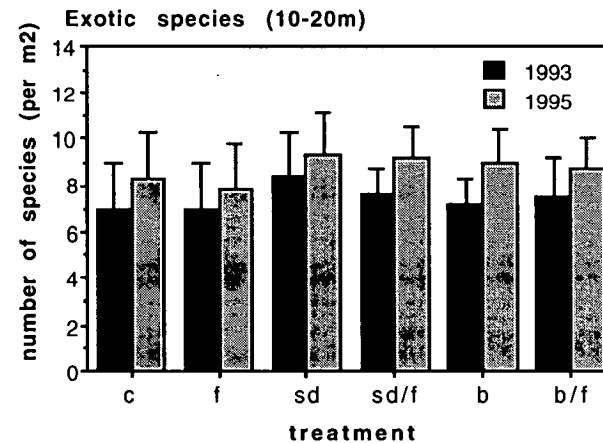
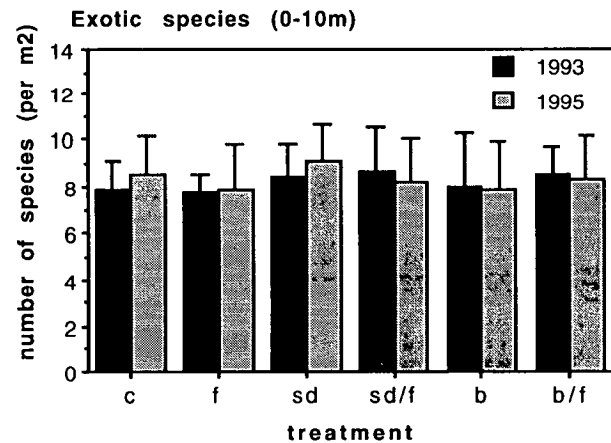
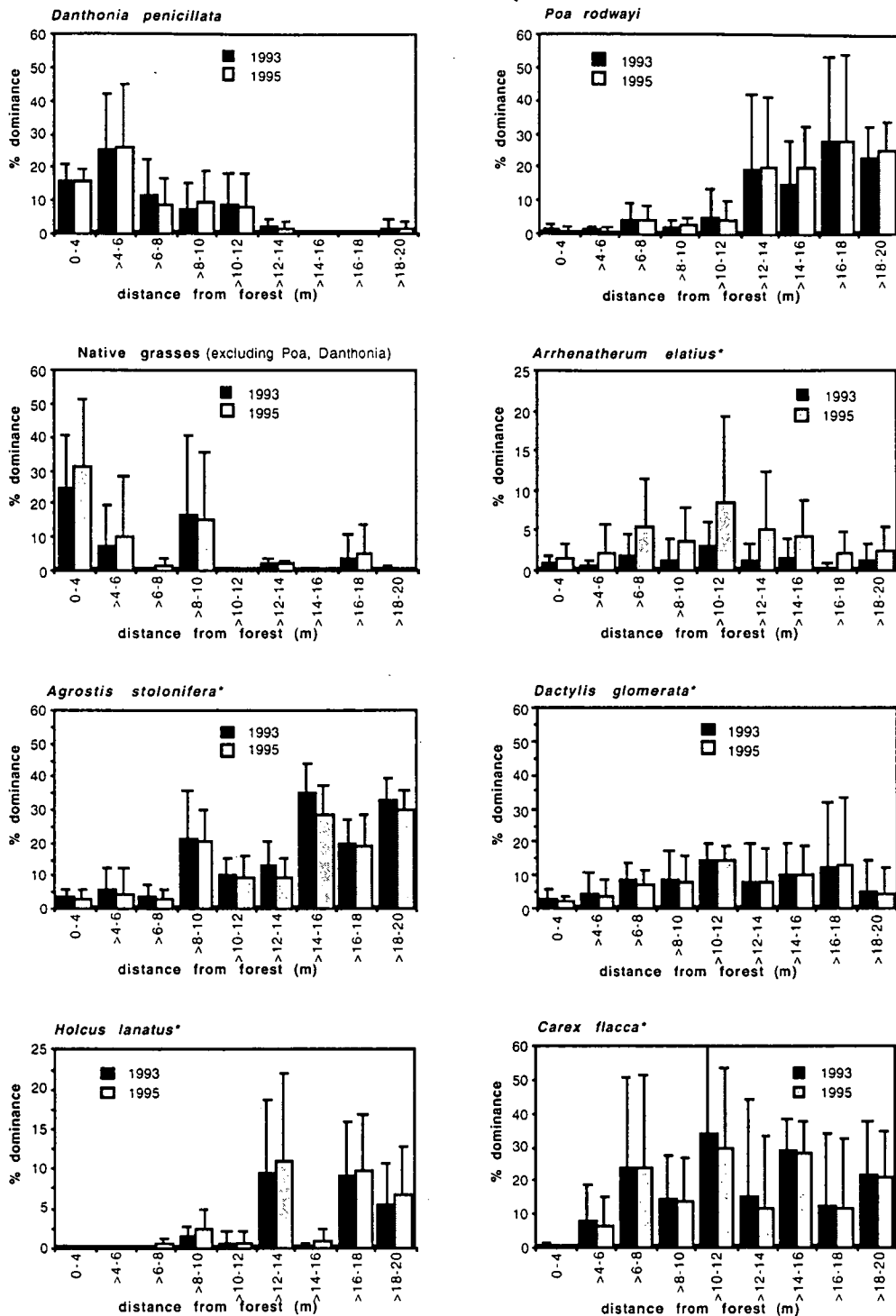


Figure 4.3 The change in dominance of species and groups of species in the control plots with distance from the forest (* denotes exotic species. Error bars = standard error).



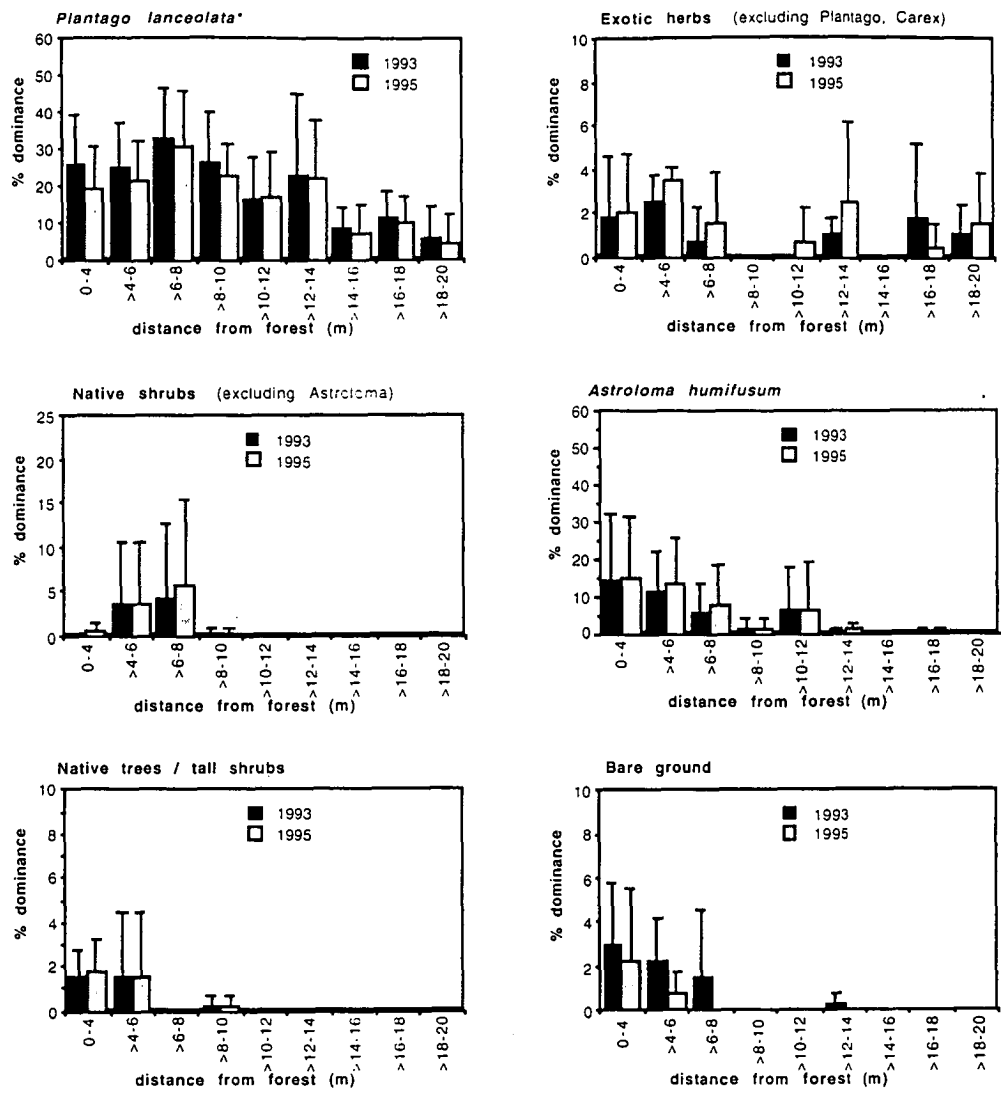
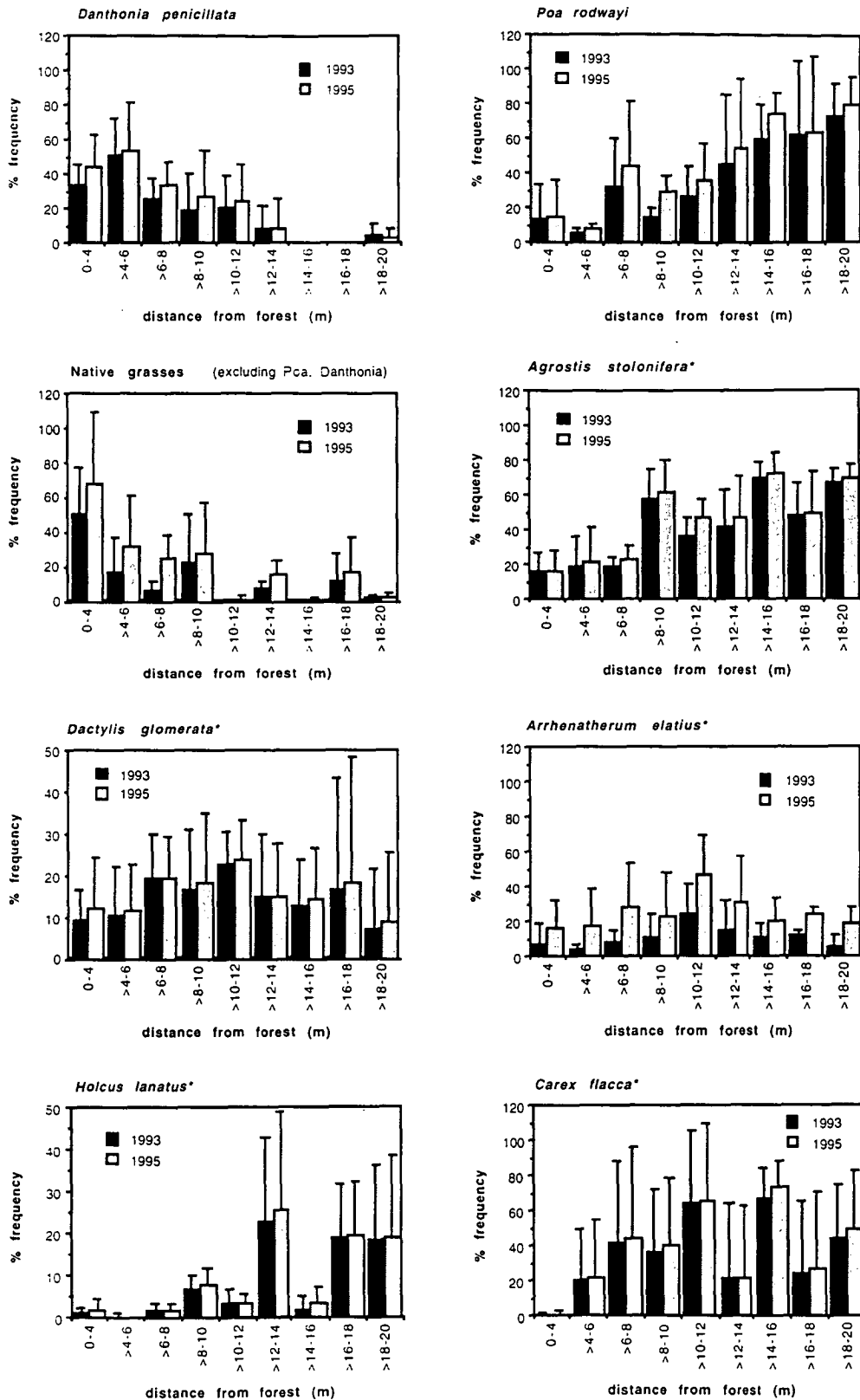
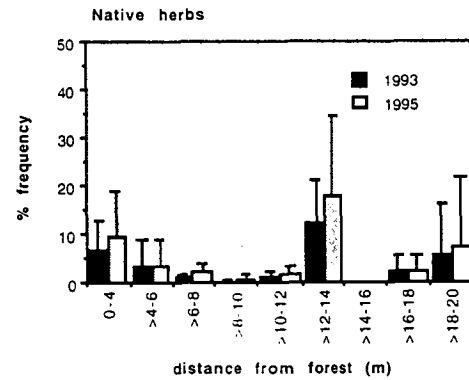
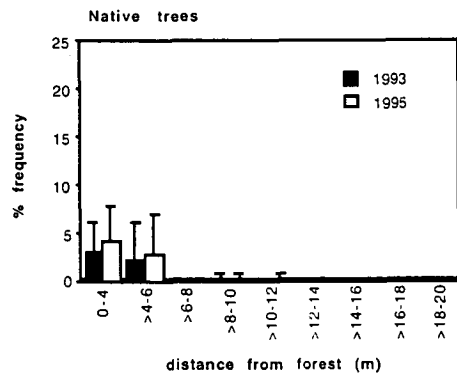
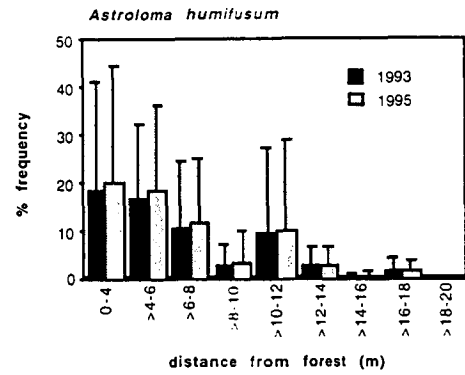
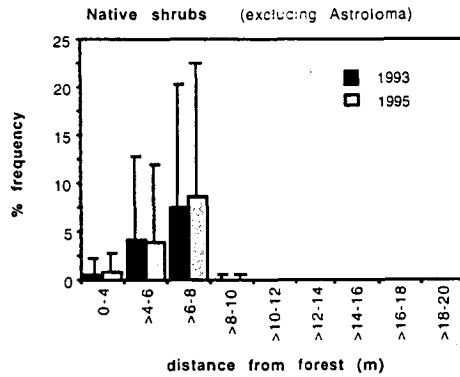
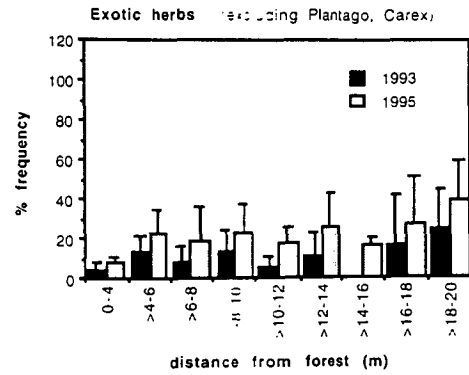
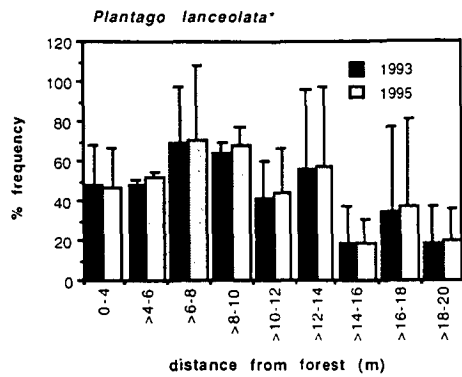


Figure 4.4 The change in frequency of species and groups of species in the control plots with distance from the forest (* denotes exotic species. Error bars = standard error).





The Response of Species to the Treatments

The results of the two-way analysis of variance showed that treatment and distance from the forest did not tend to interact. Of the 35 analyses, only five showed a significant interaction. In these cases, the interactions were due to large decreases in dominance or frequency of the species *Astroloma humifusum* and *Holcus lanatus* due to burning in one or two of the blocks. These species are fire-sensitive and the large decreases in dominance and frequency occurred where these species had attained greatest cover in the pasture. Therefore, these significant interactions between distance and treatment were not consistent and were not due to some factor(s) that varies systematically with distance from the fence. The results presented below are the results of the one-way analysis of variance, which averages the effect of the treatment over distance.

Frequency Data

Treatments versus the control:

The frequency of *Danthonia* spp. increased significantly relative to the control following the burning + fencing treatment (table 4.4; appendix 4.2). Apart from *Danthonia* spp., none of the treatments significantly improved the frequency of any native or exotic species relative to the control.

The frequencies of exotic grasses (as a group) and some individual species (*Agrostis* and *Dactylis*) were significantly reduced by soil disturbance and burning (with or without fencing) relative to the control (table 4.4). The frequencies of the mat shrub *Astroloma humifusum* and the native grass *Poa rodwayi* were reduced by both burning treatments. Burning + fencing reduced the frequency of

Table 4.4 The effect of treatments on the frequency of species and groups of species. Only species and groups of species with significant differences between treatments are shown ($p < 0.01$. Fisher's LSD). The direction of the mean change in frequency is shown in parentheses. * denotes exotic species.

Treatment (abbreviation)	Control (c)	Fenced (f)	Soil Disturbed (sd)	Soil Disturbed & Fenced (sd/f)	Burnt (b)	Burnt & Fenced (b/f)
Control (c)	---					(b/f > c) <i>Danthonia</i>
Fenced (f)	(c > f) <i>Agrostis</i> *	---			(b > f) <i>Danthonia</i>	(b/f > f) <i>Danthonia</i>
Soil Disturbed (sd)	(c > sd) Exotic grasses* <i>Agrostis</i> * <i>Dactylis</i> *		---			(b/f > sd) <i>Danthonia</i>
Soil Disturbed & Fenced (sd/f)	(c > sd/f) Exotic grasses* <i>Agrostis</i> *	(f > sd/f) Exotic grasses*		---		
Burnt (b)	(c > b) Exotic grasses* <i>Agrostis</i> * <i>Dactylis</i> * <i>Astroloma</i> <i>Poa</i>	(f > b) <i>Dactylis</i> * <i>Poa</i>	(sd > b) <i>Poa</i>		---	
Burnt & Fenced (b/f)	(c > b/f) Exotic grasses* <i>Agrostis</i> * <i>Dactylis</i> * <i>Plantago</i> * <i>Astroloma</i> <i>Poa</i>	(f > b/f) Exotic grasses* <i>Dactylis</i> * <i>Astroloma</i>	(sd > b/f) <i>Plantago</i> * <i>Astroloma</i>	(sd/f > b/f) <i>Dactylis</i> *	(b > b/f) <i>Plantago</i> *	---

Plantago lanceolata, though burning alone tended to increase the frequency (appendix 4.2). The frequency of *Agrostis stolonifera* declined following fencing of the plots.

Comparisons between treatments:

The native grass *Danthonia* was promoted more by burning (with and without fencing) than the fenced treatment alone (table 4.4). The frequency of *Poa* decreased significantly with burning relative to fencing. *Astroloma* decreased with burning + fencing compared with fencing.

Soil disturbance + fenced and burnt + fenced both decreased the frequency of exotic grasses compared with just fencing.

Dominance data

Treatments versus the control:

Relative to the control, several species were significantly more dominant as a result of one or more treatments (table 4.5). *Danthonia* responded positively to soil disturbance and burning + fencing treatments. *Carex flacca* also increased with soil disturbance. *Plantago* and bare ground increased with burning.

Exotic grasses—either as a group or individual species—were less dominant with either of the soil disturbance or burning treatments. These treatments also reduced the native grass *Poa rodwayi*, except for soil disturbance. *Astroloma* was adversely affected by burning.

Table 4.5 The effect of treatments on the dominance of species and groups of species. Only species and groups of species with significant differences between treatments are shown ($p < 0.01$, Fisher's LSD). The direction of the mean change in dominance is shown in parentheses. * denotes exotic species.

Treatment (abbreviation)	Control (c)	Fenced (f)	Soil Disturbed (sd)	Soil Disturbed & Fenced (sd/f)	Burnt (b)	Burnt & Fenced (b/f)
Control (c)	---		(sd > c) <i>Carex flacca</i> * <i>Danthonia</i>		(b > c) Bare ground <i>Plantago</i> *	(b/f > c) <i>Danthonia</i>
Fenced (f)		---	(sd > f) <i>Carex flacca</i> * <i>Danthonia</i>		(b > f) Bare ground <i>Danthonia</i>	(b/f > f) <i>Danthonia</i>
Soil Disturbed (sd)	(c > sd) Exotic grasses* <i>Dactylis</i> *	(f > sd) Exotic grasses*	---	(sd/f > sd) <i>Dactylis</i> *	(b > sd) <i>Plantago</i> *	
Soil Disturbed & Fenced (sd/f)	(c > sd/f) <i>Poa</i>			---	(b > sd/f) Bare ground	
Burnt (b)	(c > f) Exotic grasses* <i>Dactylis</i> * <i>Holcus</i> * <i>Astroloma</i> <i>Poa</i>	(f > b) Exotic grasses* <i>Dactylis</i> * <i>Astroloma</i>	(sd > b) <i>Astroloma</i>	(sd/f > b) <i>Dactylis</i> * <i>Astroloma</i>	---	
Burnt & Fenced (b/f)	(c > b/f) <i>Dactylis</i> * <i>Holcus</i> * <i>Astroloma</i> <i>Poa</i>	(f > b/f) <i>Astroloma</i>	(sd > b/f) <i>Astroloma</i>	(sd/f > b/f) <i>Dactylis</i> * <i>Plantago</i> *	(b > b/f) <i>Plantago</i> *	---

Comparisons between treatments:

Relative to the fencing treatment, burning and soil disturbance reduced the dominance of exotic grasses and *Astroloma*, but increased the dominance of *Danthonia*, *Carex* and bare ground (table 4.5). Burning increased the dominance of *Plantago* relative to soil disturbance, but reduced the dominance of *Astroloma*.

Discussion

The Effectiveness of Treatments in Facilitating the Establishment of Native Species

With respect to enhancing the re-establishment of native species there were negative aspects associated with each of the treatments applied in this experiment (table 4.4; 4.5). Some treatments failed to reduce the frequency or dominance of exotic species. Those treatments which did reduce exotics failed to promote many native species and/or reduced the frequency or dominance of some native species. There was very little germination of native seeds observed in any of the plots over the course of the experiment (1993–1995) and in the following year (1996). This result occurred regardless of the treatment type.

The hypothesis that the absence of grazing (fencing treatment) increases the rate of native re-establishment was not supported by the data. In the relatively short length of this study, fencing marginally increased the frequency and dominance of the exotic species present (appendix 4.2). Fencing also led to a noticeable increase in the height of the grass sward, compared with the other treatments.

In Australia, a number of studies have examined the changes in the vegetation structure and composition with the exclusion of grazing animals. Initially, the response is typically an increase in structural complexity as shrub and tree species gain dominance in the predominantly grassy vegetation (Wimbush & Costin 1979; Leigh *et al.* 1987; Williams & Ashton 1987; Gibson & Kirkpatrick 1989; Pettit *et al.* 1995). Unlike those study sites, the pasture in this study had very few or no shrubs present when the fences were erected and only very small areas of bare ground.

The results of the experiment suggest that the grasses will continue to dominate the fenced plots in the pasture. In the long-term, it seems likely that species richness will fall in fenced plots if disturbance is required to disrupt competitive exclusion by the grasses (Huston 1979; Gibson & Kirkpatrick 1989). If the grazing pressure prior to fencing had been greater and resulted in large areas of bare ground, then fencing may have allowed greater opportunities for re-establishment from seed.

The alternative hypothesis, that more severe disturbance facilitates an increase in the rate of re-establishment, provides a better explanation of the results. However, the evidence is not strong. Many exotic species were significantly adversely affected by burning and soil disturbance but the response of native species was small and inconsistent (table 4.4; 4.5).

The exotic grasses can adversely affect the growth of native species through competition and/or allelopathy (McConnaughay & Bazzaz 1991; Myster & Pickett 1992; Fensham & Kirkpatrick 1992; Nepstad *et al.* 1996). Since these grasses were the dominant group of species in the pasture, it seems logical that treatments which significantly reduce their influence could facilitate the re-establishment of native species.

For example, competition for space and resources would ease, at least temporarily, following burning and soil disturbance (table 4.4).

However, native species did not tend to fill the void left by these exotic grasses. There was no significant increase of natives species, except for *Danthonia* following burning + fencing (table 4.4) and soil disturbance (table 4.5).

Burning significantly increased the dominance of the exotic herb *Plantago lanceolata* (table 4.5). This species quickly regenerates from a thick tap-root to produce a flat rosette that occupies a large proportion of the bare ground created (Christensen & Burrows 1986). The rapid regeneration and rosette life-form would reduce the chances of seedling establishment in the close vicinity. The negative effects of species such as *Plantago* and *Hypochoeris radicata* (flat/versatile hemicryptophytes) on seedling regeneration of native species has been demonstrated (Gilfedder & Kirkpatrick 1993; Zacharek 1997).

Interestingly, fencing the burnt plots reduced the dominance of *Plantago* (table 4.5). The main differences between the burnt and burnt + fenced plots were a larger proportion of bare ground in the burnt plots and the taller grassy vegetation in the burnt + fenced plots (table 4.5). Preferential grazing of the young regenerating shoots of tall grass species—such as *Poa* and *Dactylis*—compared with the flat rosette of *Plantago* may be responsible for these results (table 4.4).

Gap Dynamics

Gaps as small as the seed itself can be large enough to allow germination of species in dense grassy vegetation (Rusch & van der

Maarel 1992). However, more substantial gaps are generally required for successful establishment in these situations (Noble 1980; McConnaughay & Bazzaz 1987; Goldberg & Gross 1988; Reader & Buck 1991; Williams 1992; Fensham & Kirkpatrick 1992). In grasslands, competition from the surrounding grasses are primarily responsible for the poor success of seedling establishment.

The critical factor appears to be the distance from the seedling to the roots of the competing grasses (Gross 1984; McConnaughay & Bazzaz 1990; Fensham & Kirkpatrick 1992; Kolb & Robberecht 1996). Seedling growth rates are significantly higher when grown on non-competitive ground cover such as bare ground or litter, especially for species with small seeds (Gross 1984). Therefore, the light grazing regime in these pastures, caused predominantly by rabbits, was unlikely to facilitate the germination of native species. Heavy grazing which creates large gaps is more likely to encourage changes in the composition of pastures (Noy-Meir *et al.* 1989; Bullock *et al.* 1994).

The soil disturbance treatment produced small gaps (around 5 cm in diameter) with bare ground. These gaps were mostly short-lived and recolonised vegetatively by the surrounding grasses. Small gaps can provide suitable sites for annual species (Goldberg & Gross 1988) and increase species richness in the short-term (Reader & Buck 1991).

However, these gaps are unlikely to permanently alter the composition or structure of the abandoned pastures (Reader & Buck 1991). Of the native species, only the grass *Danthonia* was able to take some advantage of these small gaps (table 4.5).

The burning treatment created larger gaps than the soil disturbance treatment. However, the grasses and other hemicryptophytes were able to regenerate quickly because their roots and buds were relatively

protected from the fire (see also Noy-Meir 1989; McIntyre *et al.* 1995; Zacharek 1997). In the burnt + fenced plots, the grasses resprouted before most seeds emerged and the gaps were rapidly revegetated. As a result, few seedlings successfully established.

The burnt (unfenced) plots maintained larger areas of bare ground even a year after the fire, but very few species were able to establish from seed. These plots may have been preferentially grazed because of the availability of more palatable young shoots of seedlings and resprouters.

Seedling Establishment

The availability of suitable microsites for germination or 'safe sites' may also limit the effectiveness of this treatment. Low moisture availability after the clearance of vegetation can lead to high seedling mortality, even though consumption of resources should be lower (Tyler & D'Antonio 1995). The lack of microsites which maintain soil moisture (*e.g.* depressions) could result in high levels of seedling mortality (Fowler 1986; Battaglia & Reid 1993). The holes created in the soil disturbance treatments may have provided a better microsite for germination but they may have been too small, surrounded by taller vegetation and only disturbing a small volume of the root mass.

The rainfall conditions during the experiment were generally close to the long-term average, except for very dry conditions in June 1994 and December 1994 (appendix 4.3). These dry months followed seasons when peak germination would have been expected—autumn and spring (Marsden-Smedley *et al.* 1997). These short periods of drought may not affect established plants but could have killed young seedlings with shallow root systems.

Small-scale soil disturbance created by animal diggings has been shown to promote the germination of several native species in Tasmanian grassy woodland and grassland communities (Pyrke 1994). However, there was no significant response to soil disturbance by native species in this pasture community. Burning would have killed many seeds on or close to the soil surface, especially in the plots with higher fuel loads (see appendix 4.1). This loss of seeds should be compensated by the heat and/or smoke stimulating the germination of seeds (from a wide range of species), assuming there was a soil-stored seed bank at the site (Warcup 1980; Bell *et al.* 1993; Dixon *et al.* 1995; Marsden-Smedley *et al.* 1997).

The most appropriate treatment to encourage native species re-establishment may not be the grazing, fire or small-scale soil disturbances tested in this study. These disturbance types can occur naturally in these pastures but there is little evidence to show whether these forms of disturbance were responsible for re-establishment in the past. Other natural (but less common or less obvious) disturbances may have been more effective, for example larger gaps produced by burrowing animals or heavy grazing which reduced the dominance of the grasses.

Seed Availability

The main assumption in this experiment was that propagules of native species were available in the pasture and would respond to either the creation of gaps (disturbed plots) or the exclusion of disturbance (fenced plots). The results of this experiment suggest that this assumption may not be true. Following the application of the disturbance treatments, the number of native seedlings observed in the plots was always low.

The main source of seed of native species was the forest adjacent to the pasture. The distance that seeds can be dispersed may limit the amount of seed present in the pasture (figure 4.2). To counter these problems, the experiment was set up on the western edge of the pasture to maximise the chance of seed being carried into the pasture with the prevailing westerly winds. The following chapter investigates whether seeds of native species are available in the pasture, or whether poor seed dispersal or seed predation limit re-establishment. The timing of good seed dispersal was also investigated to determine whether the lack of success in the disturbance experiment could have been affected by the timing of the opening up of safe sites.

If the availability of propagules limits re-establishment, then treatments such as burning that create patches of bare ground which persist long after the initial disturbance may prove to be beneficial. These conditions may enhance the chances of germination when seed finally reaches these gaps in the vegetation. These gaps will provide a more suitable site for regeneration compared with areas where the thick grassy sward regenerates more quickly following disturbance.

Burning (unfenced) was the only disturbance treatment to maintain a significant increase in bare ground from 1993 to 1995 (table 4.5). The bare ground created by the soil disturbance treatment (and those created naturally by rabbits or bandicoots) tended to be rapidly recolonised by vegetative regeneration of grass species (see also Rapp & Rabinowitz 1985; Goldberg & Gross 1988; Reader & Buck 1991).

Conclusion and Further Investigations

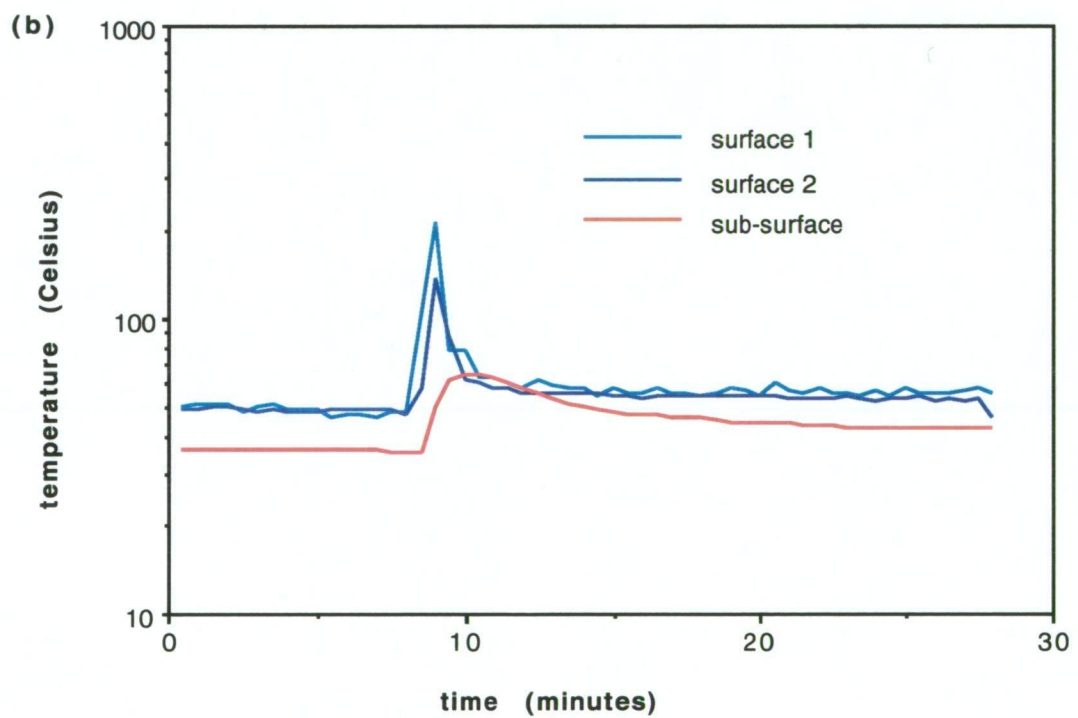
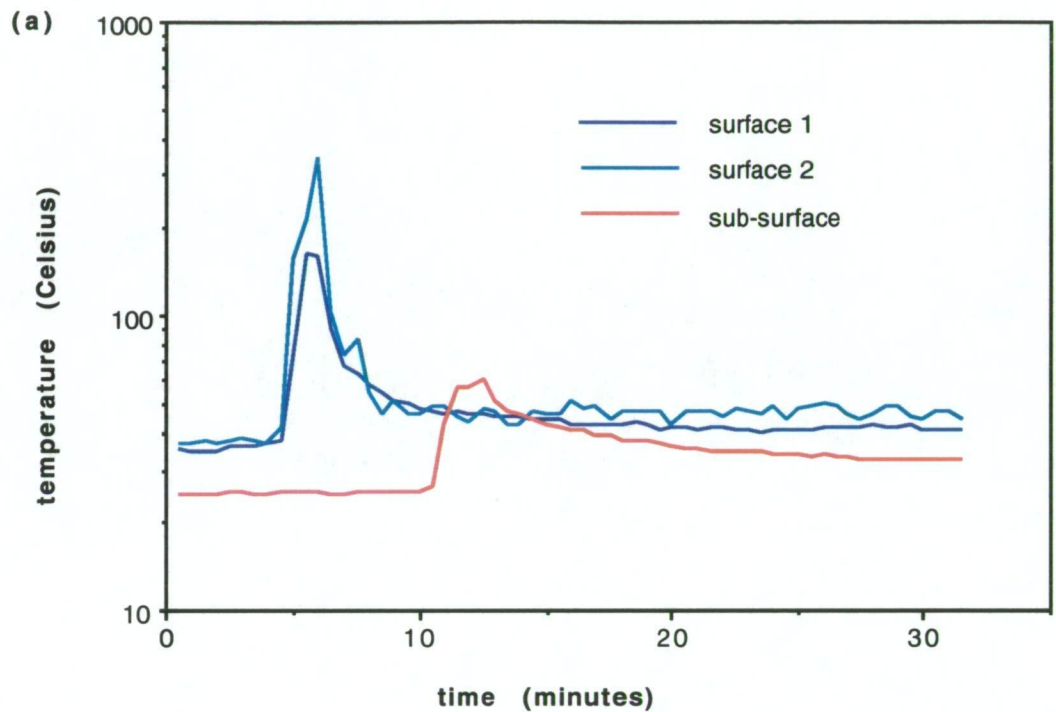
Disturbance of the pasture vegetation led to a significant reduction in the cover of exotic grasses, the dominant component of the pasture. However, there was very little re-establishment of native species to take advantage of these gaps.

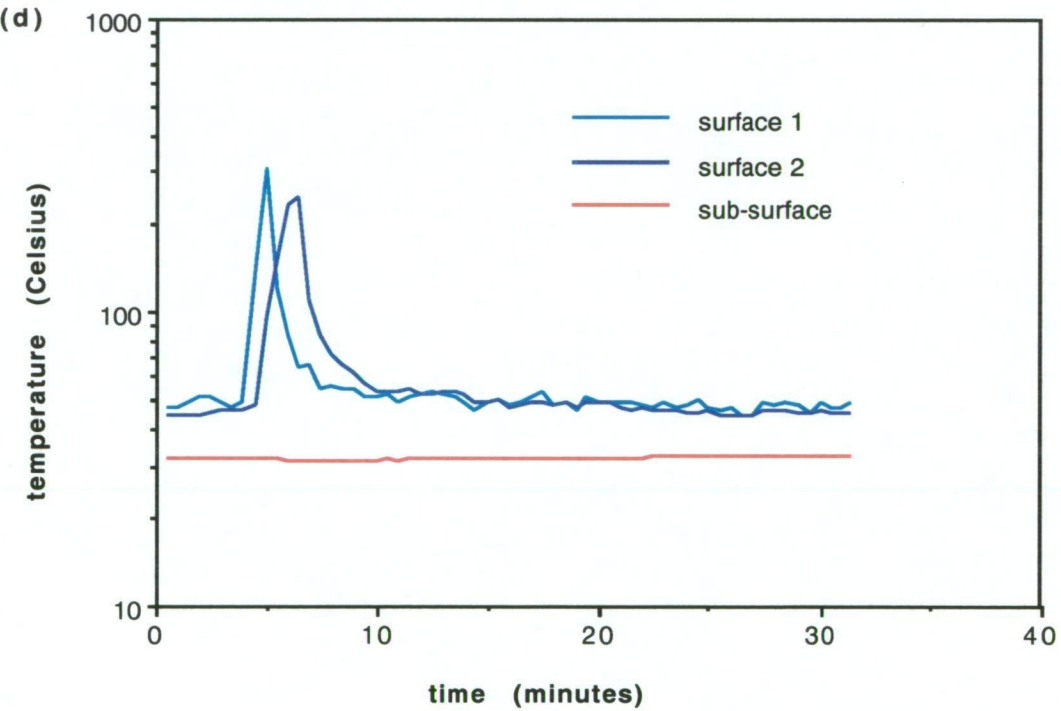
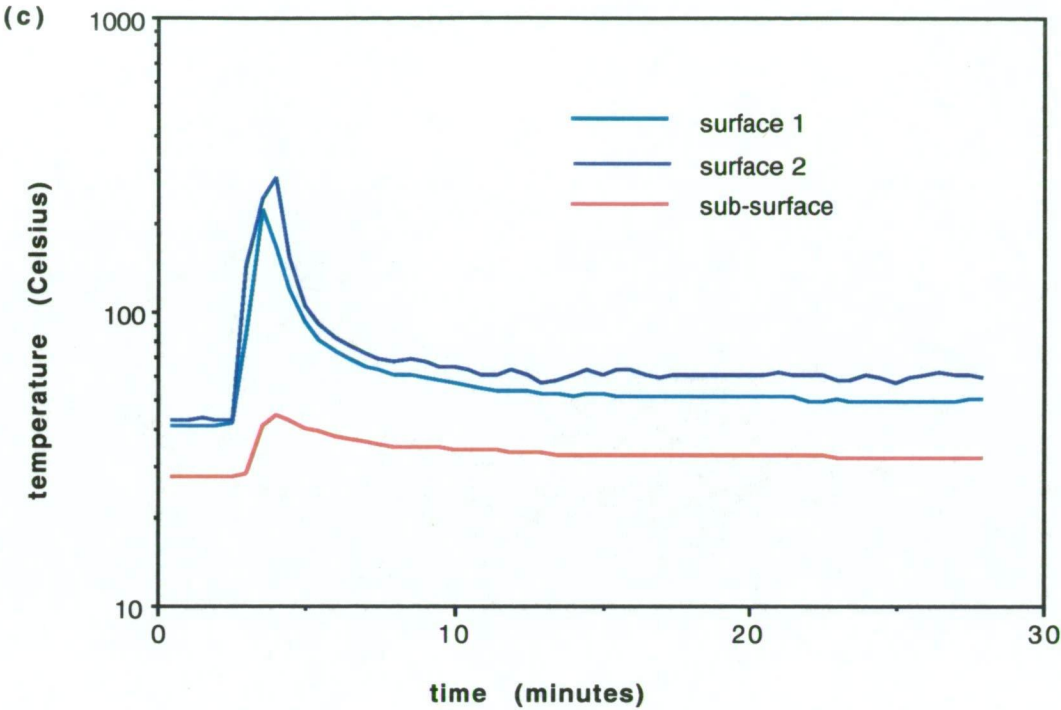
The situation may exist where the treatments appear ineffective only because there were few or no propagules of native species present in the soil where the treatments were applied. The following chapter examines seed dynamics in these pastures: the soil seed bank; the amount of seed fall into the pasture and the losses due to seed predation.

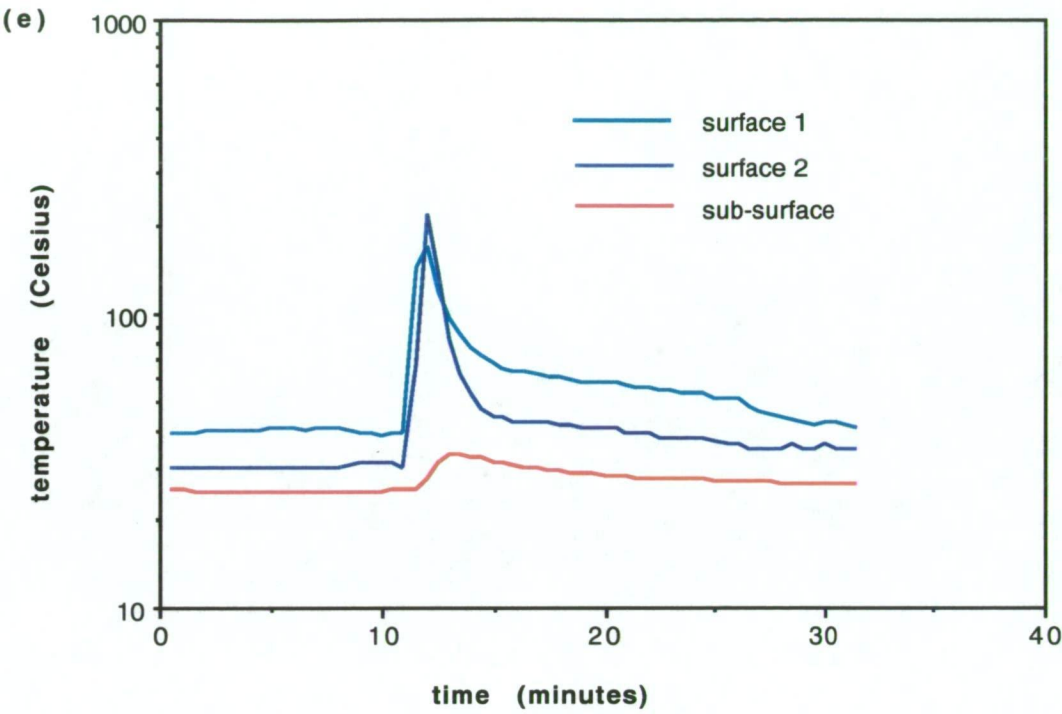
Long term data are required to test whether the disturbance treatments permanently reduced the frequency and dominance of the exotic grasses. Some studies have found that changes in composition observed following disturbance were not a true, directional change in floristics but, rather, a reversible fluctuation (Collins *et al.* 1987). Indeed, these exotic grasses were not totally eliminated and few species emerged to take the place of the exotic grasses (table 4.4; 4.5). Long term data are also needed to follow the fate of the few native species which established in these experiments. Some of the factors affecting these seedlings (frosts and herbivory) are investigated in chapter six.

The effects of the different disturbance treatments may vary depending on the season in which they are applied (Bullock *et al.* 1994; Zacharek 1997). A study examining the effects of the timing of disturbance may find that these treatments could be more effective at promoting the germination of native species in conditions other than those that occurred during the experiment (Marsden-Smedley *et al.* 1997).

Appendix 4.1 Temperatures recorded on the surface and 1 cm below the soil surface during the application of fire to the quadrats. a & b) quadrats with a relatively heavy fuel load; c) medium load; d & e) light load.







Appendix 4.2 The effects of treatments on the frequency and dominance of selected species and groups of species from 1993 to 1995.

The mean is shown for each treatment. The probability of a significant difference between each pair-wise comparison of treatments is shown (test: Fisher's LSD procedure).

* denotes exotic species.

Treatments: c = control

sd = soil disturbance

b = burnt

f = fenced

sd/f = soil disturbance + fenced

b/f = burnt + fenced

Agrostis stolonifera *
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	-1.722	c	-	0.1252	0.2046	0.1612	0.7888	0.9733
18	-4.278	f	0.1252	-	0.8165	0.9076	0.2715	0.1744
18	-3.833	sd	0.2046	0.8165	-	0.9076	0.3849	0.2592
18	-4.056	sd/f	0.1612	0.9076	0.9076	-	0.3250	0.2137
18	-2.167	b	0.7888	0.2715	0.3849	0.3250	-	0.7941
18	-1.667	b/f	0.9733	0.1744	0.2592	0.2137	0.7941	-

Agrostis stolonifera *
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	4.139	c	.	0.0038	0.0055	0.0001	0.0031	0.0038
18	-3.444	f	0.0038	-	0.9106	0.0512	0.9552	1.0000
18	-3.111	sd	0.0055	0.9106	-	0.0395	0.8662	0.9106
18	-9.278	sd/f	0.0001	0.0512	0.0395	-	0.0581	0.0512
18	-3.611	b	0.0031	0.9552	0.8662	0.0581	-	0.9552
18	-3.444	b/f	0.0038	1.0000	0.9106	0.0512	0.9552	-

Arrhenatherum elatius *
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	2.583	c	.	0.0247	0.6756	0.4950	0.6756	0.2443
18	5.444	f	0.0247	-	0.0213	0.0116	0.0213	0.3410
18	2.056	sd	0.6756	0.0213	-	0.8189	1.0000	0.1712
18	1.722	sd/f	0.4950	0.0116	0.8189	-	0.8189	0.1109
18	2.056	b	0.6756	0.0213	1.0000	0.8189	-	0.1712
18	4.056	b/f	0.2443	0.3410	0.1712	0.1109	0.1712	-

*Arrhenatherum elatius**
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	13.944	c	-	0.3860	0.9051	0.0057	0.0758	0.1644
18	16.778	f	0.3860	-	0.5169	0.0018	0.0229	0.0517
18	14.333	sd	0.9051	0.5169	-	0.0123	0.1006	0.1911
18	4.778	sd/f	0.0057	0.0018	0.0123	-	0.3772	0.2225
18	8.111	b	0.0758	0.0229	0.1006	0.3772	-	0.7346
18	9.389	b/f	0.1644	0.0517	0.1911	0.2225	0.7346	-

Astroloma humifusum
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.306	c	-	0.7582	0.8887	0.9777	0.0033	0.0039
18	0.611	f	0.7582	-	0.8844	0.8085	0.0049	0.0057
18	0.444	sd	0.8887	0.8844	-	0.9228	0.0075	0.0086
18	0.333	sd/f	0.9777	0.8085	0.9228	-	0.0098	0.0113
18	-2.667	b	0.0033	0.0049	0.0075	0.0098	-	0.9613
18	-2.611	b/f	0.0039	0.0057	0.0086	0.0113	0.9613	-

Astroloma humifusum
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.694	c	-	0.9838	0.5306	0.1029	0.0035	0.0003
18	0.667	f	0.9838	-	0.5991	0.1624	0.0115	0.0018
18	-0.167	sd	0.5306	0.5991	-	0.3814	0.0437	0.0086
18	-1.556	sd/f	0.1029	0.1624	0.3814	-	0.2485	0.0756
18	-3.389	b	0.0035	0.0115	0.0437	0.2485	-	0.5282
18	-4.389	b/f	0.0003	0.0018	0.0086	0.0756	0.5282	-

Bare ground
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	-0.444	c	-	0.9362	0.7489	0.8103	0.0013	0.0217
18	-0.556	f	0.9362	-	0.7290	0.7816	0.0042	0.0393
18	0.000	sd	0.7489	0.7290	-	0.9447	0.0114	0.0851
18	-0.111	sd/f	0.8103	0.7816	0.9447	-	0.0094	0.0735
18	4.111	b	0.0013	0.0042	0.0114	0.0094	-	0.4062
18	2.778	b/f	0.0217	0.0393	0.0851	0.0735	0.4062	-

Carex flacca *
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	-1.361	c	-	0.6303	0.0005	0.0105	0.0325	0.4288
18	-0.500	f	0.6303	-	0.0087	0.0692	0.1480	0.7879
18	5.000	sd	0.0005	0.0087	-	0.4049	0.2274	0.0180
18	3.278	sd/f	0.0105	0.0692	0.4049	-	0.7065	0.1205
18	2.500	b	0.0325	0.1480	0.2274	0.7065	-	0.2379
18	0.056	b/f	0.4288	0.7879	0.0180	0.1205	0.2379	-

Carex flacca *
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	2.972	c	-	0.2282	0.4856	0.9593	0.2282	0.0654
18	1.000	f	0.2282	-	0.6584	0.3171	1.0000	0.5756
18	1.833	sd	0.4856	0.6584	-	0.5756	0.6584	0.3171
18	2.889	sd/f	0.9593	0.3171	0.5756	-	0.3171	0.1200
18	1.000	b	0.2282	1.0000	0.6584	0.3171	-	0.5756
18	-0.056	b/f	0.0654	0.5756	0.3171	0.1200	0.5756	-

Dactylis glomerata *
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	-0.556	c	-	0.6255	0.0030	0.8452	0.0004	0.0030
18	-1.111	f	0.6255	-	0.0295	0.5541	0.0068	0.0295
18	-4.000	sd	0.0030	0.0295	-	0.0060	0.5827	1.0000
18	-0.333	sd/f	0.8452	0.5541	0.0060	-	0.0011	0.0060
18	-4.722	b	0.0004	0.0068	0.5827	0.0011	-	0.5827
18	-4.000	b/f	0.0030	0.0295	1.0000	0.0060	0.5827	-

Dactylis glomerata *
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	1.278	c	-	0.2889	0.0022	0.0559	0.0001	0.0001
18	-0.500	f	0.2889	-	0.0764	0.4550	0.0015	0.0004
18	-3.944	sd	0.0022	0.0764	-	0.3015	0.1441	0.0634
18	-1.944	sd/f	0.0559	0.4550	0.3015	-	0.0135	0.0043
18	-6.778	b	0.0001	0.0015	0.1441	0.0135	-	0.6872
18	-7.556	b/f	0.0001	0.0004	0.0634	0.0043	0.6872	-

Danthonia spp.
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	-0.083	c	-	0.6879	0.0007	0.0782	0.0013	0.0001
18	-0.556	f	0.6879	-	0.0010	0.0616	0.0018	0.0001
18	4.000	sd	0.0007	0.0010	-	0.1423	0.8699	0.3071
18	2.000	sd/f	0.0782	0.0616	0.1423	-	0.1918	0.0137
18	3.778	b	0.0013	0.0018	0.8699	0.1918	-	0.2365
18	5.389	b/f	0.0001	0.0001	0.3071	0.0137	0.2365	-

Danthonia spp
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	3.722	c	-	0.4989	0.5205	0.0747	0.0122	0.0002
18	2.611	f	0.4989	-	0.2543	0.0340	0.0061	0.0001
18	4.778	sd	0.5205	0.2543	-	0.3199	0.1026	0.0061
18	6.667	sd/f	0.0747	0.0340	0.3199	-	0.5194	0.0757
18	7.889	b	0.0122	0.0061	0.1026	0.5194	-	0.2543
18	10.056	b/f	0.0002	0.0001	0.0061	0.0757	0.2543	-

Exotic grasses
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.972	c	-	0.5616	0.0002	0.0223	0.0002	0.0356
18	-0.222	f	0.5616	-	0.0061	0.1361	0.0061	0.1839
18	-6.833	sd	0.0002	0.0061	-	0.1996	1.0000	0.1486
18	-3.778	sd/f	0.0223	0.1361	0.1996	-	0.1996	0.8699
18	-6.833	b	0.0002	0.0061	1.0000	0.1996	-	0.1486
18	-3.389	b/f	0.0356	0.1839	0.1486	0.8699	0.1486	-

Exotic grasses
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	20.167	c	-	0.0728	0.0008	0.0001	0.0001	0.0001
18	11.500	f	0.0728	-	0.1650	0.0004	0.0214	0.0040
18	3.778	sd	0.0008	0.1650	-	0.0249	0.3519	0.1268
18	-8.778	sd/f	0.0001	0.0004	0.0249	-	0.1839	0.4646
18	-1.389	b	0.0001	0.0214	0.3519	0.1839	-	0.5477
18	-4.722	b/f	0.0001	0.0040	0.1268	0.4646	0.5477	-

Exotic herbs
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.278	c	-	1.0000	1.0000	0.0996	0.0846	0.1358
18	0.278	f	1.0000	-	1.0000	0.1532	0.1347	0.1959
18	0.278	sd	1.0000	1.0000	-	0.1532	0.1347	0.1959
18	1.444	sd/f	0.0996	0.1532	0.1532	-	0.9455	0.8913
18	1.500	b	0.0846	0.1347	0.1347	0.9455	-	0.8376
18	1.333	b/f	0.1358	0.1959	0.1959	0.8913	0.8376	-

Exotic herbs
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	4.722	c	-	0.4774	0.2481	0.9514	0.8869	0.0188
18	2.778	f	0.4774	-	0.6987	0.5736	0.4604	0.0084
18	1.556	sd	0.2481	0.6987	-	0.3429	0.2613	0.0027
18	4.556	sd/f	0.9514	0.5736	0.3429	-	0.8603	0.0364
18	5.111	b	0.8869	0.4604	0.2613	0.8603	-	0.0548
18	11.222	b/f	0.0188	0.0084	0.0027	0.0364	0.0548	-

*Holcus lanatus**
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.667	c	-	0.1798	0.0153	0.0124	0.0002	0.0007
18	-0.278	f	0.1798	-	0.3378	0.3046	0.0351	0.0659
18	-1.056	sd	0.0153	0.3378	-	0.9453	0.2449	0.3733
18	-1.111	sd/f	0.0124	0.3046	0.9453	-	0.2736	0.4111
18	-2.000	b	0.0002	0.0351	0.2449	0.2736	-	0.7838
18	-1.778	b/f	0.0007	0.0659	0.3733	0.4111	0.7838	-

*Holcus lanatus**
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.806	c	-	0.2243	0.0154	0.0756	0.9621	0.0272
18	-1.333	f	0.2243	-	0.2861	0.6218	0.2740	0.3810
18	-3.500	sd	0.0154	0.2861	-	0.5650	0.0319	0.8478
18	-2.333	sd/f	0.0756	0.6218	0.5650	-	0.1137	0.7012
18	0.889	b	0.9621	0.2740	0.0319	0.1137	-	0.0502
18	-3.111	b/f	0.0272	0.3810	0.8478	0.7012	0.0502	-

Native grasses
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	1.944	c	-	0.3312	0.8033	0.0131	0.1907	0.5564
18	-0.444	f	0.3312	-	0.5307	0.1840	0.7687	0.1777
18	1.333	sd	0.8033	0.5307	-	0.0517	0.3576	0.4686
18	-4.222	sd/f	0.0131	0.1840	0.0517	-	0.2998	0.0081
18	-1.278	b	0.1907	0.7687	0.3576	0.2998	-	0.1014
18	3.389	b/f	0.5564	0.1777	0.4686	0.0081	0.1014	-

Native grasses
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	20.583	c	-	0.2496	0.5985	0.0195	0.0288	0.2005
18	15.167	f	0.2496	-	0.5870	0.2967	0.3623	0.9102
18	18.111	sd	0.5985	0.5870	-	0.1139	0.1472	0.5120
18	9.500	sd/f	0.0195	0.2967	0.1139	-	0.8940	0.3516
18	10.222	b	0.0288	0.3623	0.1472	0.8940	-	0.4244
18	14.556	b/f	0.2005	0.9102	0.5120	0.3516	0.4244	-

Native shrubs
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.222	c	-	0.7068	0.8508	0.5727	0.7068	0.1895
18	0.333	f	0.7068	-	0.8706	0.4159	0.5150	0.1444
18	0.278	sd	0.8508	0.8706	-	0.5150	0.6252	0.1940
18	0.056	sd/f	0.5727	0.4159	0.5150	-	0.8706	0.5150
18	0.111	b	0.7068	0.5150	0.6252	0.8706	-	0.4159
18	-0.167	b/f	0.1895	0.1444	0.1940	0.5150	0.4159	-

Native shrubs
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.139	c	-	0.7401	0.5381	0.8127	0.0274	0.8127
18	0.333	f	0.7401	-	0.8055	0.9346	0.0282	0.9346
18	0.500	sd	0.5381	0.8055	-	0.7427	0.0150	0.7427
18	0.278	sd/f	0.8127	0.9346	0.7427	-	0.0345	1.0000
18	-1.167	b	0.0274	0.0282	0.0150	0.0345	-	0.0345
18	0.278	b/f	0.8127	0.9346	0.7427	1.0000	0.0345	-

Native trees
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.028	c	-	0.7407	0.9122	0.4405	0.4405	0.0999
18	-0.056	f	0.7407	-	0.7024	0.3403	0.7024	0.0874
18	0.056	sd	0.9122	0.7024	-	0.5668	0.4452	0.1827
18	0.222	sd/f	0.4405	0.3403	0.5668	-	0.1827	0.4452
18	-0.167	b	0.4405	0.7024	0.4452	0.1827	-	0.0373
18	0.444	b/f	0.0999	0.0874	0.1827	0.4452	0.0373	-

Native trees
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.194	c	-	0.8139	0.9374	0.9374	0.5830	0.1838
18	0.111	f	0.8139	-	0.7858	0.7858	0.7858	0.1757
18	0.222	sd	0.9374	0.7858	-	1.0000	0.5868	0.2780
18	0.222	sd/f	0.9374	0.7858	1.0000	-	0.5868	0.2780
18	0.000	b	0.5830	0.7858	0.5868	0.5868	-	0.1047
18	0.667	b/f	0.1838	0.1757	0.2780	0.2780	0.1047	-

Plantago lanceolata *
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	-2.111	c	-	0.0992	0.4411	0.0108	0.0002	0.5375
18	0.278	f	0.0992	-	0.4430	0.4234	0.0588	0.0506
18	-1.000	sd	0.4411	0.4430	-	0.1184	0.0085	0.2306
18	1.611	sd/f	0.0108	0.4234	0.1184	-	0.2716	0.0064
18	3.444	b	0.0002	0.0588	0.0085	0.2716	-	0.0002
18	-3.000	b/f	0.5375	0.0506	0.2306	0.0064	0.0002	-

Plantago lanceolata *
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	1.778	c	-	0.5722	0.6957	0.7609	0.0214	0.0013
18	0.333	f	0.5722	-	0.4081	0.8213	0.0134	0.0200
18	2.778	sd	0.6957	0.4081	-	0.5472	0.0957	0.0018
18	1.000	sd/f	0.7609	0.8213	0.5472	-	0.0242	0.0109
18	7.722	b	0.0214	0.0134	0.0957	0.0242	-	0.0001
18	-6.611	b/f	0.0013	0.0200	0.0018	0.0109	0.0001	-

Poa rodwayi
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.861	c	-	0.6946	0.1147	0.0018	0.0010	0.0048
18	0.111	f	0.6946	-	0.3026	0.0168	0.0112	0.0339
18	-2.167	sd	0.1147	0.3026	-	0.1675	0.1261	0.2688
18	-5.222	sd/f	0.0018	0.0168	0.1675	-	0.8798	0.7817
18	-5.556	b	0.0010	0.0112	0.1261	0.8798	-	0.6685
18	-4.611	b/f	0.0048	0.0339	0.2688	0.7817	0.6685	-

Poa rodwayi
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	7.889	c	-	0.5206	0.2985	0.1335	0.0001	0.0064
18	6.278	f	0.5206	-	0.7297	0.4545	0.0012	0.0672
18	5.278	sd	0.2985	0.7297	-	0.6869	0.0035	0.1360
18	4.111	sd/f	0.1335	0.4545	0.6869	-	0.0111	0.2749
18	-3.333	b	0.0001	0.0012	0.0035	0.0111	-	0.1411
18	0.944	b/f	0.0064	0.0672	0.1360	0.2749	0.1411	-

Stipa spp.
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.639	c	-	0.5746	0.7662	0.1389	0.7662	0.2230
18	0.167	f	0.5746	-	0.8190	0.4237	0.8190	0.1242
18	0.389	sd	0.7662	0.8190	-	0.3040	1.0000	0.1897
18	-0.611	sd/f	0.1389	0.4237	0.3040	-	0.3040	0.0203
18	0.389	b	0.7662	0.8190	1.0000	0.3040	-	0.1897
18	1.667	b/f	0.2230	0.1242	0.1897	0.0203	0.1897	-

Stipa spp.
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	7.056	c	-	0.6888	0.7458	0.0061	0.5546	0.2165
18	5.889	f	0.6888	-	0.5305	0.0407	0.8688	0.4678
18	8.000	sd	0.7458	0.5305	-	0.0080	0.4284	0.1772
18	-1.056	sd/f	0.0061	0.0407	0.0080	-	0.0593	0.1825
18	5.333	b	0.5546	0.8688	0.4284	0.0593	-	0.5746
18	3.444	b/f	0.2165	0.4678	0.1772	0.1825	0.5746	-

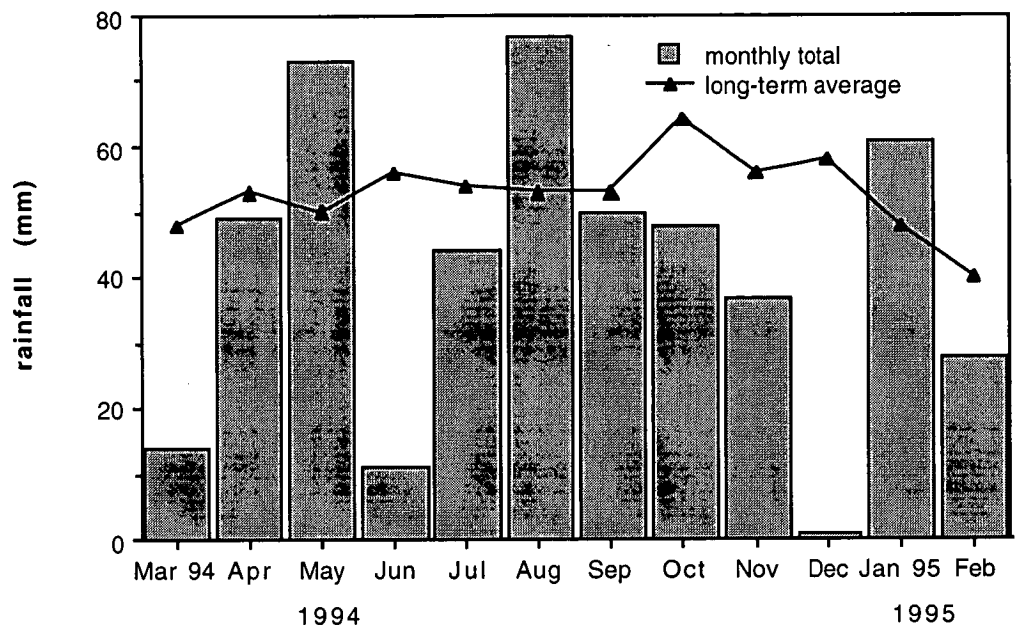
*Vicia sativa**
dominance

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	0.056	c	-	1.0000	0.3565	0.7582	0.7582	0.0224
18	0.056	f	1.0000	-	0.4244	0.7898	0.7898	0.0473
18	0.389	sd	0.3565	0.4244	-	0.2873	0.2873	0.2316
18	-0.056	sd/f	0.7582	0.7898	0.2873	-	1.0000	0.0249
18	-0.056	b	0.7582	0.7898	0.2873	1.0000	-	0.0249
18	0.889	b/f	0.0224	0.0473	0.2316	0.0249	0.0249	-

*Vicia sativa**
frequency

N	MEAN	TX.	c	f	sd	sd/f	b	b/f
36	5.806	c	-	0.3410	0.2730	0.0430	0.8563	0.0136
18	3.611	f	0.3410	-	0.9001	0.3474	0.5037	0.1823
18	3.278	sd	0.2730	0.9001	-	0.4153	0.4273	0.2265
18	1.111	sd/f	0.0430	0.3474	0.4153	-	0.1091	0.6911
18	5.389	b	0.8563	0.5037	0.4273	0.1091	-	0.0464
18	0.056	b/f	0.0136	0.1823	0.2265	0.6911	0.0464	-

Appendix 4.3 The monthly rainfall for Hobart for March 1994–February 1995
(source: Bureau of Meteorology).



Chapter Five

Seed Availability

Introduction

This chapter investigates the seed dynamics of native species in abandoned pastures. The availability of native seeds in the soil seed bank of the pasture is examined, as well as the dispersal of seed from the forest, and the level of seed predation within the pasture.

In south-eastern Australia, soil seed banks of both native and improved pastures tend to have a high density of exotic seeds (Lunt 1990; Marsden-Smedley *et al.* 1997). In pastures, the soil seed bank of native species may be depleted where cultivation has taken place and the sources of seed replenishment are remote or sparse. In these situations re-establishment of native species may require direct-seeding or planting (Venning 1991). Analysis of the soil seed bank across the pasture should determine how much native seed is available for re-establishment and the amount of potential competition from exotic germinants.

Seed dispersal is often limited if the seeds are heavy or the plants have no mechanisms to assist dispersal. Most seeds fall either beneath or in close proximity to the parent plant (Cook 1980). Even seed dispersal from tall *Eucalyptus* species is largely limited to a distance equal to twice the height of the tree (Cremer 1977). Therefore, the distance from the seed source is expected to be a major factor limiting the availability of native seeds in the pasture. However, diaspores (seeds or fruits) with features to assist with wind or animal dispersal may be less affected.

Seed predation is also an important aspect of seed bank dynamics. Considerable losses may be incurred through the agency of many ant species as well as other granivorous insects, rodents and some birds (Ashton 1979; Campbell 1982; Abbott & van Heurck 1985; Andersen & Ashton 1985; Andersen 1987; Louda 1989). However, there is almost no information on whether grazing and pasture improvement adversely affects the ant population (Andersen 1988; Andersen & McKaige 1987). The effects of seed predation may be significant, especially if re-establishment in pasture is dependent on dispersal of seed from surrounding native vegetation.

The aims of this chapter are:

- to quantify the availability of native seeds in the soil seed bank and in the seed-fall;
- to investigate whether distance from the forest limits the availability of native seeds for re-establishment in the pasture;
- to determine whether seed predation by ants occurs in pastures and to what extent these losses impact on the availability of native seeds for re-establishment.

Methods

Seed-fall

The amount of seed-fall into these pasture was measured using traps located along transects running from the forest out into the pasture and perpendicular to the fence. The traps were located along each transect at 2 m, 5 m, 10 m, 15 m and 20 m from the fence in both directions into the forest and pasture. At both Kettering and Ridgeway, there were four

transects, each with 10 traps. At Kettering, two of the four transects ran from the fence out into the pasture only. The owner of the forested area did not want the traps because he was planning to clear the understorey for grazing.

The traps consisted of a funnel attached to a fine filter (0.1 mm mesh) to catch seeds but permit the flow of water. The funnel was constructed from smooth plastic sheet (UV-stabilised) to form a conical shaped funnel with an opening at the top of 35.6 cm in diameter, approximately 1000 cm² in area. The filter was glued at the bottom of the funnel. The filter was made using two tube pots (small rectangular pots 12 cm high by 5 cm wide) with the bottom of the pots removed. The mesh was held in place between the two pots which were stacked one inside the other. This design made it very difficult for seeds to be removed by ants or other seed predators. The smooth and steeply angled surfaces in the trap prevented birds from perching and the thin lip of plastic at the entrance of the filter made it impossible for ants to climb in or out.

The traps were attached to two wooden stakes and were approximately 60 cm above the ground. The seed traps were sufficiently high off the ground that they could prevent seeds of many of the short-stature species from being collected. Since the re-establishment of native shrubs and trees has been relatively poor, it was considered more important to collect seed-fall from these taller species. It would also be difficult to design a trap which would collect seed-fall from the shortest species.

The traps were emptied every month for a period of one year. The contents of the filter were dried and then examined under a binocular microscope. The traps often collected fine material—such as the

remains of flowers of *Acacia dealbata*—which made identification of small seeds more difficult. Seeds were generally easy to identify with the exception of some very small seeds such as those of *Epacris* species. Seeds which could not be identified were placed in petri dishes in an incubator and grown until they could be identified.

The number of seeds counted was used to estimate the input of viable seed into the pasture. However, it is likely that not all the seeds were viable and, therefore, these figures are an overestimate.

An attempt was made to determine the proportion of seeds which may have been missed using the microscope examination. After the examination, the contents of the filter were transferred to a petri dish containing moist filter paper and placed in an incubator. The incubator was set for 15 hours of light with 25° C, and 9 hours of night with 17° C. Only an additional 46 seeds were identified using this method. Those seeds that did germinate were grasses.

Comparisons were made between the median number of native and exotic seeds, and also between the median number of seeds in the forest and pasture collected in the seed-fall using the Mann-Whitney *u* test. Seasonality in the seed-fall data was tested for each species using the Mann-Whitney *u* test.

Soil Seed Bank

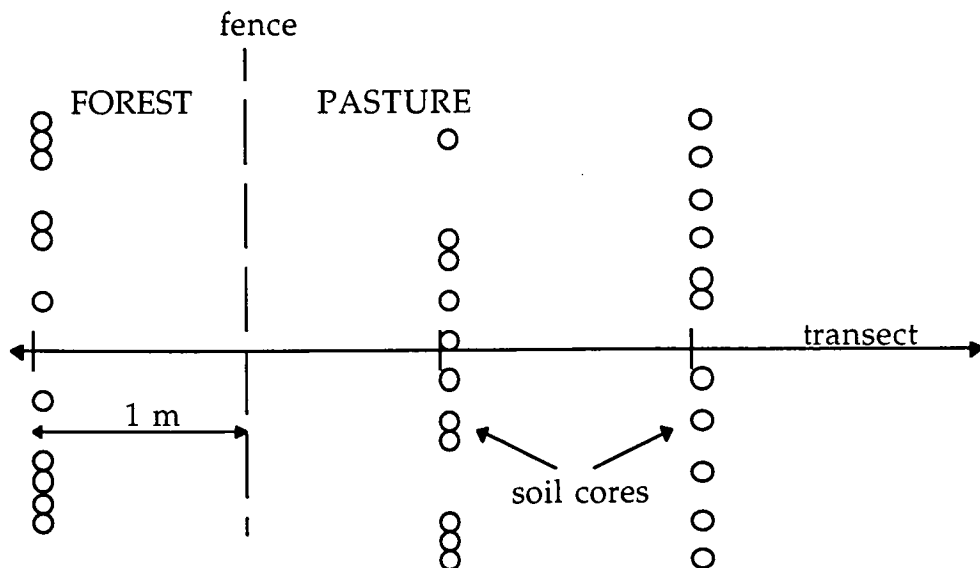
The abandoned pastures at Kettering and Ridgeway sites were selected to investigate the soil seed bank. Both sites are surrounded by natural vegetation which provides a source of native propagules for re-establishment.

Soils were collected from the pasture and the adjacent forest. The western side of the pastures was sampled. These areas of pasture should receive seed-fall of native species from the forest with the prevailing westerly winds.

Soil samples were collected along transects in both the forest and pasture. At Kettering, the transects ran perpendicular to the fence for a distance of 5 m into the forest and 10 m into the pasture. At Ridgeway, the transects were 10 m into the forest and 40 m into the pasture. There were two transects at each site.

Eleven soil cores were taken at every metre mark along the transect. The samples were taken at random distances (up to 1 m) parallel to the fence (figure 5.1). The 11 cores were bulked into a single sample. The cores were bulked to help reduce the level of variability in seed number and species composition which is typical in many soil seed banks (Benoit *et al.* 1989).

Figure 5.1 Schematic diagram of the soil seed bank sampling method.



The soil cores were 10 cm in diameter by 2 cm deep. The soil was coarsely sieved through 1 cm mesh to remove stones, litter and other debris. The soil was collected when it was relatively dry to avoid compaction of the soil and damage to the seeds during handling.

The number of seeds stored in the soil was estimated using the seedling emergence method (Gross 1990). This is a relatively accurate method of estimating the number of species stored in the soil seed bank. The estimate of the number of seeds is based on the number of viable seeds, whereas other methods (e.g. soil sieving) may provide the total number of seeds regardless of their viability. The main assumptions with this method are that all viable seeds germinate under the conditions provided and within the time constraint. Therefore, this method may underestimate the number of seeds. No treatments were applied which may overcome some seed dormancy mechanisms, for example, stratification or smoke (Bell *et al.* 1993; Marsden-Smedley *et al.* 1997).

Each bulked soil sample was placed into a single seedling tray (27 cm x 30 cm x 5 cm deep) and spread over a 2 cm layer of washed river sand. In the tray, the soil sample was approximately 2 cm deep, 1 cm below the lip of the tray.

Trays containing washed river sand and trays filled with sterilised soil were placed amongst the other trays to act as controls. Any germination on these trays would have indicated that there were seeds entering the glasshouse or seeds in the river sand contaminating the experiment.

The trays were placed in a glasshouse for a period of 12 months. Heating was used during the winter months to maintain an overnight temperature of 10° C and a maximum of around 20° C. During summer, white-wash or shade-cloth was used to keep the maximum temperature below 35° C, with a minimum of around 14° C. The temperature in the glasshouse occasionally exceeded 40° C even with the shade cloth in place. Lights were used from late autumn to early spring in order to maintain a day-length of 13.5 hours.

Seedlings emerging from the trays were counted approximately every month to maintain relatively bare soil for further germination. All seedlings were removed from the trays. Those which could be identified were discarded and the rest were transferred to pots for identification at a later stage of development.

The difference in the total number of native and exotic seeds was analysed using the Mann-Whitney *u* test. Comparisons were made between the median number of exotic and native seeds, and between the median number of seeds in the forest and pasture soil seed banks for each of the life-form groups.

The change in seed number with increasing distance from the forest was analysed using Spearman's Rank Correlation Co-efficient. Native and exotic species were analysed separately. Individual species and groups of species were analysed only if sufficient data were available.

Seed Predation

Seed predation by ants (and possibly other invertebrates) was estimated by measuring the number of seeds removed from baits. The bait

consisted of a petri dish (4 cm diameter) with two holes on opposite sides (approximately 1 cm high by 1.5 cm wide) to allow only invertebrates to enter. The petri dish was then pegged to the ground using a short piece of wire. These baits prevent disturbance and accidental loss of seeds caused by vertebrates, rain and wind.

Inside the bait a thin layer of fine sand containing the seeds was placed on the floor. All of the seeds were visible on the surface. A variety of shrub and tree species were selected because they varied in their ability to re-establish in the pasture. In each trap there were five seeds of *Leptospermum scoparium*, *Eucalyptus pulchella*, *Acacia dealbata* and *Bedfordia salicina*. The species *L. scoparium* and *E. pulchella* tended to re-establish in the pasture better than *A. dealbata*, whereas *B. salicina* was not present in the pasture.

A small area around the bait ($\approx 8\text{ cm} \times 8\text{ cm}$) was cleared of all litter and vegetation. The baits were placed on the ground close to seed-fall traps (described above) located in the pasture only. There was a total of 20 baits at each site (Ridgeway and Kettering).

This 'cafeteria' experiment was conducted once in each season (February, April, June and November). The baits were set in place early in the morning and removed at the end of three days so that the number of seeds removed could be calculated. The baits were set up only if the weather forecasts predicted three successive days of fine (sunny) weather.

Observations of invertebrates entering the baits were made hourly between 10 am and 5 pm on the first day only. The species and numbers of invertebrates carrying or eating seeds from the baits were recorded

over a period of one minute per bait. To identify these animals, individuals were collected (when necessary) and placed in a preservative (70% alcohol). Ant species were identified to the level of genus using the key in Andersen (1991).

This method provides only an indication of the actual rate and amount of seed predation in these areas. The experimental design was quite artificial because it concentrates a large number of seeds in a small area and the bait itself may interfere with the behaviour of the predators.

The rates of predation of the four species were compared between the two sites for each season using the Mann-Whitney u test. Seasonal variation in the predation rate for each species at each site was analysed using the Kruskal-Wallis H test. If a significant difference was detected by the Kruskal-Wallis H test, then the Mann-Whitney u test was used to test differences between all combinations of the seasons. The effect of distance from the forest on the predation rate for each species was tested using the Kruskal-Wallis H test.

Results

Seed-fall

Despite the height of the seed traps, seeds of some short-statured shrubs were collected, for example, *Epacris tasmanica*, which has very light seed. Seeds of grasses were also commonly collected; presumably the tall flowering culms assist with dispersal. Seed was not collected from every shrub and tree species in the vicinity of the traps.

Seed-fall was typically greater in the pasture than the forest at both sites (table 5.1). The only exception was at Kettering where the number of native seeds was not significantly different between the pasture and forest. The lowest amounts of seed-fall recorded were for exotic species in both the forests.

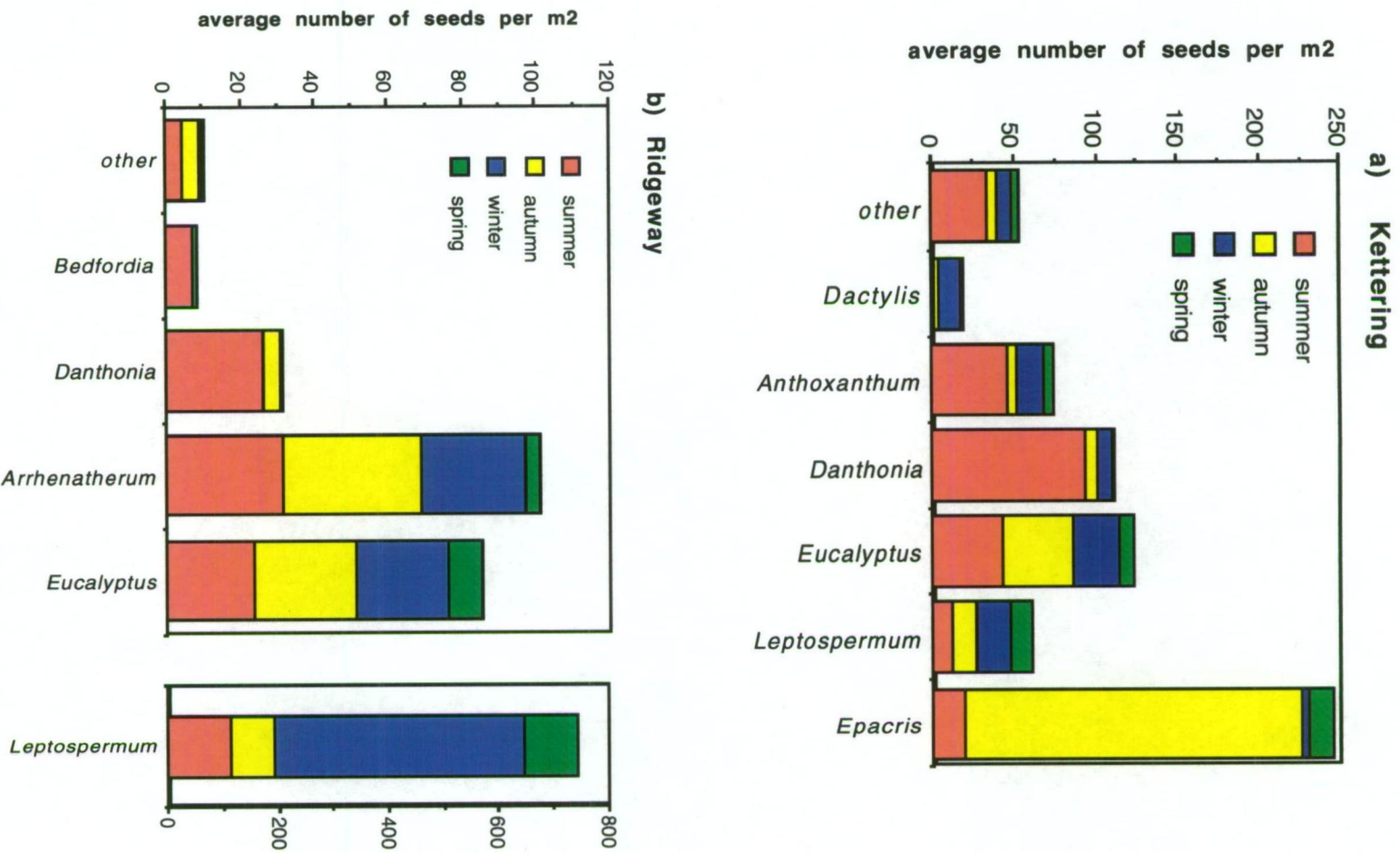
The amount of seed-fall of native species was significantly greater at Ridgeway than at Kettering in both the pasture and forest (table 5.1). Within each pasture, native seeds outnumbered exotic seeds by a factor of three at Kettering and by a factor of eight at Ridgeway.

Table 5.1 The average amount of seed-fall in the pasture and forest at Ridgeway and Kettering (number of seeds per m² per year \pm standard error). Means with different letters are significantly different: $p < 0.05$ (Mann-Whitney u test).

	forest	pasture
Ridgeway		
natives	742.5 \pm 105.1 ^A	879.5 \pm 195.9 ^B
exotics	4.5 \pm 2.1 ^C	101.0 \pm 29.6 ^D
Kettering		
natives	446.0 \pm 188.2 ^E	588.5 \pm 167.9 ^E
exotics	70.0 \pm 55.7 ^F	159.5 \pm 41.6 ^G

The two sites differed in the amount of seed-fall and the seasonal pattern of seed-fall which reaches the pasture (figure 5.2). At Kettering, most seed-fall was during summer and autumn, though the amount of seed-fall in spring was still approximately 50 seeds per m². At Ridgeway, the largest proportion of seed was shed during winter, primarily due to the large quantity of *Leptospermum* seed. At both sites, the least amount of seed fell in spring.

Figure 5.2 Seasonal patterns in the amount of seed-fall in the pasture for individual species (and the remainder). (Note: changes in scale on the Y axis).



In general, the composition of the seed-fall varied only slightly with the seasons but the amount of seed-fall changed considerably for most species (figure 5.2). At Kettering, the bulk of *Epacris* seeds fell in autumn, whereas the grasses (*Danthonia* and *Anthoxanthum*) were dispersed mainly in summer. *Leptospermum* and *Eucalyptus* maintained a fairly constant input of seed. The minor species collected in the traps were *Allocasuarina* sp., *Pultenaea juniperina* and *Acaena novae-zelandiae* (table 5.2)

At Ridgeway, seed of *Leptospermum* dominated each season's total. *Eucalyptus* and *Arrhenatherum* seeds fell in each season, while *Bedfordia* and *Danthonia* seeds fell mainly in summer (figure 5.2). The minor species collected in the traps were *Acacia dealbata*, *Banksia marginata*, *Billardiera longiflora*, *Bursaria spinosa* and *Pultenaea juniperina* (table 5.3).

At both sites, seeds of *Eucalyptus* and *Leptospermum* were collected in traps along the entire length of the transect (from the forest out into the pasture) (figure 5.3; 5.4). Seeds of *Eucalyptus* spp. at both sites tended to decrease with distance from the forest. Seeds of *Leptospermum* (at Ridgeway) and *Epacris* (at Kettering) were collected in greater numbers in the pasture than in the forest. The number of *Epacris* seeds at Kettering dropped dramatically at around 20 m from the forest. Seeds of *Cassinia* (at Kettering), *Exocarpos* and *Bedfordia* (at Ridgeway) were more common in the forest. The grasses (*Danthonia*, *Anthoxanthum* and *Arrhenatherum*) were collected predominantly in the pasture. Seed-fall from species with heavy seeds (*Exocarpos* and *Acacia*) was substantial in the forest but decreased sharply in the pasture. Seed-fall from shrubs which utilise wind for dispersal (e.g. *Cassinia*, *Bedfordia* and *Epacris*) were spread across the length of the transect in the pasture (figure 5.3; 5.4).

Table 5.2 Average amount of seed-fall per m² per year in the pasture at Kettering.

Species	Average number of seeds per m ² in the pasture	Lifeform
Native:		
<i>Acaena novae-zelandiae</i>	8	forb
<i>Allocasuarina</i> sp.	<1	shrub
<i>Cassinia aculeata</i>	12	shrub
<i>Danthonia penicillata</i>	111	grass
<i>Elymus scaber</i>	2	grass
<i>Epacris tasmanica</i>	263	shrub
<i>Eucalyptus ovata</i>	123	tree
<i>Exocarpos cupressiformis</i>	7	tree
<i>Leptospermum scoparium</i>	61	shrub
<i>Pultenaea juniperina</i>	2	shrub
Exotic:		
<i>Agrostis stolonifera</i>	18	grass
<i>Anthoxanthum odoratum</i>	118	grass
<i>Cirsium vulgare</i>	5	forb
<i>Dactylis glomerata</i>	19	grass

Table 5.3 Average amount of seed-fall per m² per year in the pasture at Ridgeway.

Species	Average number of seeds per m ² per year in the pasture	Lifeform
Native:		
<i>Acacia dealbata</i>	<1	tree
<i>Banksia marginata</i>	<1	shrub
<i>Bedfordia salicina</i>	9	shrub
<i>Bursaria spinosa</i>	3	shrub
<i>Danthonia penicillata</i>	32	grass
<i>Eucalyptus</i> spp.	85	tree
<i>Exocarpos cupressiformis</i>	6	tree
<i>Leptospermum scoparium</i>	744	shrub
<i>Pultenaea juniperina</i>	2	shrub
Exotic:		
<i>Arrhenatherum elatius</i>	101	grass
<i>Dactylis glomerata</i>	2	grass

Figure 5.3 The change in the amount of seed-fall (per year) along transects from the forest (negative distances) out into the pasture (positive distances) for individual species at Kettering. Note: scale on Y axis changes. g = grass; s = shrub; t = tree species.

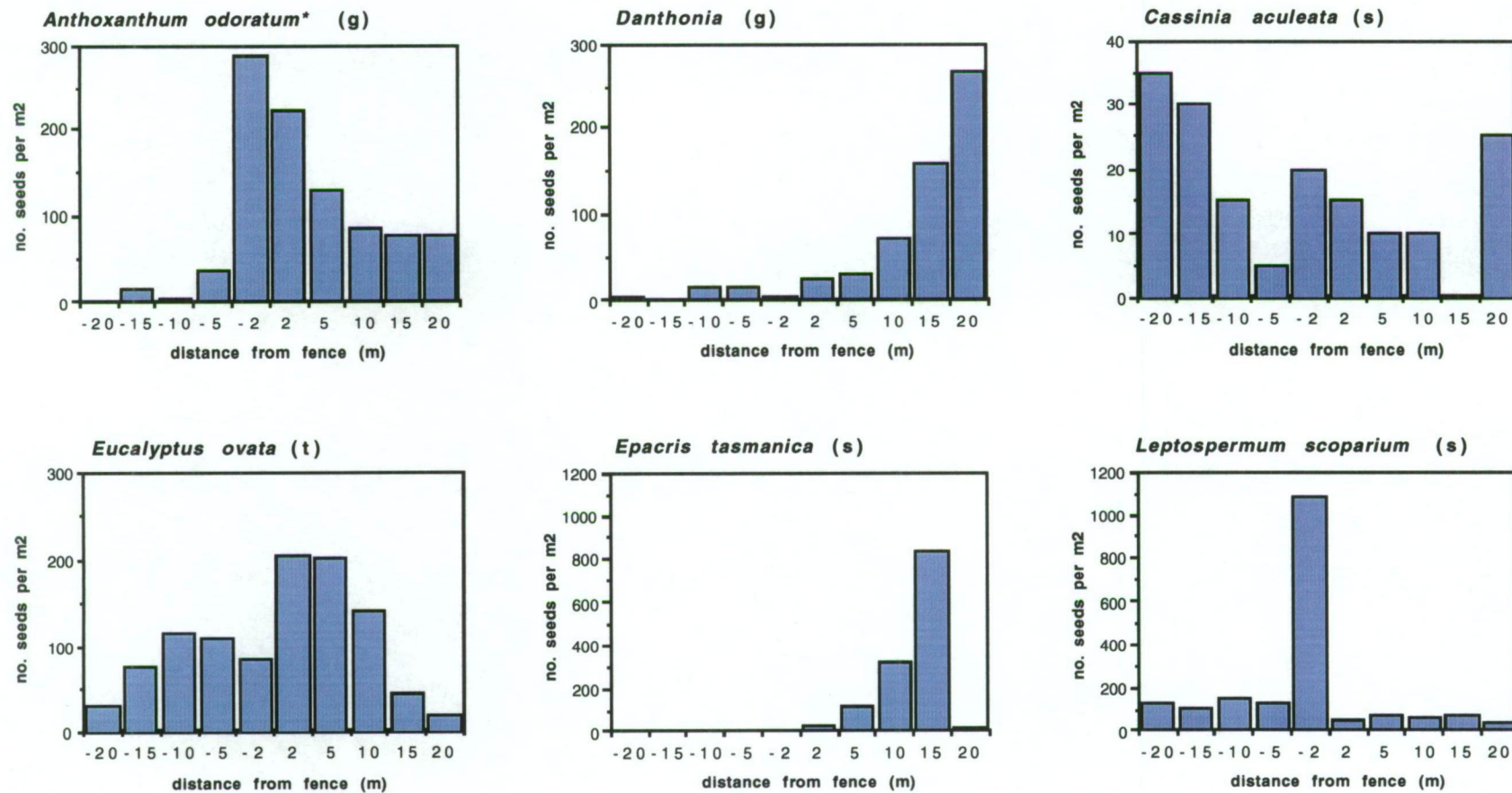
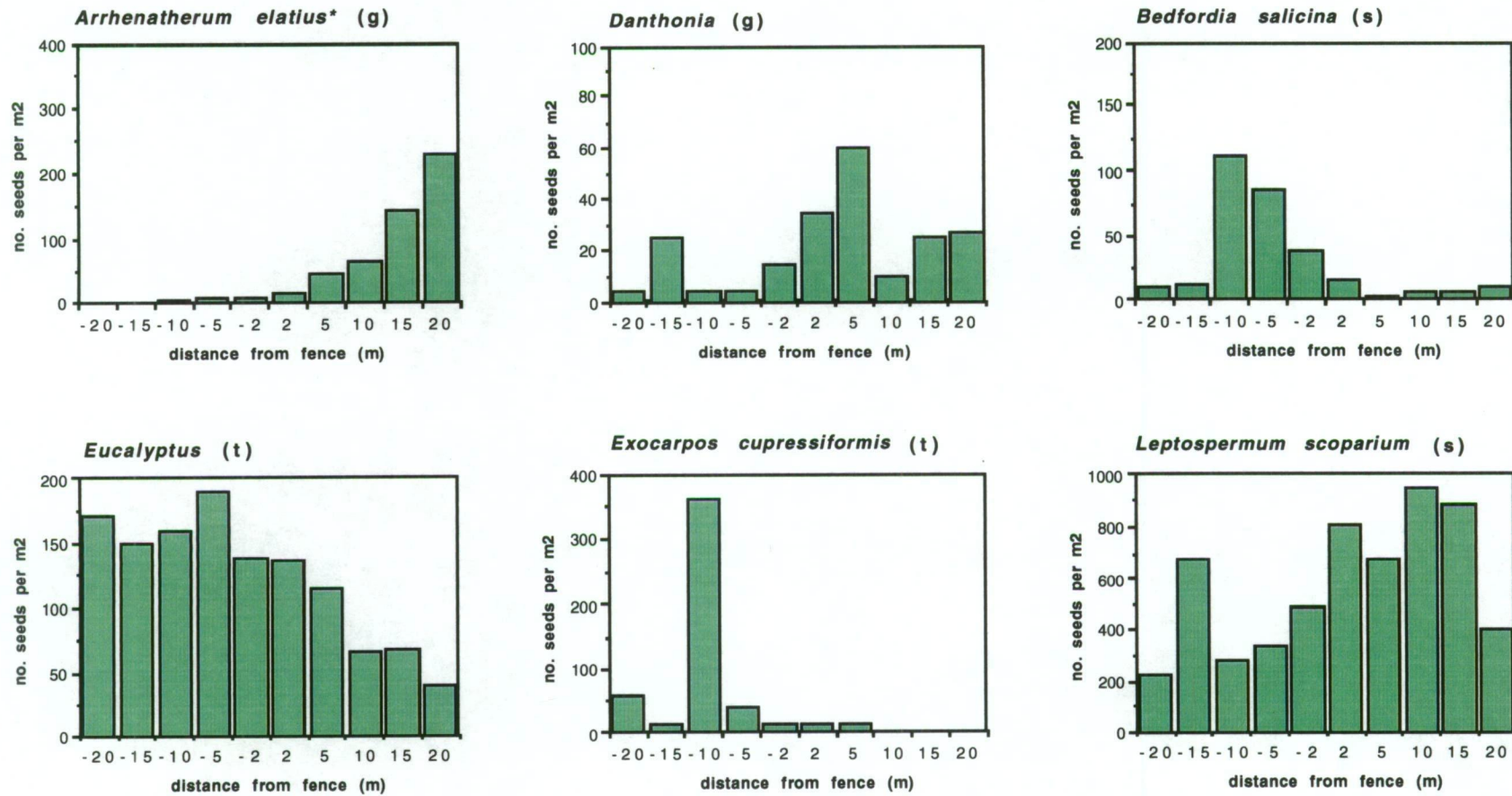


Figure 5.4 The change in the amount of seed-fall (per year) along transects from the forest (negative distances) out into the pasture (positive distances) for individual species at Ridgeway. Note: scale on Y axis changes. g = grass; s = shrub; t = tree species.



Soil Seed Banks

In both the pastures and the forests, the number of seeds per m² was highly variable especially for shrubs and tree species. However, many significantly different results were observed (table 5.4; 5.5).

In the pasture at Ridgeway, the number of native seeds was almost a tenth the number of the exotic seeds ($p = 0.0001$; table 5.4). At Kettering, however, there was no significant difference between the total number of native and exotic seeds in the pasture.

In the forest soil seed banks, the difference in the total number of native seeds and exotic seeds was significant (table 5.4). At Kettering the number of natives was greater than the number of exotics, whereas the opposite was observed for Ridgeway.

The number of native and exotic seeds stored in the soil of the forest was typically fewer than the number in the pasture (table 5.5). The seed bank at Kettering was typically larger than Ridgeway for each category. In total, native seeds out-numbered exotic seeds at Kettering only.

Herbaceous species dominated the soil seed banks at both sites. Seeds of tree species were absent in the soil seed bank at Kettering and relatively uncommon at Ridgeway. Seeds of shrubs were more common at Kettering and were more plentiful in the pasture than in the forest (table 5.5). The exotic shrub category was dominated by one species, *Erica lusitanica*.

At both sites, the number of exotic seeds was typically significantly greater in the pasture than the forest (table 5.5). At Ridgeway, the number of native seeds of each life-form was approximately equal between the forest and pasture (table 5.5). At Kettering, seeds of native graminoids were more abundant in the pasture soil, though more native forbs were found in the forest soil (table 5.5). Seeds of native shrubs tended to be more common in the pasture than the forest at Kettering but due to the highly variable data this difference was not significant ($p = 0.12$).

There was generally a higher degree of similarity between the composition of the soil seed bank and the vegetation with exotic species compared with natives (table 5.6). Native trees and shrubs were generally poorly represented in the soil seed bank ($\leq 50\%$). A few species were present only in the soil seed bank and these species were usually exotic forbs.

Only one species (*Betula pubescens*) was excluded from the analysis because it germinated in the control trays in the glasshouse, but was not present at the site. Other species (e.g. *Epilobium ciliatum*, *Senecio vulgaris* and *Cerastium glomeratum*) were glasshouse weeds which probably contaminated the trays. However, these species were also observed at the sites. An estimate of the contamination was made using the average number of seedlings of these three species germinating in the control trays. The figures for each site were corrected using these averages.

Table 5.4 The median number of seedlings germinated from the soil seed bank at Ridgeway and Kettering. Comparisons of the number of native and exotic seeds in the pasture and forest (Mann-Whitney u-test).

Number of seeds (per m ²)				
	Native	Exotic	z value	probability*
Ridgeway				
Forest				
graminoids	221	138	-1.402	ns
forbs	73	477	-3.781	***
shrubs	17	0	-3.122	**
trees	36	1	-3.153	**
Total	347	616	-2.080	*
Pasture				
graminoids	292	1050	-5.992	***
forbs	125	3235	-7.700	***
shrubs	19	2	-3.766	***
trees	5	0	-0.058	ns
Total	440	4291	-7.699	***
Kettering				
Forest				
graminoids	949	76	-2.619	**
forbs	162	201	-0.313	ns
shrubs	65	183	-2.214	*
trees	0	0	—	—
Total	1176	461	-2.611	**
Pasture				
graminoids	5970	2520	-2.987	**
forbs	36	1590	-3.797	***
shrubs	860	2534	-2.005	*
trees	0	0	—	—
Total	6866	6644	-0.038	ns

(* probability: ns = not significant; * = 0.01 < p < 0.05; ** = 0.01 < p < 0.001; *** = p < 0.001)

Table 5.5 The median number of seedlings germinated from the soil seed bank at Ridgeway and Kettering. Comparisons of the number of native or exotic seeds in the pasture and forest (Mann-Whitney u-test).

Number of seeds (per m ²)				
	Forest	Pasture	z value	probability*
Ridgeway				
Natives				
graminoids	221	292	-1.348	ns
forbs	73	125	-1.628	ns
shrubs	17	19	-0.423	ns
trees	36	5	-3.959	***
Total	347	440	-1.274	ns
Exotics				
graminoids	138	1050	-4.403	***
forbs	477	3235	-4.803	***
shrubs	0	2	-1.292	ns
trees	1	0	-0.646	ns
Total	616	4291	-4.815	***
Kettering				
Natives				
graminoids	949	5970	-3.062	**
forbs	162	36	-2.664	**
shrubs	65	860	-1.535	ns
trees	0	0	—	—
Total	1176	6866	-3.062	**
Exotics				
graminoids	76	2520	-3.065	**
forbs	201	1590	-2.939	**
shrubs	183	2534	-2.390	*
trees	0	0	—	—
Total	461	6644	-3.062	**

(* probability: ns = not significant; * = 0.01 < p < 0.05; ** = 0.01 < p < 0.001; *** = p < 0.001)

Table 5.6 The degree of similarity between the composition of the soil seed bank and the vegetation at both sites.

	Number of species in common*	Number of species in vegetation	Percentage Similarity**	No. of species present only in the seed bank
Native Species				
Ridgeway				
graminoids	8	9	89	4
forbs	6	12	50	2
shrubs	4	11	36	0
trees	2	7	29	0
Kettering				
graminoids	4	7	57	3
forbs	3	7	43	1
shrubs	3	10	30	0
trees	1	2	50	0
Exotic Species				
Ridgeway				
graminoids	6	6	100	0
forbs	14	14	100	9
shrubs	2	3	67	0
Kettering				
graminoids	4	5	80	2
forbs	9	10	90	6
shrubs	2	2	100	0

* Number of species common to both the soil seed bank and the vegetation

**Percentage Similarity = (number of species common to both the soil seed bank and the vegetation x 100) / (no. species in the vegetation)

Distance from the Forest

Kettering:

Overall, there was no significant relationship between distance from the forest and the total number of native or exotic seeds in the seed bank (table 5.7). There were few significant relationships between the number of seeds of individual species and distance from the forest

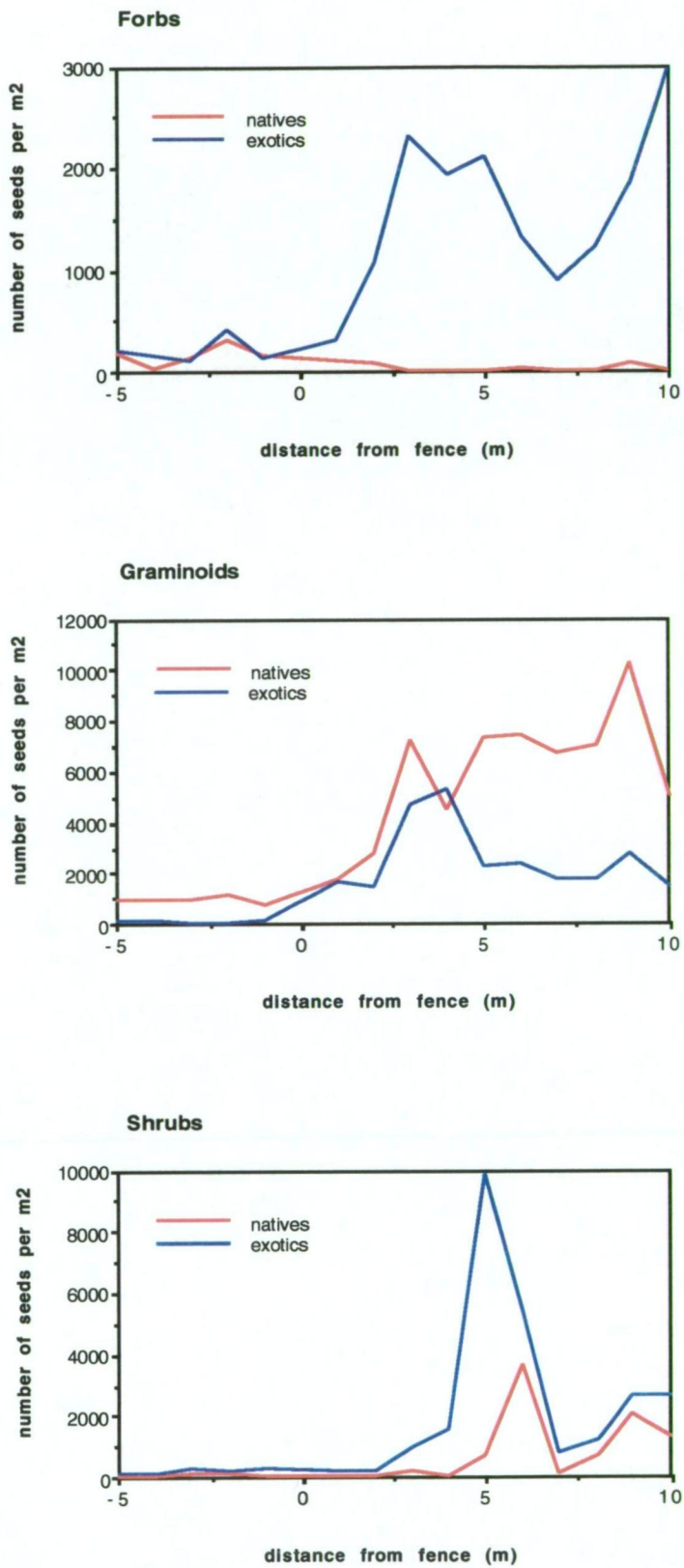
(table 5.7). However, there was a significant increase in the number of seeds of native shrubs, in particular *Epacris tasmanica*, with increasing distance into the pasture. The number of seeds of forbs, small graminoids and shrubs tended to increase ($p > 0.05$) with increasing distance from the forest (figure 5.5).

Table 5.7 The effect of distance from the forest on the number of seedlings identified from the soil seed bank at Kettering (Spearman's Rank Correlation Co-efficient).

Species / Lifeform		Increase or decrease in seedling number with distance	z value (corrected for ties)	probability
Native:				
<i>Epacris tasmanica</i>	shrub	↑	2.061	0.0393
<i>Isolepis marginata</i>	s/gr	-	0.455	ns*
<i>Poa rodwayi</i>	grass	-	0.492	ns
<i>Schoenus apogon</i>	s/gr	-	1.909	ns
<i>Stipa pubinodis</i>	grass	-	0.584	ns
Total		-	1.727	ns
Exotic:				
<i>Agrostis stolonifera</i>	grass	-	0.382	ns
<i>Anthoxanthum odoratum</i>	grass	-	-1.933	ns
<i>Centaureum erythraea</i>	forb	-	1.842	ns
<i>Dactylis glomerata</i>	grass	-	-1.829	ns
<i>Erica lusitanica</i>	shrub	-	1.618	ns
<i>Hypochoeris radicata</i>	forb	↑	2.195	0.0282
<i>Plantago lanceolata</i>	forb	-	0.636	ns
<i>Rubus fruticosus</i>	shrub	-	-1.593	ns
<i>Trifolium</i> spp.	forb	-	-0.309	ns
Total		-	0.6	ns

*ns = not significant: $p > 0.05$ s/gr = small graminoid

Figure 5.5 The density of seeds stored in the soil at Kettering. Note: scale on Y axis changes. (Positive distance = pasture. Negative distance = forest. Zero = fence.)



Ridgeway:

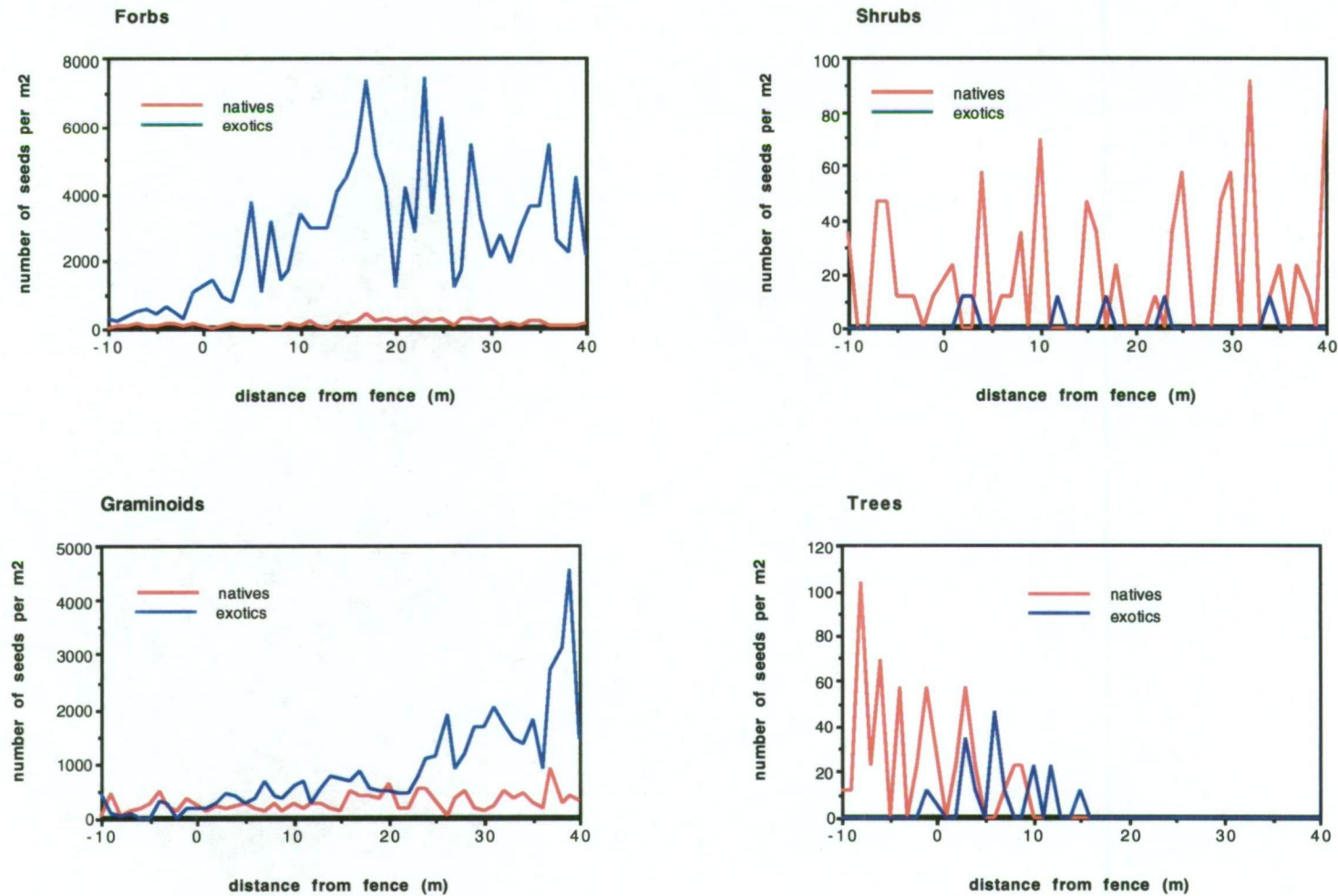
The number of seeds of native and exotic graminoid species increased significantly with distance from the forest (table 5.8). The number of seeds of native trees decreased significantly with distance from the forest. The other groups of species showed no particular trends, except the exotic forbs which tended to increase in number ($p > 0.05$) with increasing distance from the forest (figure 5.6). The number of seeds of shrub species fluctuated considerably along the transects (figure 5.6).

Table 5.8 The effect of distance from the forest on the number of seedlings identified from the soil seed bank at Ridgeway (Spearman's Rank Correlation Co-efficient).

Species / Lifeform		Increase or decrease in seedling number with distance	z value (corrected for ties)	probability
Native:				
<i>Isolepis marginata</i>	s/gr	↑	3.162	0.002
<i>Linum marginale</i>	forb	-	1.798	ns*
<i>Schoenus apogon</i>	s/gr	↑	3.622	0.0003
<i>Stipa pubinodis</i>	grass	↑	-2.92	0.0035
trees	trees	↓	-3.514	0.0004
Total		↑	2.756	0.0058
Exotic:				
<i>Agrostis stolonifera</i>	grass	↑	5.282	0.0001
<i>Anagallis arvensis</i>	forb	-	-1.044	ns
<i>Carex flacca</i>	s/gr	-	0.881	ns
<i>Centaureum erythraea</i>	forb	-	-0.052	ns
<i>Holcus lanatus</i>	grass	↑	5.314	0.0001
<i>Linum trigynum</i>	forb	-	1.309	ns
<i>Plantago lanceolata</i>	forb	-	0.423	ns
<i>Trifolium</i> spp.	forb	↑	5.292	0.0001
<i>Vicia sativa</i>	forb	↑	5.423	0.0001
Total		↑	3.505	0.0005

*ns = not significant: $p > 0.05$ s/gr = small graminoid

Figure 5.6 The density of seeds stored in the soil at Ridgeway. Note: scale on Y axis changes. (Positive distance = pasture. Negative distance = forest. Zero = fence).



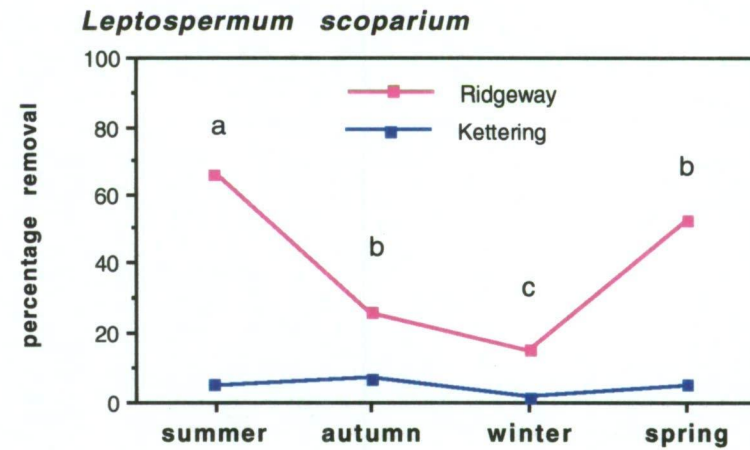
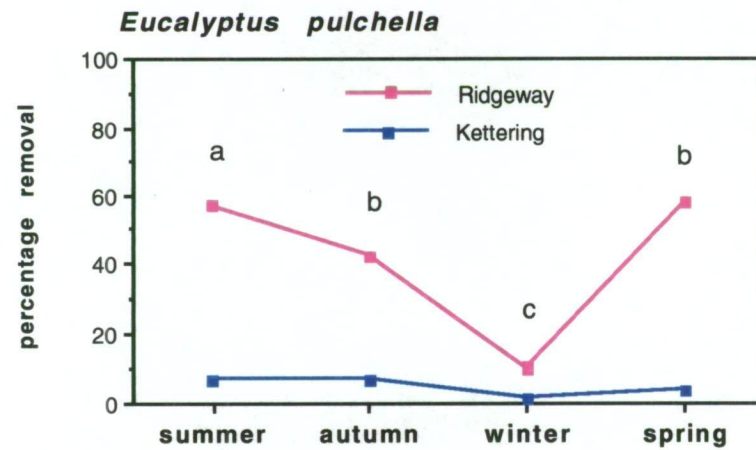
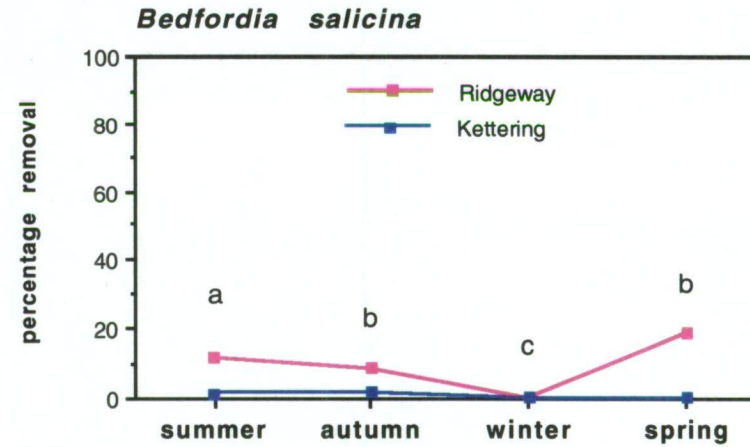
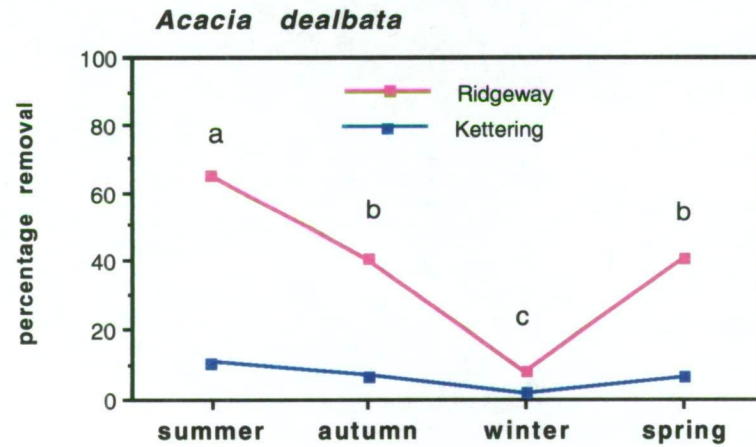
Seed Predation

Seed was removed from the baits in every season, although less was removed in winter (figure 5.7). For each species the rate of predation at Ridgeway was significantly higher than at Kettering (except *Acacia* and *Bedfordia* during winter) ($p < 0.05$). At Kettering, the predation rate was generally at or below 10% over the three-day period of the experiment, with no significant variation between the seasons ($p > 0.05$). At Ridgeway, seeds of *Eucalyptus*, *Acacia*, *Bedfordia* and *Leptospermum* were always more heavily predated ($p < 0.05$) during the warmer months of summer and spring than winter (figure 5.7). *Bedfordia salicina* seeds were generally not targeted by the ants, though predation rates were still around 10% at Ridgeway.

In each season at Kettering, the differences in the rate of seed predation between the species was minimal, except for *Bedfordia* which was rarely removed from the baits (figure 5.7). The same trend was observed at Ridgeway, however the rate of predation was substantially higher compared with Kettering. At Ridgeway, *Bedfordia* has a similar seasonal pattern to the other three species, although the rate is far lower.

Ants were the only invertebrates observed entering the seed baits (table 5.9). Three genera of ants were seen collecting or eating seeds from the baits at Ridgeway and only one genus at Kettering. Only a few ants were actually observed in the baits during the observations on the first day of each trial (<10 per 160 observations). The rate of predation was not significantly affected by the distance from the forest ($p > 0.05$).

Figure 5.7 The average rate of seed predation by ants; % removal from baits over a 3-day period. (Means with different letters (Ridgeway only) are significantly different ($p < 0.05$, Mann-Whitney u test). No significant differences between means for Kettering data).



The number of ants observed corresponds approximately to the rates of removal at each site (figure 5.7; table 5.9). Very few ants were found at Kettering, even during the summer. Ants were more common at Ridgeway, except in winter.

The ants listed in table 5.9 were all observed to remove seed from the baits and are therefore assumed to be seed harvesting or eating species. A study on seed-harvesting ants in Tasmania (Bashford 1993) describes *Iridomyrmex bicknelli* as a seed-eater, and *Rhytidoponera tasmaniensis* and *Pheidole tasmaniensis* as seed-harvesters.

Table 5.9 The total number of ants observed carrying or eating seed from the seed baits at Ridgeway and Kettering.

Site/ Ant genera	Summer	Autumn	Winter	Spring
Ridgeway				
<i>Pheidole</i>	5	2	0	2
<i>Rhytidoponera</i>	6	1	0	4
<i>Iridomyrmex</i>	7	5	1	4
Kettering				
<i>Rhytidoponera</i>	1	0	0	1

Discussion

Seed Availability

Seed Dispersal from the Adjacent Forest

The results of the seed-fall experiment show that several species of native shrub and tree are dispersed well into the pasture from the adjacent forest (figure 5.3; 5.4). The quantity of seed-fall from native species collected in the pasture was substantial. The amount of seed-fall in 12 months was approximately one fifth and one tenth the size of the soil seed bank at Ridgeway and Kettering respectively. Due to the height of the seed traps, it is likely that seed-fall from many short-statured plants would not have been collected. Therefore, the actual quantity of seed-fall is likely to be much higher and more diverse.

The quantity of seed-fall of native species varied considerably with distance from the forest. Seed-fall from species with relatively heavy seeds tended to decrease substantially with distance from the forest (e.g. *Exocarpos cupressiformis*) (figure 5.4). Taller species in the forest, such as *Eucalyptus*, were able to disperse seed (at least) 20 m into the pasture, despite the lack of a mechanism to assist seed dispersal (figure 5.3; 5.4). The presence of a (relatively) large number of individuals of *Epacris tasmanica* at Kettering and *Leptospermum scoparium* at Ridgeway in the pasture affected the pattern of seed-fall. For these two species the quantity of seed-fall increased with distance from the forest (figure 5.3; 5.4). This increase in seed-fall was presumably caused by the plants within the pasture shedding seed in addition to the seed dispersed from the forest.

The advantages of wind-dispersed seed were observed for some species, such as *Cassinia aculeata* at Kettering and *Bedfordia salicina* at

Ridgeway (figure 5.3; 5.4). Seeds were collected (at least) 20 m from the forest, despite the presence of very few plants in the pasture. Both species have a hairy pappus attached to the seed which aids wind dispersal.

In other studies, seed dispersal in abandoned pastures tended to decrease with distance from the surrounding native vegetation (Aide & Cavelier 1994; da Silva *et al.* 1996; Nepstad *et al.* 1996). In these studies, isolated trees in the pastures also contribute seeds. In abandoned pastures in Amazonia, these isolated trees also attract frugivorous birds and bats which deposit substantial numbers of viable seeds (Nepstad *et al.* 1991, 1996; Vieira *et al.* 1994; Aide & Cavelier 1994). For example, the rate of seed deposition in open pastures was around 2 seeds m⁻² yr⁻¹ versus 990 seeds m⁻² yr⁻¹ (from 22 species of tree and liana) beneath isolated trees (Nepstad *et al.* 1996).

At the sites studied in this project, only one or two species, such as *Exocarpos cupressiformis* and *Leptomeria drupacea*, produce disseminules that attract frugivorous birds or bats. Isolated trees were uncommon at both Ridgeway and Kettering and were not adjacent to the seed-fall traps. Seeds of *Exocarpos* were only collected up to 5 m within the pasture, indicating that the seed-traps were not used as perches for birds within the pasture.

Seeds of exotic species dispersed into the forest at both sites. For example, seeds of the grass *Anthoxanthum odoratum* were found up to fifteen metres from the boundary with the pasture at Kettering (figure 5.3). None of these exotic species was observed growing in the forest possibly because there was insufficient soil moisture, light or gaps in the vegetation for seedlings to establish (Amor & Stevens 1975;

Bowman & Kirkpatrick 1986; Russell 1994; Stoneman *et al.* 1994; Appleby in press).

Residual Soil Seed Bank

Some native seeds have the ability to remain viable for long periods (decades) in the soil, in particular, seeds of leguminous species with a hard seed coat (Bradbeer 1988). For example, seeds of *Acacia* spp. and *Cassia nemophila* were able to germinate following at least 40 years of storage in the soil while the land was farmed, despite the soil being ploughed (Onans & Parsons 1980). No such results were found at either Ridgeway or Kettering despite the occurrence of *Acacia* spp. (and several other species with hard seed coats) in the adjacent forest community.

The Availability of Native Seeds in the Soil Seed Bank

The density of seeds of most native species in the soil was very low. The majority of species have less than 20 seeds per m² (to a depth of 2 cm) in the pasture (appendix 5.1). The density of native seeds in the soil seed bank also varied considerably with distance from the forest (figure 5.5; 5.6). For native shrubs species, the density of seeds tended to increase with distance from the forest, although it fluctuated immensely (figure 5.5; 5.6).

At both sites, the bulk of the native component of the soil seed bank was due to just one or two sedge species which produce large quantities of seed. *Schoenus apogon* and *Isolepis marginata* accounted for approximately 80% and 50% of native seeds at Kettering and Ridgeway, respectively (appendix 5.1).

Some of the most common species collected in the seed-fall, *Leptospermum* and *Eucalyptus*, were poorly represented in the soil seed bank (appendix 5.1). It should be expected that not all the seed collected in the seed-fall traps would be viable. However, even if 50% of the seed was unviable, there was still a large discrepancy in the number of seeds collected in the seed-fall and the number germinating from the soil seed bank. Soil was collected in mid-summer (January) at Ridgeway and Kettering to analyse the soil seed bank. In December the amount of seed-fall in the pasture from *Leptospermum* was 83 and 6 seeds m⁻² at Ridgeway and Kettering respectively, and from *Eucalyptus* the seed-fall was 17 and 33 seeds m⁻².

The longevity of these seeds is probably short because the seeds germinate readily once they are released from the seed capsule on the plant. The high rate of predation of *Eucalyptus* and *Leptospermum* seeds by ants would also contribute to the rapid loss of these seeds following seed-fall (figure 5.7). In other studies, seed predation was a major factor limiting the availability of seeds in the soil (Ashton 1979; Andersen 1982; Andersen & Ashton 1985; Nepstad *et al.* 1991, 1996).

Regeneration of the genera *Eucalyptus* and *Leptospermum* from seed typically depends on disturbance such as fire. Following fire, seed is released *en masse* from the canopy (Gill 1981). This satiates the appetite of the seed-predating species and leaves plenty of seed for germination (Janzen 1971; Ashton 1979; Wellington & Noble 1985; Andersen 1987).

The number of seeds of *Epacris tasmanica* which germinated from the soil seed bank was far greater than the number of *Eucalyptus* and *Leptospermum* seeds, even though all three species have large annual seed-fall rates (appendix 5.1; figure 5.2). Seeds of *Epacris* are not

myrmecochorous (Berg 1975) and are so minute that they would easily be incorporated into the soil.

Therefore, it appears that a combination of factors which relate to the species (e.g. the amount of seed produced and seed dispersal mechanisms) and also some site-specific characteristics (e.g. the population size of the seed-harvesting ants) affect the availability of seeds of each species in the pasture.

Accuracy of the Soil Seed Bank Experiment

A number of studies have shown that there is generally a lack of similarity between the composition of the soil seed bank and the standing vegetation (Vlahos & Bell 1986; Lunt 1990; Chambers & MacMahon 1994). In soil seed bank studies, the main assumption of the germination technique is that all viable seeds will germinate. There is considerable information to suggest that seeds of many species fail to germinate unless particular germination cues are used (Auld & O'Connell 1991; Bell *et al.* 1993; Dixon *et al.* 1995; Marsden-Smedley *et al.* 1997). For example many Fabaceae species require heat-shock to break the hard seed coat. Other species respond to smoke, stratification or a combination of cues. This may explain the absence of *Acacia* and perhaps other species in the results of the soil seed bank experiment.

The Effects of Seed Predation on Seed Availability

Leptospermum scoparium and *Epacris tasmanica*

Two native shrub species that are successful recolonisers of abandoned pastures are *Epacris tasmanica* (Kettering) and *Leptospermum*

scoparium (Ridgeway). Each species appears to depend on a different strategy to re-establish.

Seeds of *Epacris tasmanica* are mostly shed in autumn (figure 5.2). This species has a persistent soil seed bank because the input of seeds (seed-fall) is less than the number of seed in the soil seed bank (figure 5.2; appendix 5.1).

Leptospermum scoparium has only a transitory soil seed bank which is predated by ants, but has plentiful seed-fall all year (figure 5.2) and an abundant canopy seed bank.

In both the above examples, there was a reliable (*i.e.* plentiful and year-round) source of seeds in the pasture. Therefore, both these species may take advantage of suitable conditions for germination throughout the year. There is little evidence in the soil seed bank or seed-fall experiments to show that other native shrub or tree species have such a reliable supply of seed in the pasture, at either Kettering or Ridgeway (table 5.2; 5.3).

Bedfordia salicina

Of the four species investigated in the seed predation experiment, *Bedfordia* seed was only lightly predated (figure 5.7). Despite *Bedfordia* seeds being collected in the seed-fall traps at Ridgeway, this species was absent from the soil seed bank. The rate of predation may equal the input of seed into the pasture, or perhaps the viability of the seed decreases rapidly. Alternatively, the sampling method used to estimate the soil seed bank may have been inadequate, considering the low number of seeds in the seed-fall (9 m² per year).

Acacia dealbata

Acacia dealbata seed would probably be the least adversely affected by seed-harvesting ants. *Acacia* seeds are collected for the elaiosome; an appendage on the seed which is a rich source of energy (Berg 1975). The seed coats of *Acacia* species are generally too thick for ants to break, so the rest of the seed is not consumed (Westoby *et al.* 1982). When ants locate *Acacia* seed the elaiosome is removed or the whole seed is carried to the nest and either buried in the nest or discarded on the surface.

The burial of *Acacia* seeds in ant nests may explain why these species were rarely detected in the soil seed bank in this study. The seeds may be buried at depths greater than the 0–2 cm sampled and they would also be concentrated around the nests. However, the *Acacia* seed may still germinate even from 8 cm below the soil surface following disturbance such as fire (Shea *et al.* 1979; Auld 1986; Appleby in press). A proportion of the *Leptospermum* and *Eucalyptus* seed which is harvested will also be stored in the nest, but these seeds are probably eaten within a short period of time (Ashton 1979).

Therefore, the extent to which seed predation affects the availability of seed is likely to vary between plant species. Species with a hard seed coat, like *Acacia* and other leguminous species, will remain viable after being harvested but their ability to germinate depends on the seed being buried close to the soil surface (Auld 1986). For species such as *Bedfordia*, *Leptospermum* and *Eucalyptus*, seed harvesting is likely to result in seed mortality. Due to the high quantity of seed of *Leptospermum* and *Eucalyptus* falling in the pasture, some seed would have a chance to germinate, if the conditions are suitable, especially in

cooler months when seed harvesting is lower (figure 5.2). Seedling recruitment will probably be limited more by the availability of safe sites than by seed predation (Andersen 1989). Rapid germination following the release of seeds of *Eucalyptus* and *Leptospermum* may be the main explanation for the lack of these species in the soil seed bank.

Predation and the Size of the Soil Seed Bank

The soil seed bank of native species was larger at Kettering—more than ten times the size of the soil seed bank at Ridgeway—despite the greater quantity of seed-fall at Ridgeway. This difference in the size of the soil seed bank could be a consequence of the difference in species composition. For example, *Epacris tasmanica* is abundant at Kettering and can produce large amounts of seed, while this is not the case at Ridgeway.

The difference in predation rates between the sites may also be a factor. The seed predation rates at Ridgeway were approximately six times the rate at Kettering (figure 5.7) based on the four species investigated. During all the visits to these sites, ants were rarely observed at Kettering, but individuals and nests were abundant at Ridgeway (table 5.9).

The main difference between the sites which could affect the size of the ant population is the aspect of the sites. At Ridgeway the area surveyed was on a north-facing slope whereas at Kettering the slope faced south. The activity of ants depends (partially) on soil temperature. The soil on southern slopes would be warmed for a shorter period of time (especially in winter) than northern slopes which are exposed to more solar radiation (in the southern hemisphere). The effect that

temperature has on ant activity was demonstrated by the substantial fall in predation rates during the cooler months (figure 5.7).

Disturbance and Seed Germination

The results of the previous chapter suggested that the availability of native seeds may be limiting the rate of re-establishment. The germination of native species would be expected following soil disturbance or burning (Purdie 1977b; Pyrke 1994). However, in the present study very little germination was observed. The results in this chapter suggest that there were native seeds (including shrubs and tree species) available either in the soil seed bank or the seed-fall.

Some studies have suggested that recruitment of native species is likely to be poor if the soil seed bank is dominated by exotic species (Lunt 1990; Hutchings & Booth 1996), especially if the exotic species can germinate at a faster rate or regenerate vegetatively following disturbance (Gilfedder & Kirkpatrick 1993; Marsden-Smedley *et al.* 1997). In this study, the vegetative regeneration of the exotic species, such as *Plantago*, *Agrostis* and *Dactylis*, may have been more rapid than the germination of native species. Native seedlings may not have survived long if competitive interactions were established between the resprouting exotic species and native germinants soon after disturbance.

These exotic species also have a large soil seed bank which probably helps maintain the dominance of these species. The density of seeds of the exotic shrub *Erica lusitanica* was extremely high in the pasture at Kettering (over 2000 seeds per m²). This species was highly successful at invading the pasture with up to 5000 seedlings per m² establishing following the removal of adult plants (unpublished data). The dense

soil seed bank appears to be a factor that increases the ability of this species to establish amongst pasture species (Mather & Williams 1990). Similarly, the greater rate of re-establishment of native woody species at Kettering (in particular *Epacris tasmanica*) compared with Ridgeway is reflected in the density of shrub and tree seeds in the soil seed bank (860 and 24 seeds per m² respectively).

Conclusion

In general, the availability of native seeds for re-establishment did not decline with distance from the forest. There was typically a plentiful supply of native seeds in the pasture either in the soil seed bank or in seed-fall. However, there tended to be only a small range of native species collected in the seed-fall traps.

For some native species, the lack of a soil seed bank in the pasture was due to poor dispersal from the adjacent forest or simply that the seeds are short-lived. For species such as *Eucalyptus* and *Leptospermum*, the lack of seeds in the soil was due, in part, to seed predation by ants.

In the pasture at Ridgeway, the quantity of seed-fall of native species was large in comparison with the size of the soil seed banks. At Kettering, the size of the soil seed bank for native species was far greater than the quantity of seed-fall. The smaller size of the soil seed bank of native species at Ridgeway may have been due to the higher rates of seed removal by ants at Ridgeway compared with Kettering.

Appendix

Appendix 5.1 A comparison of the species present in the soil seed bank of the pasture and those present in the vegetation. The average number of seeds recorded in the soil seed bank of the pasture are also presented.

**The species present in the vegetation are those recorded in both the forest and pasture.*

***Only the species present in the soil seed bank of the pasture are listed.*

Native species at Kettering			
	Species present in the vegetation*	Species present in the soil seed bank**	Average no. seeds recorded in the soil seed bank (per m ²)
Trees	<i>Eucalyptus ovata</i>	-	
	<i>Exocarpos cupressiformis</i>	-	
Shrubs	<i>Acacia verticillata</i>	-	
	<i>Cassinia aculeata</i>	<i>Cassinia aculeata</i>	1
	<i>Epacris impressa</i>	-	
	<i>Epacris tasmanica</i>	<i>Epacris tasmanica</i>	855
	<i>Leptospermum scoparium</i>	<i>Leptospermum scoparium</i>	2
	<i>Pultenaea juniperina</i>	-	
Forbs	<i>Acaena novae-zelandiae</i>	-	
	<i>Billardiera longiflora</i>	-	
	<i>Cassythra pubescens</i>	-	
	<i>Gonocarpus tetragynus</i>	-	
	-	<i>Gnaphalium collinum</i>	2
	<i>Hypericum gramineum</i>	<i>Hypericum gramineum</i>	17
	<i>Viola hederacea</i>	<i>Viola hederacea</i>	12
	<i>Wahlenbergia</i> spp.	<i>Wahlenbergia</i> spp.	5
Graminoids	<i>Danthonia</i> spp.	<i>Danthonia</i> spp.	2
	<i>Dichelachne rara</i>	-	
	<i>Diplarrena moraea</i>	-	
	<i>Ehrharta stipoides</i>	-	
	-	<i>Isolepis marginata</i>	2085
	-	<i>Juncus pallidus</i>	100
	<i>Lepidosperma laterale</i>	-	
	<i>Lomandra longifolia</i>	<i>Lomandra longifolia</i>	1
	-	<i>Luzula flaccida</i>	67
	<i>Poa rodwayi</i>	<i>Poa rodwayi</i>	140
	<i>Schoenus apogon</i>	<i>Schoenus apogon</i>	3507
	-	<i>Stipa pubinodis</i>	68

Exotic species at Kettering			
	Species present in the vegetation	Species present in the soil seed bank	Average no. seeds recorded in the soil seed bank (per m ²)
Shrubs	<i>Erica lusitanica</i>	<i>Erica lusitanica</i>	2511
	<i>Rubus fruticosus</i>	<i>Rubus fruticosus</i>	23
Forbs	-	<i>Acetosella vulgaris</i>	1
	-	<i>Anagallis arvensis</i>	9
	<i>Centaureum erythraea</i>	<i>Centaureum erythraea</i>	427
	<i>Epilobium ciliatum</i>	<i>Epilobium ciliatum</i>	10
	<i>Geranium dissectum</i>	<i>Geranium dissectum</i>	3
	<i>Hypochoeris radicata</i>	<i>Hypochoeris radicata</i>	281
	<i>Linum trigynum</i>	-	
	-	<i>Oxalis corniculata</i>	1
	-	<i>Parentucelia viscosa</i>	3
	<i>Plantago lanceolata</i>	<i>Plantago lanceolata</i>	396
	<i>Prunella vulgaris</i>	<i>Prunella vulgaris</i>	17
	-	<i>Ranunculus repens</i>	1
	-	<i>Sagina procumbens</i>	1
	<i>Senecio vulgaris</i>	<i>Senecio vulgaris</i>	8
	<i>Sonchus oleraceus</i>	<i>Sonchus oleraceus</i>	10
	<i>Trifolium spp.</i>	<i>Trifolium spp.</i>	418
Graminoids	<i>Agrostis stolonifera</i>	<i>Agrostis stolonifera</i>	2015
	-	<i>Aira caryophyllea</i>	2
	<i>Anthoxanthum odoratum</i>	<i>Anthoxanthum odoratum</i>	135
	<i>Arrhenatherum elatius</i>	-	
	-	<i>Briza minor</i>	2
	<i>Dactylis glomerata</i>	<i>Dactylis glomerata</i>	343
	<i>Holcus lanatus</i>	<i>Holcus lanatus</i>	22

Native species at Ridgeway			
	Species present in the vegetation	Species present in the soil seed bank	Average no. seeds recorded in the soil seed bank (per m ²)
Trees	<i>Acacia dealbata</i>	-	
	<i>Banksia marginata</i>	-	
	<i>Bursaria spinosa</i>	<i>Bursaria spinosa</i>	1
	<i>Eucalyptus globulus</i>	-	
	<i>Eucalyptus obliqua</i>	-	
	<i>Eucalyptus viminalis</i>	-	
	<i>Exocarpos cupressiformis</i>	<i>Exocarpos cupressiformis</i>	4
Shrubs	<i>Acacia verticillata</i>	-	
	<i>Astroloma humifusum</i>	<i>Astroloma humifusum</i>	4
	<i>Bedfordia salicina</i>		
	<i>Bossiaea prostrata</i>	-	
	<i>Cassinia aculeata</i>	<i>Cassinia aculeata</i>	6
	<i>Epacris impressa</i>	<i>Epacris impressa</i>	4
	<i>Hibbertia hirsuta</i>	-	
	<i>Leptospermum scoparium</i>	<i>Leptospermum scoparium</i>	5
	<i>Lomatia tinctoria</i>	-	
	<i>Pimelea humilis</i>	-	
	<i>Pultenaea juniperina</i>	-	
	<i>Tetratheca pilosa</i>	-	
Forbs	<i>Acaena novae-zelandiae</i>	<i>Acaena novae-zelandiae</i>	1
	<i>Billardiera longiflora</i>	-	
	<i>Cassythia pubescens</i>	-	
	-	<i>Galium gaudichaudii</i>	1
	<i>Geranium solanderi</i>	-	
	-	<i>Gnaphalium collinum</i>	1
	<i>Gonocarpus tetragynus</i>	<i>Gonocarpus tetragynus</i>	1
	<i>Goodenia elongata</i>	-	
	<i>Helichrysum scorpioides</i>	<i>Helichrysum scorpioides</i>	1
	<i>Hypericum gramineum</i>	<i>Hypericum gramineum</i>	23
	<i>Linum marginale</i>	<i>Linum marginale</i>	94
	<i>Stylidium graminifolium</i>	-	
	<i>Veronica gracilis</i>	-	
	<i>Viola hederacea</i>	-	
	<i>Wahlenbergia</i> spp.	<i>Wahlenbergia</i> spp.	3
Graminoids	<i>Danthonia penicillata</i>	<i>Danthonia penicillata</i>	5
	<i>Dichelachne rara</i>	<i>Dichelachne rara</i>	1
	<i>Diplarrena moraea</i>	-	
	-	<i>Isolepis marginata</i>	17
	-	<i>Juncus pallidus</i>	3
	<i>Lepidosperma laterale</i>	<i>Lepidosperma laterale</i>	1
	<i>Lomandra longifolia</i>	<i>Lomandra longifolia</i>	1
	<i>Luzula flaccida</i>	<i>Luzula flaccida</i>	5
	<i>Poa rodwayi</i>	<i>Poa rodwayi</i>	9
	<i>Schoenus apogon</i>	<i>Schoenus apogon</i>	197
	<i>Stipa pubinodis</i>	<i>Stipa pubinodis</i>	38
	<i>Themeda triandra</i>	<i>Themeda triandra</i>	11

Exotic species at Ridgeway			
	Species present in the vegetation	Species present in the soil seed bank	Average no. seeds recorded in the soil seed bank (per m ²)
Shrubs	<i>Erica lusitanica</i>	<i>Erica lusitanica</i>	1
	<i>Rosa rubiginosa</i>	-	1
	<i>Rubus fruticosus</i>	<i>Rubus fruticosus</i>	
Forbs	-	<i>Acetosella vulgaris</i>	10
	-	<i>Anagallis arvensis</i>	52
	<i>Centaureum erythraea</i>	<i>Centaureum erythraea</i>	2331
	<i>Cerastium glomeratum</i>	<i>Cerastium glomeratum</i>	1
	-	<i>Cirsium vulgare</i>	1
	<i>Epilobium ciliatum</i>	<i>Epilobium ciliatum</i>	34
	<i>Geranium dissectum</i>	<i>Geranium dissectum</i>	6
	<i>Hypochoeris radicata</i>	<i>Hypochoeris radicata</i>	4
	<i>Linum trigynum</i>	<i>Linum trigynum</i>	169
	-	<i>Myosotis discolor</i>	1
	<i>Oxalis corniculata</i>	<i>Oxalis corniculata</i>	6
	-	<i>Parentucellia viscosa</i>	6
	-	<i>Petrorhagia nanteuillii</i>	6
	<i>Plantago lanceolata</i>	<i>Plantago lanceolata</i>	281
	<i>Prunella vulgaris</i>	<i>Prunella vulgaris</i>	12
	<i>Ranunculus repens</i>	<i>Ranunculus repens</i>	1
	<i>Senecio vulgaris</i>	<i>Senecio vulgaris</i>	10
	-	<i>Solanum nigrum</i>	2
	-	<i>Sonchus oleraceus</i>	4
	<i>Taraxacum officinale</i>	<i>Taraxacum officinale</i>	1
	<i>Trifolium</i> spp.	<i>Trifolium</i> spp.	165
	-	<i>Veronica serpyllifolia</i>	2
	<i>Vicia sativa</i>	<i>Vicia sativa</i>	132
Graminoids	<i>Agrostis stolonifera</i>	<i>Agrostis stolonifera</i>	934
	<i>Anthoxanthum odoratum</i>	<i>Anthoxanthum odoratum</i>	1
	<i>Arrhenatherum elatius</i>	<i>Arrhenatherum elatius</i>	13
	<i>Carex flacca</i>	<i>Carex flacca</i>	33
	<i>Dactylis glomerata</i>	<i>Dactylis glomerata</i>	11
	<i>Holcus lanatus</i>	<i>Holcus lanatus</i>	58

Chapter Six

The Soil Environment and Seedling Establishment

Introduction

Many exotic pasture species require the addition of nutrients, in particular phosphorus, in order to maintain high productivity. Improving soil fertility generally decreases the abundance of species found on the original soil, while increasing the abundance of species adapted to higher nutrient soils (Clements 1983; Pywell *et al.* 1994). From the results of the present study, the improved pastures are able to remain relatively intact, despite the lack of further inputs of fertilizer and other forms of maintenance.

Over time, the soil fertility of abandoned improved pastures will fall due to processes such as leaching (especially of more mobile nutrients such as nitrate and potassium) and immobilization (particularly phosphorus) (Attiwill & Leeper 1987). However, these processes can take many years, depending on the soil type. Techniques to restore native vegetation on areas which have been fertilized include stripping the topsoil or repeated removal of crops to deplete soil nutrients, followed by reseedling (see Marrs 1985).

The presence of grasses is likely to cause other changes to the soil environment which may affect the ability of native species to re-establish. For example, soil pH can rise following the establishment of the grassy vegetation on former heathland (Pywell *et al.* 1995). Changes may also occur to the composition and abundance of soil microbes that are important for the health of native species, such as particular

mycorrhizal fungi or bacteria (Ashton & Willis 1982; Ellis & Pennington 1993).

Differences in the abundance of inoculum of mycorrhizal fungi are known to affect the competitive interactions between species (Allen & Allen 1984). For example, the lack of suitable mycorrhizal fungi in the soil beneath *Poa* grasslands was found to suppress the establishment of *Eucalyptus delegatensis* seedlings (Ellis & Pennington 1992). Succession is often accompanied or even possibly mediated by changes in the composition and abundance of mycorrhizal fungi in the soils (Reeves *et al.* 1979; Allen & Allen 1984; Johnson *et al.* 1991).

The aims of this study are to examine the effects of modification of the soil environment and soil microbes (in particular, mycorrhizal fungi) on the ability of native species to survive and compete with the introduced pasture species. Three native shrub and tree species were tested since re-establishment of woody species has been relatively poor compared with herbaceous species. These species varied in their ability to re-establish in improved pastures: *Leptospermum scoparium* (relatively good); *Eucalyptus pulchella* (moderate); and *Bedfordia salicina* (poor) (chapter 3).

In order to address these issues, the specific aims of this chapter are:

- to compare the soil nutrient status of the forest and pasture soils to find if there is a residual effect of fertilizer applications;
- to determine whether the growth and survival of the shrub and tree seedlings was adversely affected by the soil of the pasture compared with soil from the forest;

- to test whether any differences in seedling growth or survival could be attributed to a difference in soil nutrient status or the amount of mycorrhizal infection (or some other soil microbe) between the pasture and forest;
- to determine the extent that competition from the roots or the shoots of the pasture species affects the growth of native shrub and tree seedlings;
- to investigate other possible causes of seedling mortality that occur in the pastures.

Methods

Soil Nutrient Status

Soil samples were collected from the paddocks and forest at Ridgeway. Soil cores were taken in three zones: the forest (5 to 10 m from the fence); the edge of the pasture (up to 10 m from the fence) and from the centre of the pasture (greater than 15 m from the fence). Seven samples were collected from each zone. For each sample, five sub-samples were collected and bulked. The soil cores were 0–10 cm deep and 5 cm in diameter.

The samples were air-dried and then coarsely sieved to remove roots, litter and stones. The following chemical analyses were completed:

- available phosphorus using the fluoride extractable method (Jackson 1958);
- total phosphorus using the HClO_4 method (Jackson 1958);
- total nitrogen using Kjeldahl method (Jackson 1958);

- exchangeable ammonium (Rayment & Higginson 1992);
- soluble nitrate (Rayment & Higginson 1992);
- pH using the 1:5 soil/0.01M CaCl₂ extract method (Rayment & Higginson 1992);
- soil organic carbon using the Walkley and Black method (Rayment & Higginson 1992).

Differences between the forest, pasture and pasture edge were examined for each of the analyses using the Mann-Whitney *u* test (Statview 1988).

Seedling growth on different soil types—glasshouse trial

The seeds of the three species selected were sown in different soil types in order to measure the difference in growth. All the soils were collected from the Ridgeway site and the soils were all derived from dolerite rock.

The soil samples were collected from different areas; the pasture, forest, the edge of the forest and the edge of the pasture and from beneath isolated *Eucalyptus pulchella* trees in the pasture. Soil cores (8 cm diameter by 15 cm deep) were used to collect the soil. Around 40 cores were used to sample the edge of the pasture, the edge of the forest and beneath isolated trees. Around 140 cores were collected from the forest and pasture. Samples from each soil type were bulked and then sorted to remove some of the litter and objects >2 cm in diameter.

Pots were filled with either a single soil type (forest, pasture, pasture edge, forest edge, isolated tree) or a mixture of the forest and pasture

soils (see table 6.1 for the full list of soil treatments). Mixtures of forest and pasture soils were tested in different proportions varying from 75% forest / 25% pasture soil, to 10% forest / 90% pasture soil. Each species was sown (tested) in at least nine different soil types or mixtures. The pots were washed thoroughly and then sterilized before the soils were added.

Eucalyptus and *Leptospermum* seeds were also sown into pasture and forest soils which had been steam-sterilised. *Leptospermum* seeds were also sown in soils containing a mixture of sterilized and unsterilized pasture or forest soil (50% mixture) (table 6.1).

Table 6.1 The types of soil treatments and the number of pots used to test the growth of three native species.

Soil type	Species	<i>Bedfordia salicina</i>	<i>Eucalyptus pulchella</i>	<i>Leptospermum scoparium</i>
1) 100% forest soil		10	10	10
2) 75% forest/25% pasture		10	10	10
3) 50% forest/50% pasture		10	10	10
4) 25% forest/75 % pasture		10	10	10
5) 10% forest/90% pasture		10	10	10
6) 100% pasture		10	10	10
7) Pasture edge		10	10	10
8) Forest edge		10	10	10
9) Soil from beneath isolated trees in the pasture		10	10	10
10) Sterilized pasture soil (SPS)			10	10
11) Sterilized forest soil (SFS)			10	10
12) 50% SPS/50% forest soil				10
13) 50% SPS/50% pasture soil				10
14) 50% SFS/50% forest soil				10
15) 50% SFS/50% pasture soil				10

The treatments were set out in a glasshouse using a randomised block design (Neter *et al.* 1985) so that any differences in the growing conditions within the glasshouse could be detected.

The seeds were sown directly into the pots in December 1994. The pots were placed in a glasshouse for a period of 12 months. Heating was used during the winter months to maintain an overnight temperature of 10° C and a maximum of around 20° C. During summer, shade-cloth was used to keep the maximum temperature below 35° C, with a minimum of around 14° C. The temperature in the glasshouse occasionally exceeded 40° C even with the shade cloth in place. Lights were used from late autumn to early spring in order to maintain a day-length of 13.5 hours.

An excess of seed was sown in each pot. The number of seedlings was progressively reduced so that there were five evenly spaced seedlings left in each pot. The heights and dry weights of the shoot were measured at the conclusion of the experiment. The root dry weights were not measured because it was extremely difficult to separate all the roots from the soil.

The data were examined to determine whether they were normally distributed. General Linear Models were used to examine the height and dry weight data between the treatments and blocks, using the program SYSTAT (Wilkinson 1989). The GLM procedure was used to determine whether there was a significant effect due to the treatments or due to the position in the glasshouse (block). Comparisons were made between pairs of treatments by analysis of variance, using the program SYSTAT (Wilkinson 1989).

Mycorrhizal associations on seedlings grown in different soil types

The roots of seedlings grown in the different soil types (described in the previous section) were examined for the presence of mycorrhizal associations. The roots of the three species were inspected for signs of ectomycorrhizae. Histological and microscopic techniques were used to help confirm or identify fungal structures associated with mycorrhizae in the root system (for example, endomycorrhizal structures such as vesicles and arbuscules within the root).

Microscopic and histological techniques

After the seedlings were harvested, the roots were washed to remove most of the soil. A sieve with a 0.5 mm mesh screen was used to collect the fine roots. Small sections (approximately 2 cm long) of fine, young roots were picked out of the sieve and washed more thoroughly, then stored in 50% ethanol / water. Samples were collected from each of the pots.

Mycorrhizal structures can be highlighted using stains that selectively bind to the fungal tissues. The roots were prepared for staining using a technique similar to that described by Phillips & Hayman (1970). Before the roots can be stained, the cellular contents must be cleared using 10% KOH. The roots were placed in the solution of KOH and heated in a water bath at 70°C for a period of five hours. The solution of KOH was replaced after 2 hours, by which stage the solution was typically heavily pigmented. After clearing, the roots were rinsed with water and transferred to the staining solution.

The stain used was 0.05% w/v Trypan blue in lactoglycerol. The roots were placed in the stain for two days at room temperature. Following the staining, the roots were stored for a minimum of five days in jars containing 50% glycerol to allow excess stain to diffuse from the roots. The roots were examined using a compound microscope. At least ten root samples from each pot were examined under low magnification (100x) and stained structures were examined at high magnification (400x). Nomenclature of the mycorrhizal associations follows McGee (1986). The absence or presence and type of mycorrhiza(e) were noted for each pot. The incidence of mycorrhizal infection was determined by the number of pots with mycorrhizae present for each treatment and species. The difference in the incidence of mycorrhizae between the different treatments was analysed using Fisher's exact probability test (Sokal & Rohlf 1995).

Preliminary trial—factors affecting the mortality of transplanted seedlings

Before the field experiment based on the glasshouse experiment (described above) was implemented, a preliminary trial was established to examine the mortality rate of seedlings due to transplanting and other factors such as frost, pathogens and invertebrate predation. If seedling survival was adversely affected by any of these factors, then actions would be implemented in the above experiment to reduce their impact. Such action would allow better investigation of the effects of competition and soil type on seedling survival. In addition, this preliminary experiment could have indicated factors that affect the re-establishment of native species that are not being directly investigated.

Seedlings of *Bedfordia salicina* and *Leptospermum scoparium* were planted in five blocks in the paddocks at Ridgeway. The seedlings were

either planted in the grass sward with no gap (treatment 1) or a 10-cm gap in the sward (treatment 2). Within a block there were three plants of each species for each treatment (*i.e.* 12 plants per block). The seedlings were planted in a grid approximately 50 cm apart. The species and treatments were randomly allocated within the grid. Each block was fenced with chicken wire to exclude vertebrate herbivores, mainly rabbits and possums.

Prior to being planted, the seedlings were placed outside the shadehouse for four weeks in an attempt to harden them against frost. These seedlings were planted in the paddocks in August (winter).

After planting, the progress of the seedlings was checked twice a week over four weeks. The plants were checked for signs of damage by frost a day or two after each frost (the foliage of these species would blacken if killed by frost). Seedlings eaten (partially or fully) by snails or slugs were usually identified by a trail of mucilaginous material on the remains of the plant. None of the surviving seedlings were used in the experiment examining the effects of competition on seedling survival and growth (described below).

The differences in the mortality of seedlings between treatments, species and aspects were analysed by using Fisher's exact probability test (Sokal & Rohlf 1995).

Seedling survival and growth under different levels of competition and in different soil types—field trial

The growth of three species was compared in field conditions under different levels of competition from the surrounding grasses and in different soil types (pasture versus forest).

Seeds of *Bedfordia salicina*, *Eucalyptus pulchella* and *Leptospermum scoparium* were germinated in seed trays containing sterilized potting mix. Individual seedlings were transferred to tube pots (containing sterilized potting mix) soon after germination and then placed in a shadehouse (50% shade cloth). When the seedlings were well established (approximately 15 cm tall), they were planted out in paddocks at the Ridgeway site. An excess of plants was grown to ensure that plants of a comparable size could be selected.

The competition treatments were designed to test the relative importance of competition from the roots and/or shoots of the grasses on the establishment of tree and shrub seedlings. In addition, seedling growth on pasture and forest soils was compared to see whether the results of the glasshouse experiment could be replicated in the field. The treatments are listed below:

Treatment 1. Seedlings were planted into the grassy sward with a minimum of disturbance to the grasses. Only a narrow section of soil was removed, the same size as the tube pot—5 cm square by 12 cm deep. The grass shoots around the seedling were disturbed as little as possible during the planting.

Treatment 2. This treatment was exactly the same as treatment 1, except that the grass shoots were removed from around the seedling. The gap created in the sward was 10 cm in diameter.

Treatment 3. The shoots were removed as in treatment 2 and a soil core 10 cm in diameter and approximately 20 cm deep was removed and coarsely sieved to remove large roots. A seedling was then planted in the hole with the sieved pasture soil.

Treatment 4. This treatment was the same as treatment 3, except a section of plastic pipe (10 cm diameter by 20 cm long) was placed in the hole after the soil core was removed. This sleeve prevented the roots of the surrounding grasses from interacting with the roots of the seedling, but allowed water to drain through freely.

Treatment 5. The same as treatment 3, except coarsely sieved soil from the forest was used to fill the hole.

Treatment 6. The same as treatment 4, except coarsely sieved soil from the forest was used to fill the plastic pipe.

Once the experimental conditions were established, the gaps created around the seedlings were not maintained. The grasses were allowed to recolonise the soil and above-ground space, but seedlings of pasture species were removed from the soil around seedlings protected from root competition (treatments 4 and 6).

In the field, all the seedlings were protected from frost by a small piece of 50% shade cloth. Each shade cloth was approximately 10 cm x 10 cm square and held in place by a piece of wire. At the end of October 1995, the shade cloth was removed since the risk of further frost was minimal. Snail bait (a molluscicide containing Metaldehyde) was placed around the seedlings to prevent damage caused by slugs and snails. The snail bait was applied weekly.

The seedlings were planted in five blocks in three different paddocks (the same blocks used in the preliminary experiment). Within a block there were three plants of each species for each treatment (*i.e.* 54 plants per block). The seedlings were planted in a grid approximately 50 cm apart. The species and treatments were randomly allocated within the grid. Each block was fenced with chicken wire to exclude vertebrate herbivores, mainly rabbits and possums.

The height of each plant was recorded soon after the seedlings were planted in September (spring) 1995 and after three months in December 1995. The samples were uneven due to a number of seedlings dying in treatments 1 and 2. Thus differences between the blocks were tested using the Kruskal-Wallis H test for each treatment. The differences between pairs of treatments were tested using the Mann-Whitney u test. The seedling heights were measured again in January 1998, however no statistical test was applied to these data due to the lack of seedlings in most treatments.

The effects of treatment type on the survival of each species was analysed based on the number of seedlings which survived to December 1995 and January 1998. Differences between the blocks due to aspect were tested for each treatment and species using Fisher's exact probability test (Sokal & Rohlf 1995). If aspect was found to have a significant effect on seedling survival, the data were divided and then the treatments were compared. Fisher's test was also used to analyse the difference between pairs of treatments.

Results

Soil Nutrient Status

Most of the nutrients examined did not vary significantly from the forest out into the pasture (figure 6.1). The main exceptions were total and available phosphorus. Total P rose significantly from around 100 ppm in the forest to approximately 250 ppm at the edge and towards the centre of the pasture. Available P increased sharply from the edge of the pasture and the forest (4 ppm) out into the pasture (8 ppm).

Total nitrogen, soil organic carbon, exchangeable ammonium and soluble nitrate did not vary significantly from the forest to the pasture.

Glasshouse trial—Seedling growth on different soil types

The position of seedlings in the glasshouse did not have a significant effect on the results of this experiment ($p = 0.08$). None of the seedlings in the pots died in the first two months after germination as a result of damping-off caused by pathogenic fungi. However, after several months in the glasshouse, some of the seedlings were killed by damping-off when conditions in the glasshouse were very humid and warm.

Seedlings growing in the 100% forest soil treatment were usually the smallest plants. Increasing the proportion of pasture soil to the forest soil typically increased the height and dry weight of all three species tested (figure 6.2; 6.3). However, in most cases, it was only the 10% forest/90% pasture mixture that produced a significant improvement in growth (height and dry weight) over the 100% forest soil treatment. The only exception was *Eucalyptus* seedlings (dry weight only) where there was little pattern, except that seedling growth was significantly

Figure 6.1 Mean nutrient levels in the forest, pasture, and pasture edge at Ridgeway (Error bars = standard deviation. Means with no letters in common are significantly different: $p > 0.05$. Mann-Whitney u test) Note: log scale used on the Y-axes.

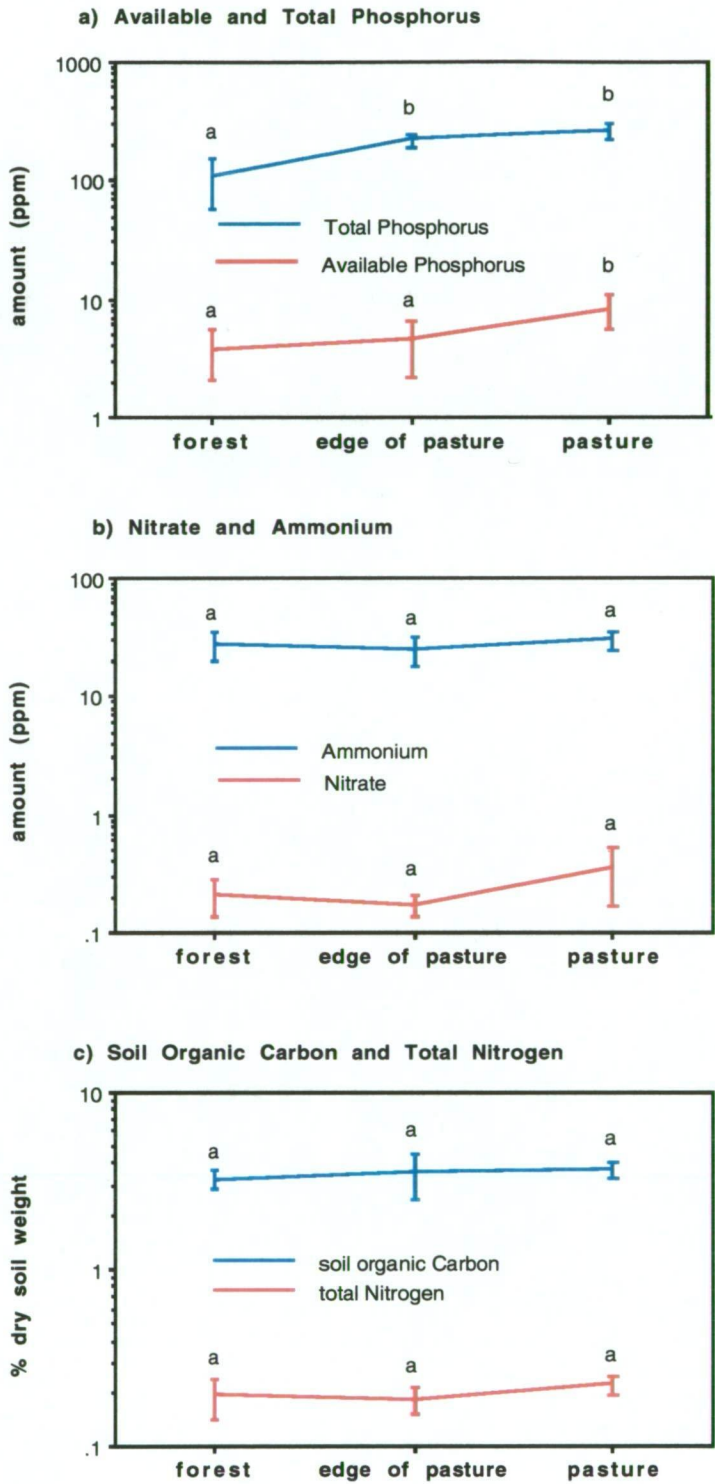


Figure 6.2 The mean heights of three species grown in the glasshouse in different soil types / treatments. (Means with no letters in common are significantly different: $p < 0.05$. ANOVA).

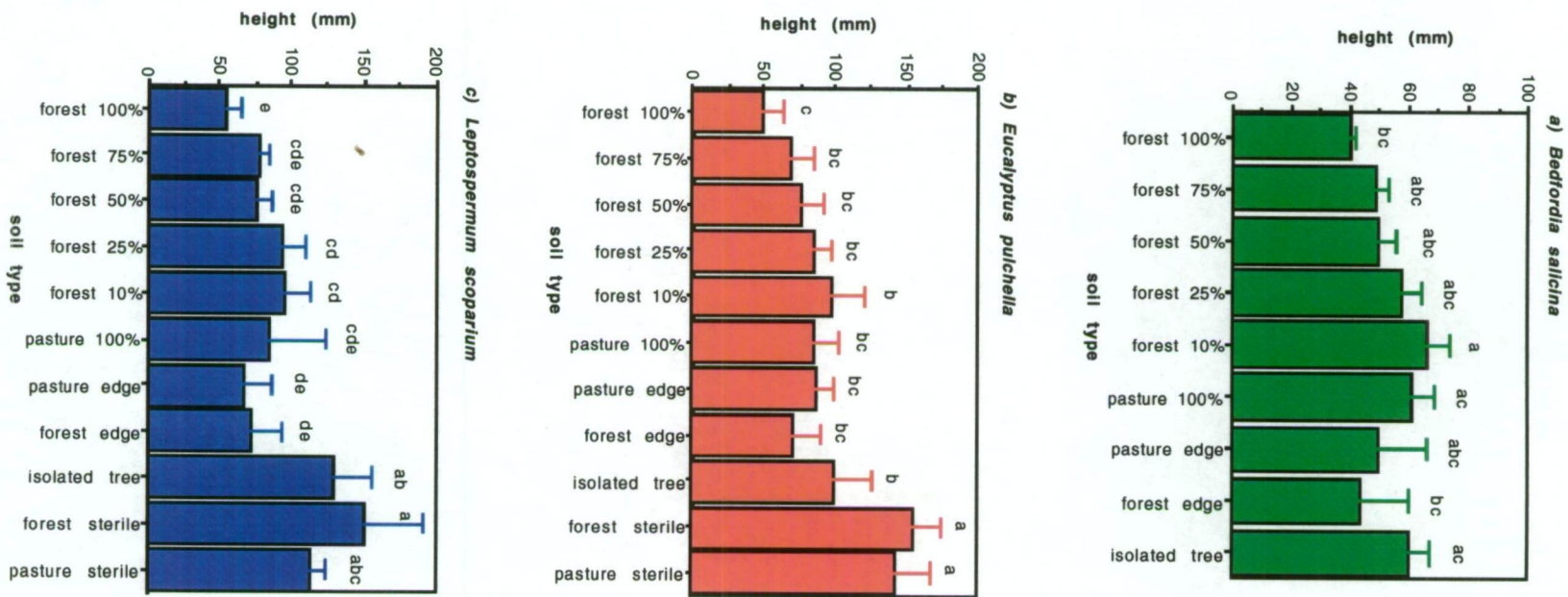
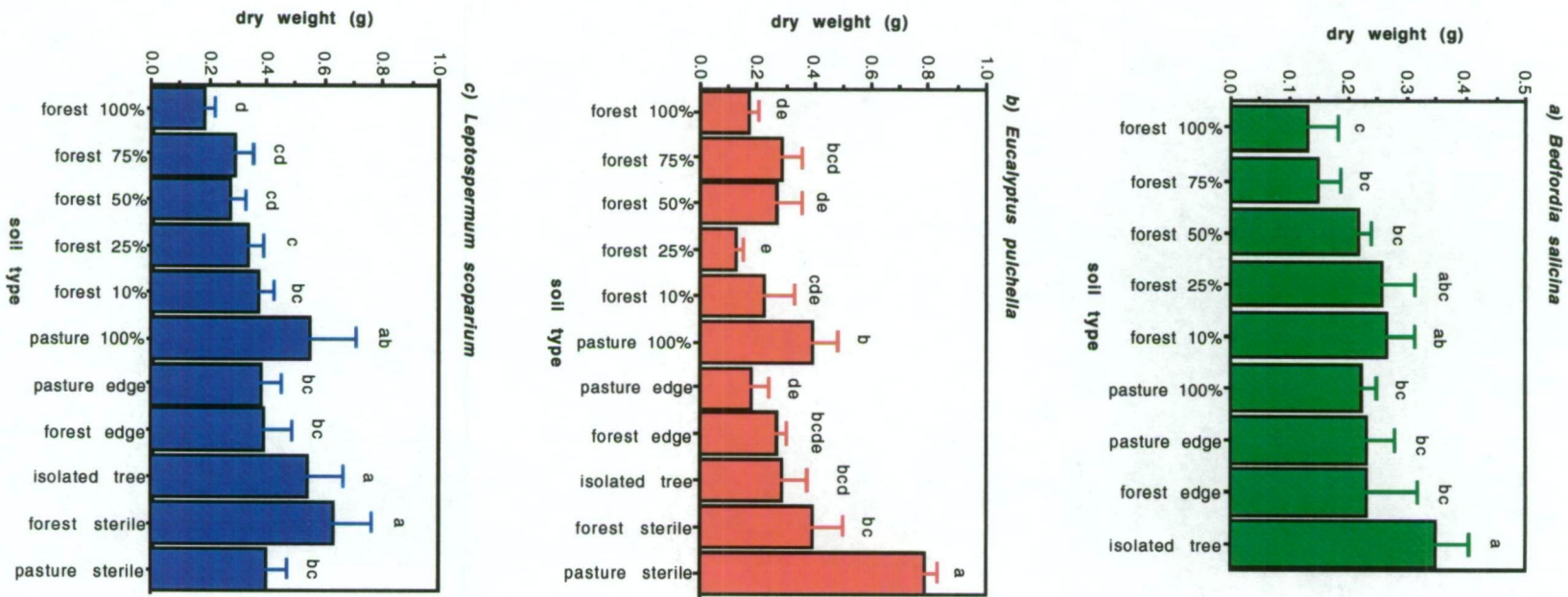


Figure 6.3 The mean dry weights of three species grown in the glasshouse in different soil types / treatments. (Means with no letters in common are significantly different: $p < 0.05$. ANOVA).



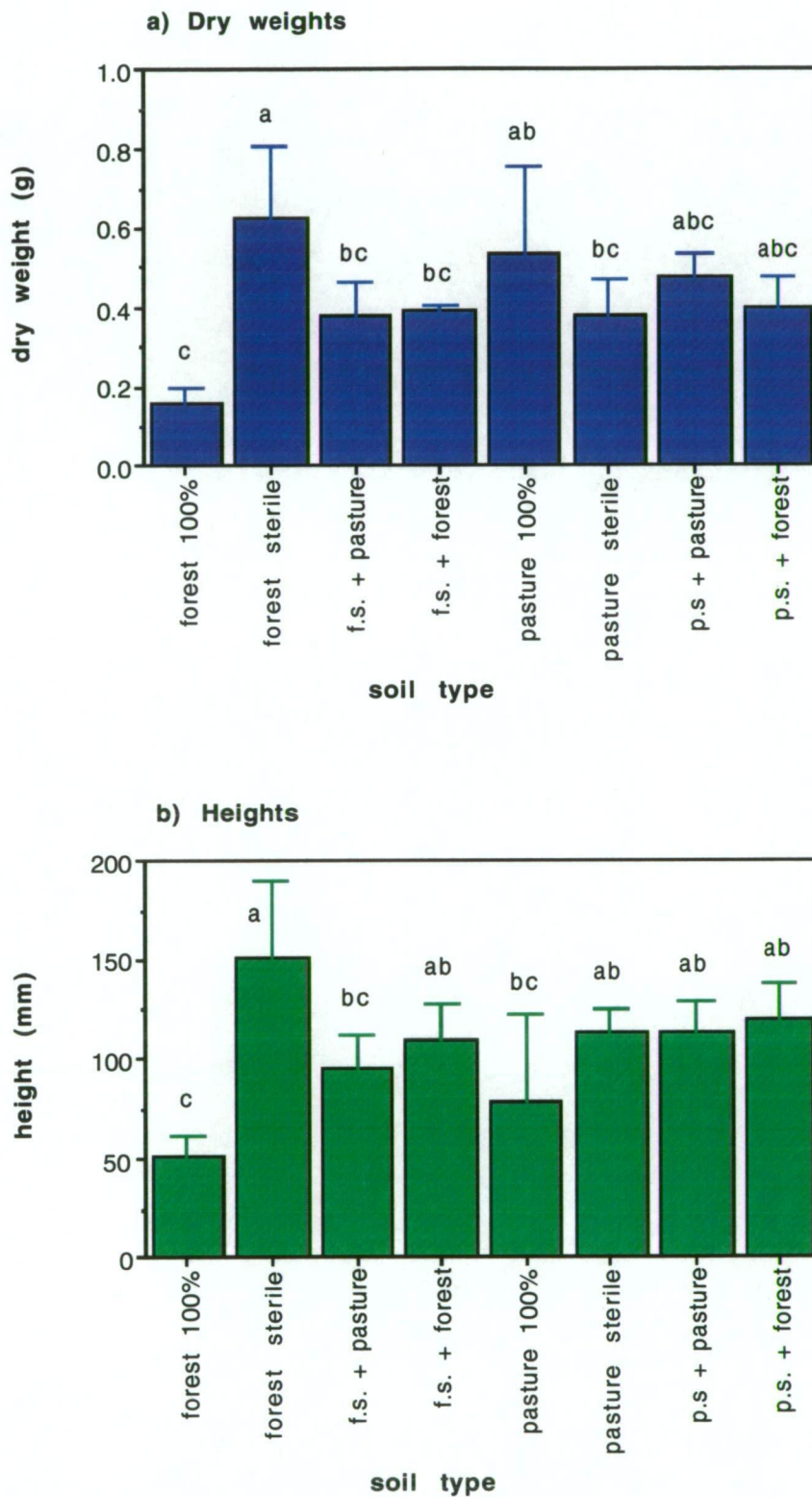
better on 100% pasture than 100% forest soils (figure 6.3). The 25% forest soil treatment also significantly improved seedling growth for *Leptospermum* compared with the 100% forest soil treatment. The 100% pasture soil treatment was frequently not significantly different to the 100% forest soil treatment. The exceptions were *Eucalyptus* and *Leptospermum* seedlings (dry weights only) (figure 6.3).

Seedlings grown in soils collected from the edge of the forest and the pasture were usually not significantly different from those grown in the 100% forest or the 10% forest soil (figure 6.2; 6.3). However, the seedlings grown on soil collected from beneath isolated trees in the pasture tended to grow significantly better than seedlings in the 100% forest soil type. With the exception of *Leptospermum* (height only), the isolated tree soils and 10% forest soil treatments were not significantly different.

The sterilized forest or sterilized pasture soil treatments generally produced the highest growth (figure 6.2b, c; 6.3b, c). These results were not always better than the 100% pasture soil treatment but were always significantly better than the 100% forest soil treatment. The sterilized forest soil treatment was usually slightly better than the sterilized pasture soil treatment, except for *Eucalyptus* dry weight.

Leptospermum seedling growth was substantially higher on the sterilized forest soil compared with the unsterilized forest soil. The addition of unsterilized soil (pasture or forest) to the sterilized forest soil produced a decrease in *Leptospermum* seedling growth which was usually significant (figure 6.4). The addition of unsterilized soils to the sterilized pasture soil did not affect seedling growth. However, there was no significant difference in seedling growth between the 100% pasture and sterilized pasture soil treatments.

Figure 6.4 The dry weights and heights of *Leptospermum scoparium* grown in different soil types / treatments. (Means with no letters in common are significantly different: $p < 0.05$. ANOVA). f.s. = sterile forest soil, p.s. = sterile pasture soil



In general, seedlings growing in forest soil were slower growing than those grown in pasture soil. In addition, the slower growth rates in forest soil could be overcome by the addition of pasture soil or by the sterilization of the forest soil.

Mycorrhizal associations on seedlings grown in different soil types

The type of mycorrhizae formed on *Eucalyptus* and *Leptospermum* seedlings were always ectomycorrhizal, whereas *Bedfordia* seedlings formed vesicular-arbuscular mycorrhizae (table 6.2). The seedlings grown in soil containing a high percentage of forest soil always produced mycorrhizae. Even the 10% and 25% forest soil treatments usually produced mycorrhizae but there were significantly less mycorrhizae on the seedlings grown in the 100% pasture soil. Similarly, the seedlings of the three species grown in soils from the pasture edge had a significantly lower incidence of mycorrhizae than the seedlings grown in the soil from the forest edge.

Of the three pasture soil treatments (isolated tree, 100% pasture and pasture edge), only the isolated tree soil significantly increased the incidence of mycorrhizae, but not for *Bedfordia*. For *Leptospermum* and *Eucalyptus* seedlings growing on soil from beneath isolated trees, the occurrence of mycorrhizae was as high as those grown in 100% forest soil.

None of the seedlings grown in the sterilized soils produced mycorrhizae.

Table 6.2 The types of mycorrhiza* associated with three native species grown on different soil types. The number of replicates (pots) which exhibited that form of mycorrhiza are shown in parentheses. (Within each species, numbers with different letters are significantly different: $p < 0.05$.)

Soil type	Species	<i>Bedfordia salicina</i>	<i>Eucalyptus pulchella</i>	<i>Leptospermum scoparium</i>
1) 100% forest soil		VAM (10) ^A	ECM (10) ^A	ECM (10) ^A
2) 75% forest/25% pasture		VAM (10) ^A	ECM (10) ^A	ECM (10) ^A
3) 50% forest/50% pasture		VAM (10) ^A	ECM (10) ^A	ECM (10) ^A
4) 25% forest/75 % pasture		VAM (9) ^A	ECM (8) ^{AB}	ECM (9) ^A
5) 10% forest/90% pasture		VAM (9) ^A	ECM (8) ^{AB}	ECM (8) ^{AB}
6) 100% pasture		VAM (1) ^B	ECM (1) ^C	ECM (2) ^C
7) Pasture edge		VAM (3) ^B	ECM (4) ^{BC}	ECM (4) ^{BC}
8) Forest edge		VAM (10) ^A	ECM (10) ^A	ECM (10) ^A
9) Soil from beneath isolated trees in the pasture		VAM (2) ^B	ECM (10) ^A	ECM (10) ^A
10) Sterilized pasture soil (SPS)		- (0) ^B	- (0) ^C	- (0) ^C
11) Sterilized forest soil (SFS)		- (0) ^B	- (0) ^C	- (0) ^C

* Type of association:

ECM = ectomycorrhizal;

VAM = vesicular-arbuscular mycorrhizal; - = none

Preliminary trial—factors affecting the mortality of transplanted seedlings

There were no other apparent cause(s) of seedling mortality except for frost damage and browsing from molluscs during the four-week period of this experiment.

Combined effects

The size of the gap around the seedlings did not have a significant effect on seedling mortality ($p = 0.26$ *Leptospermum*; $p = 0.15$

Bedfordia). On southern aspects, the combined effects of frost and browsing damage were severe on both *Bedfordia* and *Leptospermum*—around 70% mortality. On northern aspects, *Leptospermum* seedlings

had a significantly better chance of survival ($p = 0.001$). The mortality of *Bedfordia* seedlings was high regardless of the aspect.

Frost damage

On southern aspects, *Bedfordia* and *Leptospermum* seedlings suffered equal losses due to frost, regardless of the planting technique (table 6.3). On northern aspects, seedlings of *Leptospermum* planted with no gap survived better than *Bedfordia* seedlings ($p = 0.04$). When planted in 10-cm gaps, there was no difference in seedling mortality between the species on northern aspects.

There were no significant differences in the numbers of *Bedfordia* killed on north versus south aspects or between the two gap sizes. Seedlings of *Leptospermum* planted with no gap survived frosts better on northern aspects ($p = 0.002$), whereas those planted with 10-cm gaps showed no difference. These species showed no significant differences in mortality between the two gap sizes on either southern or northern aspects.

Browsing damage

Leptospermum seedlings were not browsed by snails or slugs (table 6.3). The size of the gap around the *Bedfordia* seedlings did not influence the number killed by browsing. Browsing of *Bedfordia* seedlings was greater in the blocks on northern slopes, although this result may have been affected by the smaller number of seedlings affected by frost on northern aspects. Not all of the browsed *Bedfordia* seedlings died, some only lost one or two leaves.

Table 6.3 The number of seedlings of two shrub species killed by frost and browsing on pastures at Ridgeway with northern and southern aspects. Seedlings were planted into the grass sward with either minimal disturbance to the grasses (no gap) or the grass shoots cleared away from the seedling (gap 10 cm in diameter). (Within each section numbers with different letters are significantly different: $p < 0.05$. Fisher's exact probability test.).

Species	Northern Aspects	Southern Aspects
Total (frost + browsed)		
<i>Bedfordia salicina</i>	13 ^A (n=18)	10 ^A (n=12)
<i>Leptospermum scoparium</i>	1 ^B	8 ^A
Frost-killed		
No gap		
<i>Bedfordia salicina</i>	4 ^A (n=9)	5 ^A (n=6)
<i>Leptospermum scoparium</i>	0 ^B	5 ^A
10-cm gap		
<i>Bedfordia salicina</i>	3 ^A (n=9)	3 ^A (n=6)
<i>Leptospermum scoparium</i>	1 ^A	3 ^A
Browsed		
No gap		
<i>Bedfordia salicina</i>	3 ^A (n=9)	1 ^A (n=6)
<i>Leptospermum scoparium</i>	0 ^A	0 ^A
10-cm gap		
<i>Bedfordia salicina</i>	3 ^A (n=9)	1 ^A (n=6)
<i>Leptospermum scoparium</i>	0 ^A	0 ^A

Field trial—Seedling growth on different soil types

Survival rate

After the first three months of this trial, there were no significant differences in seedling survival between the treatments where grass roots were removed from the soil around the seedling (treatments 3 to

6) (table 6.4). These results were irrespective of whether it was forest or pasture soil, or whether grass roots were able to grow back into the soil. After two years, no seedlings survived if they were planted with a minimum of disturbance to the grass sward (treatments 1) and very few seedlings survived if only the grass shoots were removed (treatment 2) (table 6.4).

Differences in aspect rarely affected the survival of the three species tested. However, fewer *Leptospermum* seedlings survived the first three months on southern aspects in treatments 1 and 2. This was despite the seedlings being protected from frost (table 6.4). Over the same period, no *Leptospermum* seedlings died with treatments 1 and 2 on the northern aspects. After two years, only 14 of the original 90 *Leptospermum* seedlings survived. More seedlings survived in the treatments where grass roots were excluded (treatments 4 and 6).

After the first three months, the survival of *Eucalyptus* seedlings was not adversely affected by any treatment ($p > 0.05$). Over the two-year period of the experiment, no *Eucalyptus* seedlings emerged through the grass sward. By the end of the two-year period all but two seedlings were dead. Both were growing in forest soil with grass roots excluded.

Bedfordia seedlings that experienced the highest levels of competition (treatments 1 and 2) had a significantly lower chance of survival in the first three months ($p < 0.05$). Where the roots and shoots of the surrounding grasses had been removed (treatments 3 to 6), most seedlings survived. However, after two years, only treatments 3 and 5 were significantly better than treatments 1 and 2. In both treatments 3 and 5, the roots of the grasses were able to grow back into the soil around the *Bedfordia* roots. Only 24 of the original 90 seedlings survived over the two-year period.

Table 6.4 The survival of seedlings of three species planted in pasture at Ridgeway under different levels of competition and in different soils (with protection from vertebrate and mollusc herbivory, as well as frost). A census was taken three months and two years after planting. Fifteen individuals were planted per species per treatment. (Within each species, numbers with no letters in common are significantly different: $p < 0.05$. Fisher's exact probability test.)

Census date/ Treatment *	<i>Bedfordia salicina</i>	Number of survivors		
		<i>Eucalyptus pulchella</i>	<i>Leptospermum scoparium</i>	
			Aspect	
Dec 1995			North	South
1	2 ^A	13 ^A	9 ^A	3 ^A
2	7 ^B	15 ^A	9 ^A	1 ^A
3	14 ^C	15 ^A	9 ^A	6 ^B
4	14 ^C	15 ^A	9 ^A	6 ^B
5	15 ^C	15 ^A	9 ^A	6 ^B
6	15 ^C	15 ^A	9 ^A	6 ^B
Dec. 1997				
1	0 ^A	0 ^A	0 ^A	
2	2 ^{AB}	0 ^A	1 ^{AB}	
3	7 ^C	0 ^A	3 ^{AB}	
4	4 ^{BC}	0 ^A	4 ^{BC}	
5	8 ^C	0 ^A	0 ^A	
6	3 ^{ABC}	2 ^A	6 ^{BC}	

* Planting Treatment. Seedlings planted with:

- 1 minimal disturbance to surrounding grasses
- 2 grass shoots removed (10 cm diameter)
- 3 grass shoots removed and roots removed from soil core (10 cm diameter)
- 4 same as 3 + plastic sheath around soil core
- 5 grass shoots removed and forest soil used to fill core
- 6 same as 5 + plastic sheath around soil core

Growth after three months

After the first three months, no significant differences were found in seedling growth (increase in height) between the five blocks ($p > 0.05$).

The growth of the pasture grasses was vigorous, reaching heights of around 40 cm (excluding the heights of the flowering stems). Rainfall in the second half of 1995 was approximately 90 mm above the average for this period (appendix 6.1).

The growth of all three shrub and tree species were significantly lower where the roots of the surrounding grasses were not disturbed (treatments 1 and 2) (figure 6.5). The differences between treatments 1 and 2 were not significant, except for seedlings of *Eucalyptus pulchella*.

Preventing the regrowth of grass roots back into the soil core usually caused only a slight (not significant) increase in seedling growth (figure 6.5). The only exception was *Bedfordia* seedlings grown in forest soil (treatments 5 and 6), where the increase in seedling height was significantly greater without competition from grass roots.

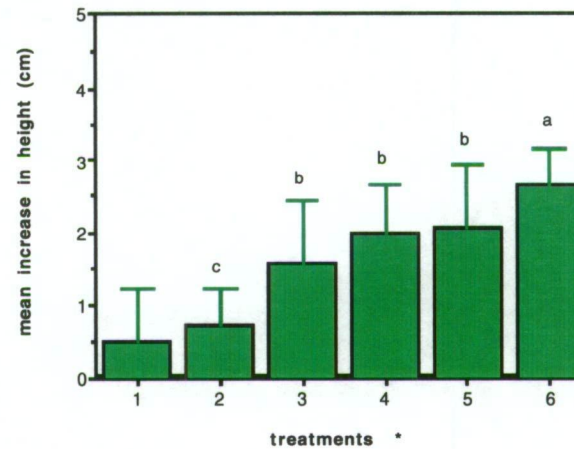
Replacing the soil around the seedlings with forest soil had no significant effect on the growth of *Leptospermum* seedlings. *Bedfordia* seedlings protected from competition with grass roots grew taller with forest soil rather than pasture soil. *Eucalyptus* seedlings not protected from root competition grew taller with forest soil.

Figure 6.5 The mean increase in the height of three species grown in the field, three months after planting. Seedlings planted under different levels of competition and in different soils. Means with no letters in common are significantly different: $p < 0.05$, Mann-Whitney u test.

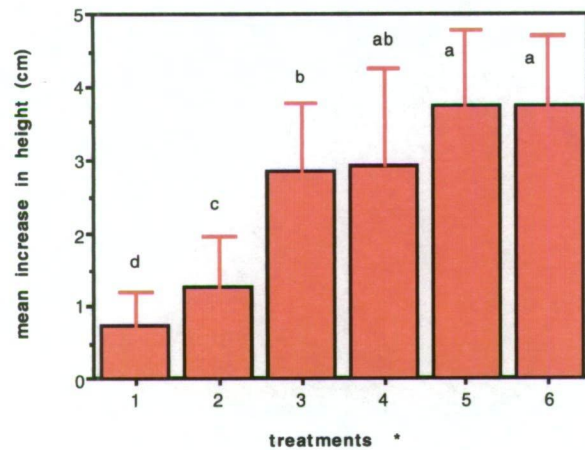
* Planting Treatment. Seedlings planted with:

- 1 minimal disturbance to surrounding grasses
- 2 grass shoots removed (10 cm diameter)
- 3 grass shoots removed and roots removed from soil core (10 cm diameter)
- 4 same as 3 + plastic sheath around soil core
- 5 grass shoots removed and forest soil used to fill core
- 6 same as 5 + plastic sheath around soil core

a) *Bedfordia salicina*



b) *Eucalyptus pulchella*



c) *Leptospermum scoparium*

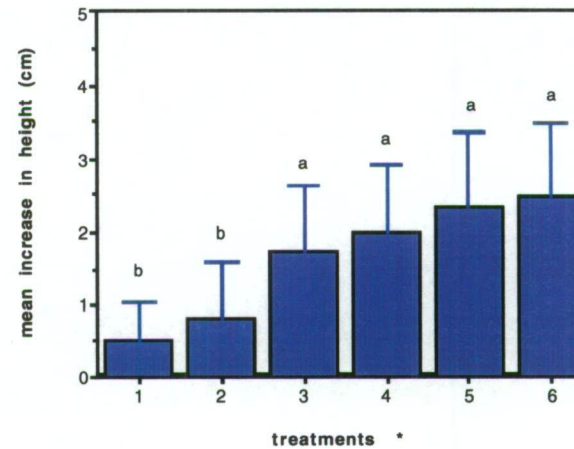
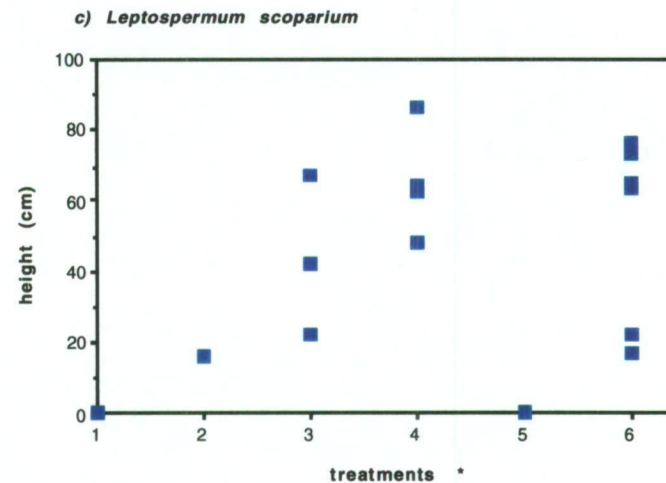
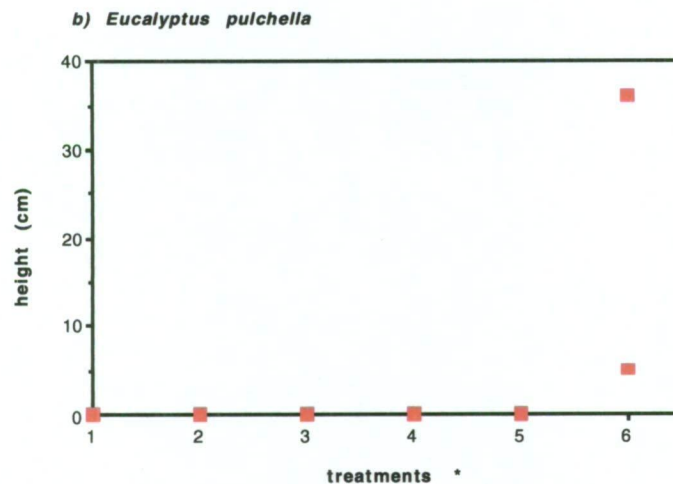
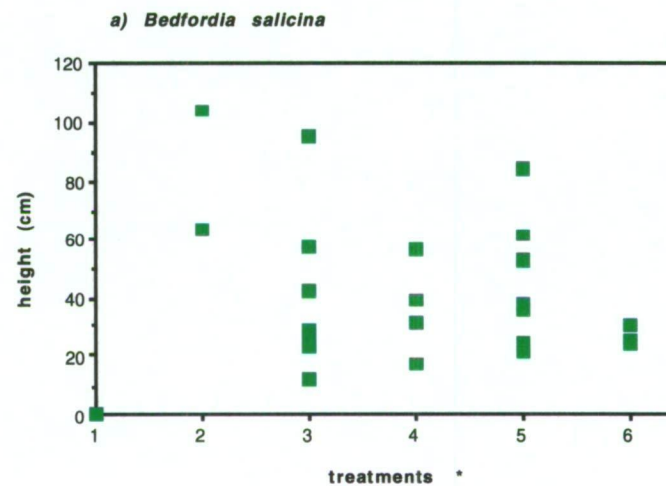


Figure 6.6 The heights of individual seedlings of three species grown in the field, two years after planting. Seedlings planted under different levels of competition and in different soils.

* Planting Treatments. Seedlings planted with:

- 1 minimal disturbance to surrounding grasses
- 2 grass shoots removed (10 cm diameter)
- 3 grass shoots removed and roots removed from soil core (10 cm diameter)
- 4 same as 3 + plastic sheath around soil core
- 5 grass shoots removed and forest soil used to fill core
- 6 same as 5 + plastic sheath around soil core



Growth after two years

Only one of the two remaining *Eucalyptus* seedlings appeared healthy and emerging through the grass sward (figure 6.6). Within each treatment (except treatment 1), the heights of *Bedfordia* and *Leptospermum* seedlings tended to vary greatly. In most treatments, the seedlings of both species were able to at least double in height (*i.e.* reach 30 cm) after two years. The heights of *Bedfordia* seedlings planted in treatment 2 were greater than those where grass roots were excluded (treatments 4 and 6), although there were very few seedlings left in treatments 2 and 6. *Leptospermum* seedlings tended to grow better in pasture soil protected from grass roots (treatment 4).

Discussion

The effects of soil nutrient status on the survival of seedlings

Both the field and glasshouse trials showed that the pasture soil does not adversely effect seedling growth or survival of the selected species. Seedling growth appeared to follow the trend in soil phosphorus. Seedlings grown in soil from the forest had the lowest growth, those from the forest edge and pasture edge were intermediate, while those on the pasture soil were the highest (figure 6.2; 6.3). However, seedling growth on pasture soils was not usually significantly greater than the growth on forest soil.

The restoration of native vegetation can be impeded if the soil nutrient status has been raised, such as through the application of superphosphate (Hedde & Specht 1975; Specht *et al.* 1977; Clements 1983; Marrs 1985; Pywell *et al.* 1994). In the present study, thirty years after the pasture was abandoned, the soil nutrient status of the pasture and forest soils were generally very similar, except for phosphorus (P)

(figure 6.1). While nitrogen (N) and P were applied to the soil of the pasture when the area was farmed, phosphorus would not be leached from the soil because it is bound strongly to soil particles (Attiwill & Leeper 1987). Following the cessation of farming (and, therefore, further fertilizer applications) the concentration of N generally decreases while available P may remain high (Gough & Marrs 1990).

It may be significant that natural re-establishment of most native species was best in the areas where the level of available P was significantly lower than the pasture (*i.e.* the pasture edge). Other studies have shown that high soil P (usually in combination with disturbance) tends to favour establishment of exotic species (Clements 1983; Hobbs & Atkins 1988).

In this study, the growth of *Eucalyptus*, *Leptospermum* and *Bedfordia* seedlings did not (usually) vary significantly between the soil collected from the forest, the forest edge, the pasture edge and the pasture. This suggests that the difference in P availability does not affect seedling growth. However, these results are probably confounded by the higher incidence of mycorrhizal infections on the roots of seedlings growing in the forest soil (table 6.2).

There is evidence to suggest that some *Eucalyptus* species may not form mycorrhizae where available P exceeds 5 ppm (Mullette 1976). Similarly, the seedlings in the pasture at Ridgeway formed very few mycorrhizae on soils where available P was 8 ppm. However, the degree of mycorrhizal infection is not always correlated with the availability of P (Abbott & Robson, 1991; Allsopp & Stock 1994).

The effect of soil type on mycorrhizal infection of seedlings

Alternatively, the lower rate of mycorrhizal infections on pasture soils could be related to the availability of spores and other infective material in the pasture. If the grasses form mycorrhizae they are of the VAM type (Allen & Allen 1990), whereas *Leptospermum* and *Eucalyptus* typically form ectomycorrhizae—although there is some evidence that young seedlings may briefly form VAM (Lapeyrie & Chilvers 1985). There is no overlap in the fungal species that form VAM (phycomycetes, of the family Endogonaceae) and those which form ECM (basidiomycetes, ascomycetes and zygomycetes) (Rovira *et al.* 1983). The mycorrhizal fungal population of a particular vegetation type tends to reflect the mycorrhizae associated with the species present (Hamel *et al.* 1994).

Therefore, the lack of host material in the pasture would mean there is little inoculum of ectomycorrhizal fungi. In addition, soil disturbance (ploughing) during the establishment of the improved pasture would drastically reduce the amount of inoculum (Reeves *et al.* 1979; Allen & Allen 1980; Jasper *et al.* 1989). The presence of ectomycorrhizal fungi in the pasture would depend on dispersal from the forest. Therefore, the probability of *Leptospermum* and *Eucalyptus* seedlings being infected with a suitable mycorrhizal fungus could be low. However, the presence of inoculum of ectomycorrhizal fungi in the soil beneath isolated trees suggests that some degree of infection is possible.

Even though *Bedfordia* seedlings form VAM, the amount of infection was also low for this species (table 6.2). The mycorrhizal fungi present in the pasture may not necessarily be species that would typically infect *Bedfordia*. The high rate of infection of *Bedfordia* seedlings grown in 90% pasture/10% forest soil compared with 100% pasture soil shows

that this species would tend to produce mycorrhizae if a source of inoculum was available.

A high correlation between spore numbers in the soil and infection of plant hosts does not always occur (Hayman 1970; Daft & Nicolson 1972; Read *et al.* 1976; Furlan & Fortin 1977). It has been suggested that the principal source of inoculum is not necessarily spores but rather infected roots of the host plant or mycelium in the soil (Read *et al.* 1976). The seedlings of *Leptospermum* and *Eucalyptus* tested on pasture-soil (not including the pasture edge) were only lightly infected by ectomycorrhizal fungi. However, these species were able to form ectomycorrhizae from soils beneath isolated trees in the pasture (table 6.2). This demonstrates that infection of ectomycorrhizal plants can occur in pastures away from the edge of the forest. However, the probability that seedlings will be infected is much higher in soils from in or close to the forest or from beneath the few trees that have managed to establish in the pasture.

Mycorrhizae and Competition with Grasses

The species composition and abundance of soil microbes can play an important role in controlling the vegetation at a particular site. For example, the establishment of *Eucalyptus delegatensis* on *Poa* grasslands in north-eastern Tasmania was inhibited by the lack of suitable mycorrhizal fungi in the soils of the grassland (Ellis & Pennington 1992). Inoculation of the grassland soil with only a small quantity of soil from the *E. delegatensis* forest overcame this inhibitory effect. Similarly, the addition of a small quantity of forest soil from Ridgeway marginally increased the growth of native shrub and tree species in the pasture soil. In the present study, the inhibitory soil was the forest soil, rather than the grassland (pasture) soil.

Even though the incidence of mycorrhizae was greater when seedlings were grown in some forest soil ($\geq 10\%$), this did not result in greater seedling growth compared with seedlings grown in the 100% pasture soil. The higher levels of available and total phosphorus in the pasture soil may explain this difference. There appeared to be some additive effect of mycorrhizal infection and higher soil nutrient status on seedling growth, which resulted in a significant increase in seedling growth on the 10% forest soil mix compared with growth on 100% forest soil.

There was some evidence that mycorrhizae were more beneficial when the shrub and tree seedlings were grown in competition with the pasture species. In the field, seedling growth after three months was typically greater (sometimes significantly) with forest soil (containing mycorrhizal inoculum), whereas under glasshouse conditions (with ample moisture and light) the seedlings grew better in pasture soil (containing little or no mycorrhizal inoculum) (figure 6.2; 6.3; 6.5). Mycorrhizae may only be beneficial when competition applies sufficient stress on the plants such that the advantages of the mutualistic association outweigh the costs to the plant (Allen & Allen 1984, 1990; Grime *et al.* 1987). In highly competitive environments such as these pastures, the inability of shrub and tree seedlings to form mycorrhizae may be critical (see Miller 1979). Similarly, in the establishment of plantations of eucalypt (and other ectomycorrhizal species), seedlings are being inoculated with suitable mycorrhizal fungi to maximise growth and survival (Castellano 1993).

This difference in the results from the glasshouse and field experiment was unexpected. The lack of sufficient data after two years also makes interpretation of these results difficult. Further testing under controlled

(glasshouse) conditions is required to determine whether competition from grasses can affect the results of these experiments.

The Effects of Soil Sterilisation

Following sterilization of the forest soil, no mycorrhizal infection of the seedling roots occurred (table 6.2), although seedling growth was substantially higher than for seedlings grown on unsterilized forest soil (figure 6.4). This suggests that seedling growth was restricted by some factor present in the soil. It is unlikely to be mycorrhizal fungi since mycorrhizae increase the supply of soil nutrients to the plant, and are particularly important in soils where nutrients (especially phosphorus) are deficient (Bowen 1973; Sanders *et al.* 1975 Abbott & Robson 1977). The exact cost/benefit to the plant in terms of growth as a result of mycorrhizal associations varies but it would at least balance if the plants were to survive in competition with non-mycorrhizal species.

The steam-sterilisation process may have increased the availability of some soil nutrients. The heating process could increase the decomposition rate of organic matter within the soil which releases more nutrients. However, there was no similar increase in seedling growth on pasture soils that were sterilised, even though the percentage of soil organic carbon was very similar in the forest and pasture.

There was no evidence of invertebrates attacking the roots when the roots were examined during the harvesting of the seedlings.

It would appear that there was some inhibitory factor(s) present in the forest soil that was responsible for the slower seedling growth. This

inhibitory factor(s) was not present or as abundant in the pasture soil since seedling growth was better on pasture soil and there was no difference in growth between the sterilized and unsterilized pasture soil for *Leptospermum* (figure 6.4). The inhibitory factor(s) may be a plant pathogen present in the soil and, therefore, seedling growth would be faster if the sterilization process killed these pathogens. Allelopathic substances produced by plants in the forest can also have a detrimental effect on seedling growth (del Moral *et al.* 1978; May & Ash 1980). The heat produced by a ground-fire or, in this case, steam sterilization, may breakdown allelopathic substances in the soil and remove the inhibitory effect on seedlings.

Inhibition of Seedlings in Forest Soil

The inhibition of seedlings growing in the soil from the forest was not unexpected. It could result from a variety of factors, including the presence of pathogens or allelopathic substances as discussed above. Seedling establishment in this situation is often more successful following disturbance where there is partial sterilisation of the soil, such as fire (Ashton & Willis 1982).

In the present study, the mixing of a small proportion (10%) of inhibitory forest soil with less inhibitory pasture soil, tended to improve seedling growth (figure 6.2; 6.3). The small proportion of forest soil provided native seedlings with a source of inoculum of mycorrhizal fungi that was absent from the pasture soil (table 6.2). The addition of a greater proportion of forest soil probably introduces too much of the inhibitory factor(s) for the benefit of the mycorrhizae to show in the results.

In this way, altering the balance and/or composition of soil microbes can result in improved seedling growth (see Ellis & Pennington 1993). Similarly, Ashton & Willis (1982) found that the proportion of healthy *Eucalyptus regnans* seedlings increased as the ratio of the number of *Penicillium janthinellum* + *P. simplicissimum* colonies to *Cylindrocarpon destructans* + bacteria colonies in the mature forest soil exceeded 1:1.

Therefore, there is an element of risk in restoration techniques that utilise soils collected from undisturbed sites to inoculate degraded sites with desirable soil microbes. Inoculating sites or native plants with particular species of microbes (whether they be mycorrhizal fungi or bacteria) that are known to be of benefit are far more likely to be successful (see Castellano 1993).

The effects of invertebrate browsing on seedling establishment

The effects of vertebrate browsing on seedling establishment have been well documented for many plant communities. In Australia, most studies have focused on the effects of sheep, rabbits and cattle as well as native vertebrate browsers (e.g. Winbush & Costin 1979; Gibson & Kirkpatrick 1989; Leigh *et al.* 1989; Tremont 1994). Seedling recruitment, as well as the survival and fecundity of adult plants, can be adversely affected by invertebrate browsing (Brown & Grange 1989; Kelly 1989; Rees & Brown 1992; Hanley *et al.* 1995).

The study by Hanley *et al.* (1995) demonstrated that the impact of mollusc browsing on seedling emergence was sufficient to influence the composition and abundance of species in the grasslands. In the present study, the *Leptospermum* seedlings were not browsed, whereas the *Bedfordia* seedlings were severely browsed by slugs and snails soon

after they were planted (table 6.3). The browsing pressure on non-grass species in the pasture is likely to be high, since trials have indicated that grasses are unpalatable to molluscs (Grime *et al.* 1968), may be as a result of the high levels of silica in their leaves (Cottam 1985).

Bedfordia seedlings were never observed in the pasture. This is despite *Bedfordia* seeds being collected in the seed traps in the pasture (Chapter 5). The selection of *Bedfordia* seedlings by molluscs may, in part, explain the lack of *Bedfordia* re-establishment in the pastures at Ridgeway.

The preference for *Bedfordia* seedlings could be related to the palatability or structure of the seedlings. The leaves of *Bedfordia* seedlings were wider and longer (around 5 x 1.5 cm) than *Leptospermum* which tended to be small (1 x 0.3 cm) and attached to a much thinner and weaker stem. Like *Eucalyptus* species, *Leptospermum* tend to have high levels of oils and phenolic compounds in the leaves, however, whether these compounds are toxic to molluscs is not known. Not all the *Bedfordia* were completely eaten, and given the short length of this experiment it is possible that the losses due to browsing by molluscs could be even higher (see Kelly, 1989).

The Effects of Aspect and Frost on Seedling Survival

Seedlings of *Leptospermum* and *Bedfordia* appeared to survive frost better when planted within a 10-cm gap in the surrounding grasses compared with no gap in the grass (table 6.3). During frost conditions, the thick grass sward would raise the height above the ground that freezing temperatures occur (Oke 1987). The seedlings planted with no gap in the grass sward were approximately the same height as the

surrounding grasses, and therefore the growing tip and many of the leaves on the seedlings would be exposed to freezing (*i.e.* lethal) temperatures. In the 10-cm gaps, the active cooling surface, and therefore the coldest temperatures, would be closer to the ground, away from most of the leaves and the growing tip of the seedlings (Oke 1987). If shorter seedlings were planted, the 10-cm gaps would not provide this 'protection'.

Therefore, to avoid frost damage, seedlings germinating in the grass sward (*i.e.* no gap around the seedling) need to grow taller in a shorter period of time than those which germinate in gaps. This is difficult to achieve when competition is likely to be high, given the close proximity of the surrounding grasses.

The larger surface area of leaves of *Bedfordia* (compared with *Leptospermum*) is likely to make this species more susceptible to frost. In addition, the leaves of *Leptospermum* (and *Eucalyptus* species) generally have a more waxy cuticle which would offer more frost protection.

The difference in frost damage between north- and south-facing slopes relates to the duration and severity of the frosts. The frosts on northern slopes (in the southern hemisphere) would be less severe because the soil would store more heat than on southern slopes. The frosts would also be shorter in duration because the sun would warm these slopes first, the following morning (Oke 1987). As a consequence, the more frost-resistant species, *Leptospermum*, was not as badly affected on slopes with a northern aspect, regardless of the size of the gap in the grasses (table 6.3).

The effects of Competition on Seedling Survival and Growth

After the first three months there was generally little difference in seedling survival between the each of the competition treatments in the field (table 6.4). However, the seedlings used were quite well established when planted. It is likely that if the seedlings were transplanted into the pasture at a younger, smaller stage of development, there may have been more contrast between the treatments.

Overall, there was evidence that shoot competition has little effect on both the survival and growth of these shrubs and tree seedlings compared with root competition (table 6.4; figure 6.6). The seedlings were either killed or grew more slowly when planted in amongst the roots of the grasses (treatments 1 and 2). There is also substantial evidence in the literature, as reviewed by Wilson (1988), that root competition is usually more important. Removing the influence of the roots (either temporarily or permanently) always significantly increased the seedlings growth. These results are similar to other studies which have found that increasing gap size or excluding root competition increases seedling growth (Noble 1980; Snaydon & Howe 1986; Aguilera & Lauenroth 1993; Morgan 1997).

The heavy rainfall in late winter and early summer promoted extremely good growth of the grasses and, as a result, most of the seedlings were overgrown (appendix 6.1). The lack of light penetration and suppression of growth at this critical phase in the establishment of these seedlings is the most likely explanation for the poor growth and eventual death of almost all (85%) of the seedlings. Unlike many other studies in which root competition had been excluded, in the present study the above-ground gaps were not large or long-term. However,

these small gaps are probably more realistic of the size of gaps produced naturally in these pastures.

Conclusion

In the first three months, these three native species were more likely to survive and establish faster if they were planted in gaps in the grass sward. When the native tree and shrubs seedlings were transplanted into the grass sward without the roots of the grasses being disturbed, 97% of the seedlings were dead after two years (table 6.4). When protected from frost and herbivory, *Bedfordia* seedlings were more likely to survive than *Leptospermum*, whereas almost all *Eucalyptus* seedlings died.

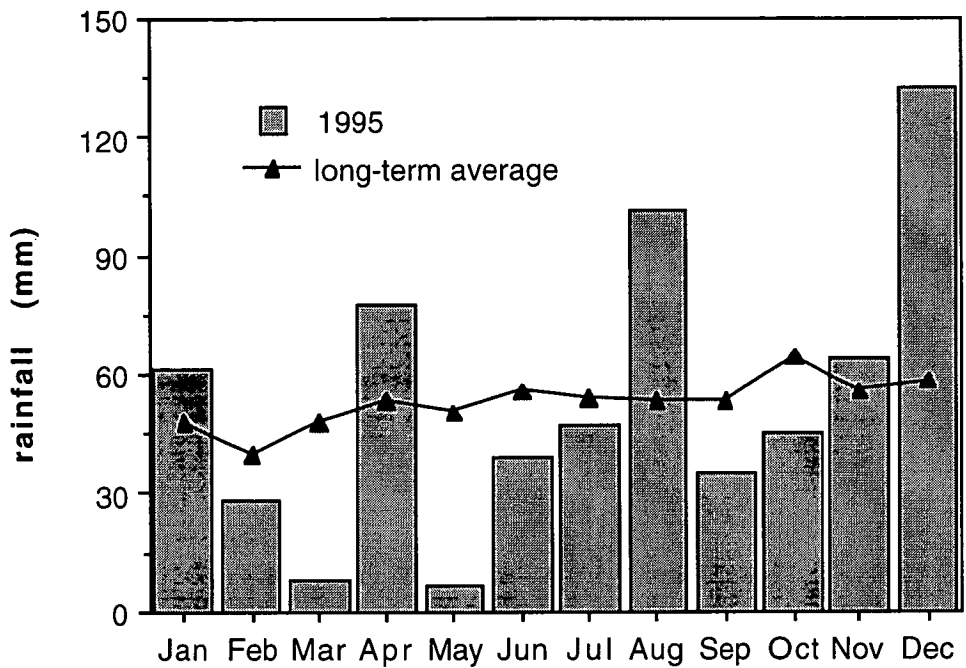
The three species tested were usually unable to form mycorrhizae when grown in the pasture soil. Even at the pasture edge, mycorrhizal colonization rates were low. This is likely to adversely affect the ability of all three woody species to compete with the grasses. Despite this, seedling growth tended to be greater in the pasture soil. This could be due to the greater availability of phosphorus in the soil.

Bedfordia salicina seedlings were highly susceptible to damage caused by frost and browsing by snails and slugs. In both the field and glasshouse, these seedlings increased in height and weight slower than the other two species tested. These factors could account for the lack of re-establishment of *Bedfordia* in the pasture. However, provided that the seedlings are protected from frost and browsing, this species appears capable of re-establishment.

Fewer *Leptospermum* seedlings established on south-facing aspects, even when protected from the effects of frosts. *Eucalyptus* seedlings showed no such effect. Unfortunately, the effects of invertebrate browsing and frost were not tested on *Eucalyptus* seedlings, due to a lack of available seedlings.

During the period of rapid grass growth in spring and summer 1995, the *Eucalyptus* seedlings were smothered and suppressed. More *Leptospermum* (and *Bedfordia*) seedlings were able to maintain (at least) the same height as the grasses. The difference in growth form of the young *Leptospermum* and *Eucalyptus* seedlings may account for these differences. *Leptospermum scoparium* seedlings appeared to have a greater degree of apical dominance than *Eucalyptus pulchella* seedlings.

Appendix 6.1 The monthly rainfall for Hobart in 1995 and the long-term monthly average (source: Bureau of Meteorology).



Chapter Seven

General Discussion

The aims of this thesis are:

- to examine the factors that inhibit or facilitate the natural re-establishment of native species on improved pastures;
- to determine the relative impacts of these factors on the rate of re-establishment and the extent of re-invasion.

In the preceding chapters, the effects of particular factors on the rate of re-establishment were examined (aim 1). This chapter examines the relative importance of these factors on the process of natural re-establishment (aim 2) and the implications of these results as a whole for restoration work.

The relative importance of factors affecting the re-establishment of native plants

Competitive Exclusion

Disturbance may result in conditions suitable for germination of native species but the proximity of the roots and shoots of pasture species will determine whether establishment is likely to be successful (McConnaughay & Bazzaz 1987, 1991; Wilson 1988; Morgan 1997). In the present study, gaps up to 10 cm in diameter were not sufficient to facilitate native re-establishment (chapters 4 & 6). The composition of improved pastures was very stable because the vegetation rapidly recovered from disturbance and there were typically no gaps in the

vegetation for other species to establish (chapters 3 & 4). Following disturbance, the pasture grasses and associated exotic weeds, such as *Plantago lanceolata*, could regenerate rapidly from the root system (rhizomes and tap roots) and/or from protected buds at the base of the shoots. In addition, the shoot and root systems of the grasses were dense (and competition intense) close to the soil surface where seedlings were attempting to establish.

There is sufficient data in the literature to suggest that larger gaps are more likely to assist establishment of native seedlings (Noble 1980; McConnaughay & Bazzaz 1987, 1991; Morgan 1997). The creation of large gaps away from the edge of the pasture was very uncommon (*e.g.* rabbit burrows). It is likely that the main reason for successful re-establishment at the edge of the pasture was due to the more open nature of the ground-cover vegetation (*i.e.* large gaps).

The Edge of the Pasture

The reduction in exotic grass cover beneath a taller canopy is likely to be due to competition for light, moisture and nutrients, and possibly the release of allelopathic compounds (May & Ash 1990; Fensham & Kirkpatrick 1992; Nepstad *et al.* 1996; Appleby *in press*). At the edge of the pasture, the re-establishment of native species was highly correlated with the presence of litter produced by the trees and shrubs in the adjacent forest, and with a more open grass sward (chapter 3). The litter may provide suitable microsites or 'safe sites' to protect seedlings from the extremes in soil temperature, reducing soil desiccation and providing some protection from browsing animals (Battaglia & Reid 1993; Kirkpatrick 1997). However, it is also likely that the correlation between litter and re-establishment merely reflects the proximity of eucalypts and tall shrubs, and that the influence of these tall species on the grasses below was crucial.

The presence of exotic grass seeds in the forest soils, but the lack of their invasion into the forests at Kettering and Ridgeway, implies that these grasses cannot cope with forest conditions. The native species that form the understorey in these open forests should be better adapted than the exotic grasses to the conditions beneath the tall canopy. The transition from an exotic to a native understorey is not a rapid process and may depend on the length of time needed to form a tree canopy and root system that can suppress the exotic grasses.

There was a plentiful source of native seeds for a few species—including a range of tree and shrub species—throughout the year at the edge of the pasture (chapter 5). This was due to the large quantity of seed-fall and the good seed dispersal capabilities of several native species. Despite this, the availability of native seeds in the soil seed bank was relatively low in the pasture due, in part, to seed predation by ants.

Other factors also played a role in facilitating re-establishment of native species at the edge of the pasture. Firstly, the availability of inoculum of ectomycorrhizal fungi in the pasture soil was high close to the edge of the forest (chapter 6). A number of native shrub and tree species, including the dominant species of eucalypt, are likely to form ectomycorrhizae (May & Simpson 1997). Secondly, frost was more likely to damage seedlings growing in the open than those growing beneath the canopy at the edge of the pasture (Oke 1987). And thirdly, available phosphorus was significantly lower towards the edge of the pasture which would not favour exotic species. It is likely that the presence of tall, woody native species at the pasture edge would provide host material for ectomycorrhizal fungi, protect seedlings from frost and reduce available soil nutrients.

"

Therefore, the conditions around the edge of the improved pastures facilitated re-establishment. The creation of large gaps in the grass sward is an important requirement to encourage native seedling establishment. The chances of conditions being suitable for native re-establishment away from the edge are few, shown by the few isolated trees in the pasture. The conditions which were unsuitable for exotic pasture species were restricted to the edge of the pasture. The pace of native re-establishment is, therefore, likely to be restricted to the pace at which the tree and shrub canopies and root systems spreads from the edge of the pasture and from around isolated trees.

The difference in the rate and extent of re-establishment between the sites investigated

At the sites studied in this project, the extent of re-establishment was poorly correlated with age since abandonment. The improved pasture at Ridgeway—abandoned since 1967—still resembles a pasture, whereas one of the native pastures at Mornington—abandoned since 1970—could not be easily distinguished from the surrounding forest. However, given the small number of sites investigated in this study, no correlation between age and the extent of re-establishment could be established. Other studies have found that the factors which affect the rate of re-establishment relate to the conditions and history of farming specific to each site (Onans & Parsons 1980; Uhl *et al.* 1988; Nepstad *et al.* 1991; Zeng & Whelan 1993; Motzkin *et al.* 1996).

How do differences in the type of pasture explain the difference in the rate of re-establishment?

Variation in the rate of re-establishment relates to the intensity of the disturbances that created and have maintained the pasture (Onans &

Parsons 1980; Uhl *et al.* 1988; Nepstad *et al.* 1991; Motzkin *et al.* 1996). The differences in the rate of re-establishment between improved and native pastures suggest that it is the degree of modification of the site caused by disturbance which determines the rate of re-establishment and, therefore, the resilience of the native community. The degree of modification (*i.e.* pasture improvement) will determine the chances of recovery from elements *in situ* (Grubb & Hopkins 1986). Two key factors are discussed below.

1). Ploughing removes most of the native vegetation and prevents species from resprouting. Ploughing also reduces the available soil seed bank by mixing the more diverse and larger soil seed bank near the surface with lower soil layers (Cavers & Benoit 1989). Therefore, one would expect a faster rate of recovery and a greater diversity of native species on the native pastures compared with the improved pastures. Similarly, if the topsoil was scalped by bulldozers when the pasture was established, natural re-establishment would be much slower (Nepstad *et al.* 1991).

In improved pastures, native species would have to regenerate from what remains of the soil seed bank (Onans & Parsons 1980), but also probably rely on dispersal from outside sources (Hobbs & Mooney 1993). However, after years of agricultural use, the soil seed bank is typically dominated by weed species (Conn *et al.* 1984; Nepstad *et al.* 1991; Marsden-Smedley *et al.* 1997). In addition, dispersal does not always provide a reliable and plentiful source of seed for each species (Conn *et al.* 1984; Nepstad *et al.* 1991). The sites chosen in this study were adjacent to undisturbed forest to provide a suitable source of propagules of native species. In these pastures, there was a significant influx of seeds of several native tree and shrub species from the forest.

Ploughing also reduces the amount of inoculum of mycorrhizal fungi (Allen & Allen 1980). In the present study, the inoculum of suitable mycorrhizal fungi for the native species tested was significantly lower in the improved pastures compared with the forest (table 6.2). While many native species are facultative mycotrophs, the formation of mycorrhizae could be advantageous when competing with grasses in abandoned pastures. The inability of the native seedlings to form mycorrhizae could explain the high mortality of the seedlings planted in the pasture (table 6.4). Some studies have shown that the ability to form mycorrhizae can be a mechanism which facilitates succession or, in this case, re-establishment (Reeves *et al.* 1979; Allen & Allen 1984; Johnson *et al.* 1991).

2). The addition of fertilizers should favour the sown exotic grasses which are generally not adapted to low soil fertility (Hedde & Specht 1975; Specht *et al.* 1977; Clements 1983; Hobbs & Atkins 1988). Sowing exotic grasses and adding fertilizers results in increased competition for any native species that may attempt to re-establish.

In general, pasture establishment will be successful and permanent on more fertile soils. For example, on the fertile basalt plains of western Victoria, native species are typically completely replaced following pasture improvement (Lunt 1991). Similar results were found in the Goulburn district of New South Wales, although native species were still abundant where disturbance associated with clearing and cultivation was limited (Robinson *et al.* 1993).

Conversely, it is difficult to establish improved pastures on sites with relatively low natural soil fertility and a dry climate. In these situations there is poor establishment of the pasture species, and native species may begin to re-establish while the pasture is still grazed by domestic

animals (Robinson *et al.* 1993; Zacharek 1997). Similarly, the rate of re-establishment was faster at Mornington where the soil fertility and rainfall are lower than at either Ridgeway or Kettering (chapter 2, 3). In sections of the pasture at Kettering, where the more fertile topsoil had been lost as a result of erosion, the re-establishment of native trees and shrubs was well developed.

Therefore, the degree of intervention that is required to restore the native vegetation at a site depends primarily on whether it is improved or native pasture—assuming there is a source of native seeds available nearby. Native pastures have been less severely disturbed and modified than improved pastures, and native species appear able to naturally regenerate in a relatively short period of time. Improved pastures have been more severely modified to produce a dense sward of exotic grasses. The modifications to the land and the presence of a dense sward of exotic grasses makes it more difficult to establish native species. From the results of this study, it seems likely that improved pastures require an interventionist approach to restoration if native forests are to be re-established in the period of a generation.

Assisting Regeneration on Abandoned Pastures

The results of this project indicate that the restoration of native forests on abandoned improved pastures should be feasible, even though the rate of natural re-establishment is slow. The factors investigated which prevented or slowed native species re-establishing were not insurmountable.

There were a number of results that suggested that the rate of re-establishment could be faster if the conditions for seedling establishment were suitable. Native seeds were able to disperse far into

the pasture (chapter 5), but the availability of safe sites for establishment was limiting further re-establishment away from the edge of the pasture. Native species grown in soil from the pasture were able to grow at a faster rate than those grown in forest soil, despite the lack of mycorrhizae (chapter 6).

The results of this study show that an approach that creates the conditions for further establishment of native species, whilst suppressing exotic grasses, would be an effective way of increasing the rate of re-establishment. Plantations of native trees and/or tall shrubs would provide a number of advantages. Once established, the canopy of tall native vegetation would facilitate the re-establishment of more native species in a similar way that establishment occurs at the edge of the pasture with the forest.

There are a number of methods that have been used in order to increase the rate of native species re-establishment on abandoned improved pastures—including direct-seeding and tree plantations (Pryor & Clarke 1964; Venning 1991). Disturbance of the grass sward that creates gaps that are both large and remain free of grasses for a long period of time appear to be important requirements for successful establishment of the native forest species. The natural disturbance regimes at the pastures investigated were not sufficient to facilitate further re-establishment (chapter 4). Methods such as the application of herbicides or ploughing provide more substantial disturbance that will kill the exotic grasses.

Plantations of trees have been recommended for regenerating abandoned pastures in Amazonia where exotic grasses impede the regeneration of native forest species (Nepstad *et al.* 1991; Vieira *et al.* 1994; da Silva *et al.* 1996). The trees not only reduce the cover of grasses

but also increase the availability of seeds for re-establishment by providing perches for frugivorous birds as well as seed from the plant itself (Vieira *et al.* 1994). The tree seedlings could be inoculated with suitable ectomycorrhizal fungi that would provide a source of inoculum for other native species that form ectomycorrhizae. Once established, the trees would suppress the exotic grasses and provide protection for emerging seedlings from frost and extremes in temperature.

Conclusion

In this study, natural re-establishment in native (unimproved) pastures was progressing at a relatively fast rate. This is most likely due to the less severe disturbance and modification of these sites compared with improved pastures.

Natural re-establishment in improved pastures was typically restricted to the edge of the pasture and, to a lesser extent, beneath isolated trees in the pasture. In general, these are the most favourable areas for native species to establish. The availability of native seeds was generally not limiting the rate or extent of re-establishment.

Therefore, it is likely that the natural rate of re-establishment will continue to be slow on abandoned improved pastures. To restore these areas at a faster rate will require methods, such as the creation of plantations, that facilitate the establishment of native seedlings by suppressing the cover of exotic grasses.

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