

**Soil disturbance by native mammals  
and the germination and establishment  
of plant species**

by

*Francis*  
**Adrian<sub>^</sub>Pyrrke BSc(Hons)**

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

Department of Geography and Environmental Studies  
University of Tasmania  
Hobart

January 1994

## Declaration

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

*Adrian Pyke*

Adrian Pyke

### 5. Access to, and copying of, thesis

The thesis copy lodged in the University Library shall be made available by the University for consultation but, for a period of two years after the thesis is lodged, it shall not be made available for loan or photocopying without the written consent of the author and in accordance with the laws of copyright.

After a thesis has been examined, the following authority will apply. Please complete your request, and sign below.

(i) I ~~agree~~/do not agree that the thesis may be made available for loan.

(ii) I ~~agree~~/do not agree that the thesis may be made available for photocopying.

(iii) I note that my consent is required only to cover the two-year period following approval of my thesis for the award of my degree. After this, access to the Library copy will be subject only to any general restrictions laid down in Library regulations.

Signed: \_\_\_\_\_

Date: \_\_\_\_\_



Lodged in Morris Miller Central Library: \_\_\_\_\_

from which date the two years embargo will apply



## Abstract

This thesis investigates disturbances created by the digging of small native mammals and their role in the germination and establishment of native plant species in eastern Tasmania, with a particular focus on species considered to be rare or threatened. At least 15 rare and endangered plant species live in habitats where digging appears to be common. Soil disturbances, which are created by bettongs, bandicoots and echidnas, can be prolific, particularly on soils of lower fertility. Turnover rates of up to 2.9% of the ground surface per annum were recorded. Diggings by bettongs, and to a lesser degree by bandicoots, are spatially associated with trees in dry sclerophyll and grassy woodlands and forests. The understorey varies in species composition depending on the degree of tree influence, so not all understorey species are close (at the scale of several metres) to where digging disturbances are most abundant.

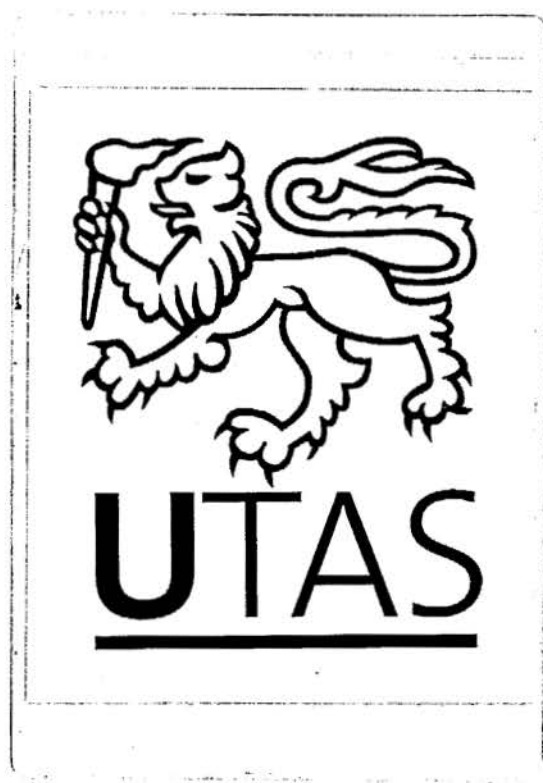
Digging creates small patches of bare ground which, on sandy soils, can be a harsh environment with low nutrient and moisture availability. However, diggings provide better conditions for the germination of many species, particularly those with small seeds and perhaps also some species which have hard-seeded dormancy. This latter effect may be a result of the considerable soil heating imposed by direct solar radiation on bare soil. Several species had higher densities of seedlings on animal diggings, although mortality rates were generally very high on both digging disturbances and undisturbed areas. Seedlings died faster, at the same rate, or slower on diggings compared with undisturbed areas, depending on the species and the circumstances. Simulated animal disturbances proved to be effective in stimulating germination, and more substantial survival of seedlings was recorded in these experiments than on natural diggings.

Many plant species in this study have seed stored in the soil at depth. Digging probably brings buried seed to the surface which would otherwise not germinate.

Rare or threatened species which were found to benefit from either natural diggings or simulated disturbances included *Lepidium hyssopifolium*,

*L. pseudotasmanicum*, *Lasiopetalum micranthum*, *Vittadinia muelleri* and *Velleia paradoxa*. No rare species appeared to be completely dependent on animal digging for a regeneration niche, but the potential exists to use mechanical disturbance as a management tool for some species.

The density of an exotic annual grass, *Briza maxima*, was considerably less on larger digging mounds compared with undisturbed areas, even three years after the creation of the mounds. There was evidence that native seedlings were experiencing less competition from *B. maxima* on these mounds and perhaps have a better opportunity for establishment.



## Acknowledgements

This thesis was funded by the Endangered Species Program of the Australian National Parks and Wildlife Service (now called the Australian Nature Conservation Agency) and an Australian Postgraduate Research Award. I am greatly indebted to a large number of people who contributed to the thesis both directly and indirectly:

- David Ashton has been a great source of inspiration.
- Jamie Kirkpatrick, my supervisor, was a tireless source of help, encouragement and ideas throughout this project.
- Rod Fensham conceived the idea and the need for the study.
- Jasmyn Lynch, Louise Mendel, Ana Blake, Andrew Zacharek, Alistair Wells, Jason Good, Louise Gilfedder, Jenny Dyring and Rebecca Cannell all helped in the field or the laboratory.
- Jill Hickie, Emma Pharo, Michael Askey-Doran and Kerry Bridle gave major contributions in the field and the laboratory, surrendered the wellbeing of their poor knees to science, consumed vast quantities of Danish pastries and provided me with great company in the field.
- Mark Chladil contributed expertise with datalogging and other equipment and helped in the field.
- Dennis Charlesworth analysed the soil samples.
- Robert Riggall, Chris Viney and John Youl made their properties available at Tunbridge, Westwood and Powranna respectively.
- Phil Watson gave support and shared a keen interest in my work at the Waverley Flora Park.
- Glen McPherson gave considerable help with statistics.
- Neville Scarlett, Dennis Morris and Alex Buchanan identified plants.
- Mike Driessen and Greg Hocking gave advice and help with mammal biology and trapping.
- Peter Cornish gave invaluable technical support at various stages.
- Kerrie Green made the bureaucratic necessities seem like a picnic (for me in any case).
- Michael Askey-Doran, Phil Cullen, Louise Gilfedder, Ian Lunt and Mark Neyland made valuable comments on various parts and drafts of this thesis.
- Shirley Grosvenor proofread the entire thesis.
- my mother, Pamela Judd, looked after my young son on too many occasions to count, and proofread most of the thesis.
- Mary Maher did some proofreading, but more importantly, gave me considerable love and support throughout and remained unbelievably patient to the end.

## Contents

Abstract .....	i
Acknowledgements .....	iii
Contents .....	iv

### Chapter 1

General Introduction .....	1
Disturbance mechanisms .....	1
Small-scale disturbance by mammals .....	2
Small-scale disturbance by mammals in Australia .....	5
<i>Small-scale disturbance by native mammals in Tasmania</i> .....	5
<i>Mammal disturbance and rare plant species in Australia</i> .....	8
Questions asked in this thesis .....	9

### Chapter 2

The Distribution of Native Mammal Digging in Relation to Rare Plant Species, and Study Site Descriptions. ....	12
Introduction .....	12
Methods .....	12
Survey Results and Discussion .....	13
Descriptions of rare species and study sites .....	17
<i>Rare Species Descriptions</i> .....	20
<i>Study Site Descriptions</i> .....	23

### Chapter 3

The Effects of Digging on the Properties of Surface Soil .....	28
Introduction .....	28
Methods .....	28
<i>Bandicoot hole depth and disturbance area</i> .....	28
<i>Soil moisture</i> .....	28
<i>Soil nutrients</i> .....	29
<i>Soil temperatures</i> .....	30
<i>Data analysis</i> .....	31
Results .....	33
<i>Bandicoot hole depth and disturbance area</i> .....	33
<i>Soil moisture</i> .....	33
<i>Soil nutrients</i> .....	33
<i>Soil temperatures</i> .....	34
Discussion .....	42
<i>Comparisons with other studies</i> .....	42
<i>Soil moisture</i> .....	43
<i>Soil nutrients on diggings</i> .....	44
<i>Soil temperatures</i> .....	45
<i>Conclusion</i> .....	46

## Chapter 4

<b>The Frequency of Diggings and the Spatial Pattern of Diggings in Relation to Trees and Understorey .....</b>	<b>47</b>
<b>Introduction .....</b>	<b>47</b>
<b>Methods .....</b>	<b>48</b>
<i>Rates and season of diggings .....</i>	<i>48</i>
<i>Spatial pattern of diggings in relation to trees and vegetation .....</i>	<i>48</i>
<i>Data Analysis .....</i>	<i>50</i>
<b>Results .....</b>	<b>53</b>
<i>Rates and season of digging .....</i>	<i>53</i>
<i>Spatial pattern of diggings and trees: 10 x 50 m transect at Bellerive .....</i>	<i>55</i>
<i>Digging in relation to understorey and trees: 0.4 x 0.8 m quadrats .....</i>	<i>56</i>
<i>Digging in relation to trees and understorey: 1 x 1 m quadrats .....</i>	<i>58</i>
<i>Mammal trapping .....</i>	<i>61</i>
<b>Discussion .....</b>	<b>87</b>
<i>Rates and season of digging .....</i>	<i>87</i>
<i>Spatial pattern of diggings and trees .....</i>	<i>90</i>
<i>Digging in relation to understorey and trees .....</i>	<i>91</i>
<i>Conclusion .....</i>	<i>94</i>

## Chapter 5

<b>The Germination and Establishment of Seedlings on Diggings .....</b>	<b>96</b>
<b>Introduction .....</b>	<b>96</b>
<b>Methods .....</b>	<b>96</b>
<i>Annandale .....</i>	<i>97</i>
<i>Bellerive .....</i>	<i>97</i>
<i>Chimney Pot Hill .....</i>	<i>99</i>
<i>Dukes Marshes .....</i>	<i>99</i>
<i>East Risdon .....</i>	<i>100</i>
<i>Hospital Creek .....</i>	<i>100</i>
<i>Kellevie Road .....</i>	<i>101</i>
<i>Old Coach Road .....</i>	<i>101</i>
<i>Powranna .....</i>	<i>101</i>
<i>Westwood .....</i>	<i>102</i>
<i>Data Analysis .....</i>	<i>102</i>
<b>Results .....</b>	<b>105</b>
<i>Annandale .....</i>	<i>105</i>
<i>Bellerive .....</i>	<i>107</i>
<i>Chimney Pot Hill .....</i>	<i>111</i>
<i>Dukes Marshes .....</i>	<i>112</i>
<i>East Risdon .....</i>	<i>112</i>
<i>Hospital Creek .....</i>	<i>112</i>
<i>Kellevie Road .....</i>	<i>113</i>
<i>Old Coach Road .....</i>	<i>114</i>
<i>Powranna .....</i>	<i>116</i>
<i>Westwood .....</i>	<i>116</i>
<b>Discussion .....</b>	<b>143</b>
<i>Lepidium hyssopifolium at Annandale .....</i>	<i>143</i>
<i>Velleia paradoxa and other species at Bellerive .....</i>	<i>145</i>

<i>Odixia achlaena</i> , <i>Dodonaea filiformis</i> , and <i>Acacia genistifolia</i> at Hospital Creek .....	149
<i>Lasiopetalum micranthum</i> at the Old Coach Road .....	150
<i>Brunonia australis</i> at Westwood .....	152
Other study sites .....	153
Methodological and data analysis considerations .....	154
Conclusions .....	155

## Chapter 6

### Experiments on Disturbance: Simulated Animal Digging, Burning and Germination Trials .....

Introduction .....	157
Methods .....	158
<i>Lasiopetalum micranthum</i> field and laboratory experiments .....	158
<i>Lepidium hyssopifolium</i> simulated digging experiment .....	161
<i>Lepidium pseudotasmanicum</i> simulated digging experiment .....	161
<i>Stackhousia gunnii</i> and <i>Vittadinia muelleri</i> simulated digging experiment .....	162
<i>Odixia achlaena</i> pot germination experiment .....	163
Data Analysis .....	164
Results .....	165
<i>Lasiopetalum micranthum</i> field and laboratory experiments .....	165
<i>Lepidium hyssopifolium</i> simulated digging experiment .....	167
<i>Lepidium pseudotasmanicum</i> simulated digging experiment .....	168
<i>Stackhousia gunnii</i> and <i>Vittadinia muelleri</i> simulated digging experiment .....	170
<i>Odixia achlaena</i> pot germination experiment .....	171
Discussion .....	180
<i>Lasiopetalum micranthum</i> .....	180
<i>Lepidium hyssopifolium</i> .....	183
<i>Lepidium pseudotasmanicum</i> .....	184
<i>Stackhousia gunnii</i> and <i>Vittadinia muelleri</i> .....	185
<i>Odixia achlaena</i> .....	186
Conclusions .....	187

## Chapter 7

### Seed Stored in the Soil at Various Depths in the Habitats of Rare and Endangered Species .....

Introduction .....	188
Methods .....	188
Results .....	192
Annandale .....	192
Bellerive .....	193
East Risdon .....	193
Hospital Creek .....	194
Old Coach Road .....	194
Discussion .....	204
Conclusions .....	209



## Chapter 8

### The Relationship Between Bandicoot Diggings, Exotic Species and the Survival of Native Seedlings ..... 210

Introduction .....	210
Methods .....	210
<i>Exotic species removal experiment on bandicoot mounds</i> .....	210
<i>Briza maxima density on bandicoot diggings and competition effects</i> .....	211
<i>Briza maxima removal experiment</i> .....	212
<i>Data Analysis</i> .....	213
Results .....	214
<i>Exotic species removal experiment on bandicoot mounds</i> .....	214
<i>Briza maxima density on bandicoot diggings and competition effects</i> .....	214
<i>Briza maxima removal experiment</i> .....	215
Discussion .....	222
<i>Competition between exotic species and native seedlings</i> .....	222
<i>Digging disturbance and Briza maxima density</i> .....	223
<i>Hand weeding of Briza maxima</i> .....	225
<i>Conclusion</i> .....	226

## Chapter 9

### Synthesis and Conclusions ..... 227

Microscale succession and plant growth on simulated and natural diggings.....	227
Germination on simulated and natural diggings.....	228
Survival of seedlings on simulated and natural diggings .....	230
A comparison of fire and mechanical soil disturbance .....	233
Influence of trees on the spatial patterns of digging and understorey .....	235
Digging intensity and soil fertility.....	236
Digging and soil stored seed .....	237
Conclusions.....	238
Recommendations for future research.....	240

### References..... 242

### Appendix 1 Summary of the survey of mammal digging in the habitats of rare plants..... 254

### Appendix 2 Complete floristic data from the 1 x 1 m grid quadrats at Bellerive. 262

### Appendix 3 Summary of survivorship until December 1992 and total counts of seedlings and ramets for all mapped species at Bellerive..... 263

### Appendix 4 Complete list of vascular plant species mentioned in this thesis..... 265

### Appendix 5 Management implications for rare species..... 270

## Chapter 1

### General Introduction

#### Disturbance mechanisms

Disturbance is widely recognised as an important and natural process in many ecosystems, and has been defined as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment' (White & Pickett, 1985; Collins, 1987). Earlier this century, there was a tendency to consider only large scale disruptions, that is, those which affected areas of size many orders of magnitude greater than the organisms in the community being discussed, as 'disturbance' phenomena. It virtually required a paradigm shift, using a different set of terms, to discuss 'disturbances' which tended to be similar in area to the size of the organisms in the community. This conceptual transfer is no longer considered necessary, and 'disturbance' is now considered to encompass a continuum of widely varying spatial and temporal scales, with many possible origins (White, 1979; Pickett & White, 1985). The definition of disturbance given above is adopted in this thesis, despite the fact that it represents only one end of a continuum if one considers that some disturbances may range from discrete and highly disruptive, to continuous and only slightly disruptive (e.g. grazing, trampling, wind)(see also Hobbs & Huenneke, 1992).

Disturbances have been classified as either endogenous or exogenous (White, 1979). An endogenous disturbance is created by the organisms themselves; for example, the death and falling over of a tree creates a canopy gap and soil disturbance. An exogenous disturbance is one that is independent of the community, e.g. strong winds. There is a continuum on this axis as well because not all disturbances are completely exogenous (White, 1979). For example, wildfire may have had an external origin such as lightning, but its intensity and therefore ultimate impact may be influenced by the morphology and chemistry of the plant species in the community. Similarly, tree falls are often a result of strong winds, and the location of digging by mammals may be influenced by the spatial location of plant species (Chapter 4).



This study is concerned with the mechanical disturbance of soil by small mammals. Within the framework of the brief typology of disturbance given above, this kind of disturbance is small-scale, both spatially and temporally, and is only partly exogenous.

### Small-scale disturbance by mammals

In recent years, it has been recognised that small-scale disturbance is important in maintaining species richness, by creating gaps in an otherwise continuous community (Grubb, 1977; White, 1979; Pickett & White, 1985). The effect of small-scale disturbances created by digging mammals has been the focus of considerable attention, particularly in North America. Digging disturbances in native prairie vegetation by gophers (Mielke, 1977; Collins & Barber, 1985; Loucks *et al.*, 1985; Hobbs & Mooney, 1985; Spencer *et al.*, 1985; Williams & Cameron, 1986; Hobbs & Hobbs, 1987; Gibson, 1989; Martinsen *et al.*, 1990; Hobbs & Mooney, 1991), badgers (Platt, 1975; Gibson, 1989), prairie dogs (Bonham & Lerwick, 1976) and various other mammals (Gibson, 1989) have been studied. Similarly, digging disturbances by gophers in old-fields (Tilman, 1983; Inouye *et al.*, 1987; Reichman, 1988), exotic grassland (Peart, 1989) and woodlands (Davis *et al.*, 1991a; Davis *et al.*, 1991b) and moles in old-fields (Goldberg & Gross, 1988; Reader & Buck, 1991) have been investigated. Meanwhile, work in other parts of the world has reported on the importance of moles in chalk grassland in Britain (Watt, 1974), rabbit scrapings on sand-dunes in The Netherlands (Burggraaf - van Nierop & van der Meijden, 1984), mole rats in Israel (see Heth, 1991) and porcupine diggings in a desert in Israel (Guttermann *et al.*, 1990; Shachak *et al.*, 1991).

Several studies have examined the effects on vegetation of small-scale disturbances created artificially, either by attempting to simulate real animal disturbances (Rabinowitz & Rapp, 1985a; Rabinowitz & Rapp, 1985b; Rapp & Rabinowitz, 1985; Belsky, 1986; Klinkhamer & De Jong, 1988; Collins, 1989), or by examining the effects of artificial gaps of a range of sizes (McConnaughay & Bazzaz, 1987; McLendon & Redente, 1990) or intensity (Armesto & Pickett, 1985), or by simply examining the importance of small artificial gaps *per se* (Carson & Pickett, 1990).

Some studies have concluded that in the communities examined, small-scale disturbances created by mammals are important in maintaining species richness and in enabling the persistence of some plant species, particularly herbs, at the expense of dominant grasses (Platt, 1975; Bonham & Lerwick, 1976; Burggraaf - van Nierop & van der Meijden, 1984; Armesto & Pickett, 1985; Hobbs & Mooney, 1985; Collins, 1989; Martinsen *et al.*, 1990; Reader & Buck, 1991). However, one study found no effect on species richness when gophers were excluded (Williams & Cameron, 1986), while others have concluded that such disturbances are either unimportant (Belsky, 1986; Novoplansky, 1984, reported in Heth, 1991), of little relevance relative to other factors (Carson & Pickett, 1990), or of relevance only to annual species and not the common perennial species (Goldberg & Gross, 1988).

A common finding has been the recognition of a distinct suite of species which colonises disturbances. These have been labelled 'fugitive species' and are often annuals or biennials (Watt, 1974; Burggraaf - van Nierop & van der Meijden, 1984; Collins, 1989; Gibson, 1989), but also perennials (Platt, 1975). They usually have distinctive life-history characteristics which are not necessarily equivalent to the ruderal habits of exotic short-lived plants (Platt, 1975). Small-scale disturbance may be important for maintaining species richness even when a distinct guild of species is not recognised (Hobbs & Mooney, 1985), or the disturbance influence may be manifest in other ways. For example, some plant species may have enhanced reproduction or growth on disturbances, due to a reduction in competition for resources (Hobbs & Mooney, 1985; Davis *et al.*, 1991a), or there may be differential survivorship due to variation in ability to survive burial underneath digging mounds (Davis *et al.*, 1991b).

Some studies have described microscale succession on animal disturbances. A common trend in these studies is the replacement of less competitive early colonisers by more competitive species (Watt, 1974; Platt, 1975; Collins, 1989; Martinsen *et al.*, 1990).

Some plant communities are subject to recurrent disturbances of varying spatial scales and frequencies from a variety of sources. For example, some prairies are not only burnt and grazed on a large scale, but also subject to

localised soil disturbances of varying sizes from different animal species (Collins & Barber, 1985; Collins, 1989; Gibson, 1989). In these cases, each of the different disturbances induces different responses from the vegetation, leading to spatial heterogeneity in floristic composition and community structure (Collins, 1989; Gibson, 1989), with combinations of disturbances having a cumulative effect on species richness (Collins & Barber, 1985). The location of disturbances within the landscape will to a certain extent influence the species which can colonise because dispersal distances are limited (Hobbs & Mooney, 1985), with colonisers being a subset of the local seed pool (Gibson, 1989).

It is necessary to be explicit about spatial scale when discussing the enhancement of species richness by disturbance. In particular, it is important to identify whether species richness is considered to be greater over an area large enough to be inclusive of both disturbed and undisturbed patches, or only within the disturbed patches. This is not stated clearly in all of the studies which have been mentioned thus far, but it is assumed that most authors would be referring to species richness over the broader community, with variation at a smaller spatial scale.

While small-scale disturbances are almost certainly important in reducing interspecific competition and hence allowing the persistence of less competitive species (Watt, 1974), they also create patches which are physically and chemically different from the undisturbed vegetation, due to soil mixing and the upheaval of sub-surface soil. Soils on animal disturbances are often poorer in nutrients such as nitrogen and phosphorus and drier than surrounding undisturbed soil (Spencer *et al.*, 1985; Inouye *et al.*, 1987; Novoplansky, 1984, reported in Heth, 1991; Reader & Buck, 1991), although sometimes moister (Platt, 1975). However, the long term accumulation of gopher diggings is believed to be responsible for the formation of much larger raised areas called 'mima' mounds, which are of greater fertility and moisture holding capacity than inter-mound areas (Mielke, 1977). The holes of some shallow diggings act as a trap for water, organic matter and seeds, thus creating a regeneration 'oasis' in desert areas (Guterman *et al.*, 1990).

## Small-scale disturbance by mammals in Australia

In Australia, the effect of fire as a broad area disturbance phenomenon in vegetation has been widely studied, although our understanding of the potential outcomes of different fire regimes (i.e. season, intensity, frequency) is still very incomplete. At the other end of the spatial scale, studies of more localised disturbance events are far less common. There has been some work on forest gap dynamics (e.g. Webb *et al.*, 1972; Read & Hill, 1988; Barker, 1992); grazing and trampling by animals (in so far as they are discrete and disruptive) by direct observation (Scott, 1985) and experimental simulation (Williams & Ashton, 1987); and some observations on soil disturbance created by the digging of exotic animals such as rabbits (Leigh *et al.*, 1987). The effects on native vegetation of small-scale mechanical soil disturbances created by *native* animals have not been examined at all in Australia. I emphasise native animals because the interest is in the disturbance as a 'natural' phenomenon.

Soil disturbance by the indigenous Australian people was probably considerable and may have been a feature of a wide range of vegetation types, given the variety and ecological amplitude of the species whose roots, tubers and tuberoids were dug up for food (Gott, 1982; 1983). Such digging is now very limited because of changes in lifestyle, particularly in southern Australia.

### *Small-scale disturbance by native mammals in Tasmania*

Australia had a healthy abundance of digging marsupials and monotremes at the time of European occupation. However, many of these species are now either extinct, extremely depleted, or still common only on off-shore islands such as Tasmania where foxes are absent (Strahan, 1983) and habitat destruction is often less advanced.

In Tasmania, the common digging marsupials and monotremes are the Tasmanian bettong (*Bettongia gaimardi*), the long-nosed potoroo (*Potorous tridactylus*), the southern brown bandicoot (*Isodon obesulus*), the eastern barred bandicoot (*Perameles gunnii*), the short-beaked echidna (*Tachyglossus aculeatus*)

and the common wombat (*Vombatus ursinus*). All but one of these species dig exclusively to extract food from the soil; wombats also dig burrows in which to live. Soil disturbance by all of these species can be extensively manifest in the landscape, at least in suitable habitat.

The Tasmanian bettong lives in dry eucalypt forests and woodlands in eastern Tasmania which have an open understorey, from sea-level to 1050 m (Driessen *et al.*, 1990; Rounsevell *et al.*, 1991). This species feeds primarily on the fruiting bodies of hypogean fungi, although other fungi, vascular plant material including fruit and seeds and invertebrates are eaten in smaller quantities (Taylor, 1992c). Its diggings for fungal sporocarps are far more common on geological substrates that form soils of lower fertility, are more abundant in winter (Taylor, 1992a) and are spatially associated with trees at the micro-scale due to mycorrhizal associations with tree roots (Chris Johnson, pers. comm.; Claridge *et al.*, 1993a).

The long-nosed potoroo lives in a wide range of habitats, but in dry areas tends to stay in wet gullies where the undergrowth is denser (Rounsevell *et al.*, 1991). Hypogean fungi constitute a major part of the diet of this species (Claridge *et al.*, 1993b), but vascular plant material and arthropods form a larger proportion than in the diet of the Tasmanian bettong (Bennett & Baxter, 1989). Diggings down to 15 cm depth formed by the long-nosed potoroo have been reported as being evenly distributed around trees, within a radius of 2 m (Claridge *et al.*, 1993a).

Mycophagous marsupials such as bettongs and potoroos probably play an important role in forest ecology by dispersing the spores of ectomycorrhizal fungi and inoculating tree roots (Lamont *et al.*, 1985; Malajczuk *et al.*, 1987; Claridge *et al.*, 1992). Successful inoculations of *Eucalyptus* roots with spores of the genus *Mesophellia* from the faeces of potoroos and bettongs have been performed, with evidence that digestion is a necessary pre-treatment for the spores of some fungi (Lamont *et al.*, 1985; Claridge *et al.*, 1992). Additionally, it has been hypothesised that a co-evolutionary relationship between trees, fungi and bettongs may be dependent on fire (Taylor, 1991). Although there has been some debate on this hypothesis (Claridge, 1992; Taylor, 1992b), fire does stimulate the fruiting of some hypogean fungi (Chris Johnson, pers. comm.).



Bandicoots have a more varied diet than bettongs and potoroos. The southern brown bandicoot is an opportunistic forager, eating a wide range of invertebrates, plant material and fungi from both above and below ground, with seasonal variation in diet depending on what is available (Heinsohn, 1966; Quin, 1985). The eastern barred bandicoot is believed to have a very similar diet and ecology (Heinsohn, 1966), although there is apparently some niche separation on the basis of habitat preference. The southern brown bandicoot prefers denser vegetation, living in heathlands, sedgeland and open-forests, whereas the eastern barred bandicoot prefers grassy woodlands and pasture (Heinsohn, 1966; Rounsevell *et al.*, 1991).

No detailed ecological description of the digging habits of bandicoots has been published, although Heinsohn (1966) gives a brief anecdotal account. The eastern barred bandicoot was found to dig small conical holes which resemble the shape of the snout, from 1.3 to 15 cm deep. Heinsohn observed that one foraging southern brown bandicoot dug 21 holes in a 26 minute period. The holes ranged in diameter from 2.5 to 25 cm and ranged in depth from 1.3 to 7.6 cm. Heinsohn also observed that one southern brown bandicoot dug a hole 38 cm deep and 13 cm in diameter at ground level in sandy soil and noted that holes of various sizes were common in this substrate.

The short-beaked echidna is very widespread in virtually all vegetation types in Tasmania and may be found wherever there is an abundance of ants and termites, which are the main component of their diet, although other invertebrates are eaten (Augee, 1983; Smith *et al.*, 1989; Rounsevell *et al.*, 1991). Smith *et al.* (1989) gave a detailed account of echidna diggings on the New England Tablelands, NSW. The majority of diggings were conical pits and snout holes, usually with a raised rim and ranging in depth from 4-20 cm. Digging activity peaked in November, with 10.8 diggings ha<sup>-1</sup> month<sup>-1</sup>, with zero digging in June and July.

The common wombat is also extremely widespread in virtually every vegetation type in Tasmania, with the possible exception of rainforest (Rounsevell *et al.*, 1991). Wombats feed primarily on grass, but also eat sedges and roots of trees and shrubs. They dig burrows up to 20 m long for refuge (McIlroy, 1983). Burrow entrances can have a mound of excavated soil covering

several square metres. There is no published account of soil disturbance created whilst foraging, but I have observed shallow scrapes with uprooted grass tussocks associated with abundant wombat faeces in treeless *Poa* dominated vegetation. Such disturbance appears to be localised, but I have seen more widespread scratchings in subalpine woodland dominated by *Eucalyptus coccifera* and *E. gunnii*.

### *Mammal disturbance and rare plant species in Australia*

While the importance in Australia of mycophagous mammals for the ecology of trees has been mentioned, the possibility of soil disturbance by mammals creating a regeneration niche for plants has not been studied on this continent. There have been some suggestions that this may be the case, particularly for rare and endangered plant species. An endangered terrestrial orchid in Victoria, *Thelymitra epipactoides*, was found to regenerate only on open bare ground where there had been some kind of soil or community disturbance. Diggings by echidnas were common in the orchid's habitat and hypothesised to be of importance, although the colonisation of diggings was not directly studied (Calder *et al.*, 1989). The endangered herb *Lepidium hyssopifolium* is thought to require some kind of disturbance to regenerate, which may include animals scratching in litter (Cropper, 1987).

Several rare or endangered herbs, graminoids and shrubs in Tasmania have been observed colonising the bare soil on the edges of tracks and recently created road cuttings (e.g. *Lasiopetalum micranthum*, *Velleia paradoxa*, *Odixia achlaena*, *Odixia angusta*, *Gahnia rodwayi*, *Vittadinia cuneata*, *Helichrysum costatifructum*, *Lepidium pseudotasmanicum*). Given that these species utilise soil disturbance created by humans, it is of interest to examine whether this disturbance is an analogue of a more natural disturbance such as digging by small mammals.

Plant species can be categorised as 'rare' on the basis of a number of criteria, an elegant typology of which has been proposed by Rabinowitz (1981). Seven forms of rarity are recognised on the basis of large or small geographic range, wide or narrow habitat specificity and large or small local population size. Of the five of these categories that seem likely to occur

(Rabinowitz, 1981b), four are discussed here in the context of disturbance. The first involves species which are found over a wide geographic range in a number of habitats, but always in very low numbers. Although such species are common in nature, they have been neglected in conservation biology (Rabinowitz, 1981b; Grubb, 1986; McIntyre *et al.*, 1993). It has been suggested that some short-lived dicotyledonous species fit this category and persist in a grassland in Britain due to small-scale disturbances creating a regeneration niche (Grubb, 1986). Some work in grasslands in the United States dismissed this likelihood for similarly classified sparse grassland species (Rabinowitz & Rapp, 1985a; Rabinowitz & Rapp, 1985b; Rapp & Rabinowitz, 1985).

The second category involves species which have a small geographic range, narrow habitat specificity, but large local populations. The third category differs only in that populations are always small (i.e. rare species in every sense), and the fourth category includes species with a wide geographic range, a very specific habitat requirement, but usually large populations (i.e. habitat specialists). For all of these categories, the availability of appropriate disturbance mechanisms may be relevant. The first category has already been discussed. While species in the second category are sometimes geographic endemics that may be related to climatic refugia (Kirkpatrick & Brown, 1984), a restricted disturbance requirement may be another factor. Similarly, species in the third category may be thus distributed because of lack or loss of appropriate disturbance and species in the fourth category may be dependent on a *disturbance phenomenon* which is habitat specific.

### Questions asked in this thesis

This thesis has a particular focus on the ecology and regeneration requirements of rare and endangered plant species. However, there are potentially many questions to be asked about small-scale disturbance by mammals in Tasmania in relation to *many* plant species, not only the rare ones. Since so little is known, many of the questions are self-evident. For example:



- Q1 *Which rare plant species live in habitats where small-scale disturbance by mammals is also present? (Chapter 2).*
- Q2 *What physical and chemical changes to the soil are induced by digging? (Chapter 3).*
- Q3 *How common is digging in the landscape and at what times of the year does it occur? (Chapter 4).*
- Q4 *Do seedlings of plant species (including rare species) germinate and/or survive preferentially on ground disturbed by mammal digging compared with adjacent undisturbed ground? (Chapter 5).*
- Q5 *In a more general sense, do seedlings of plant species germinate and/or survive preferentially on mechanically disturbed ground per se? (Chapter 6).*

Many of the habitats where small mammals dig in Tasmania are woodlands (Rounsevell *et al.*, 1991) and the digging of some mammals is not random but is associated with trees (Taylor, 1992a; Claridge *et al.*, 1993a). In woodlands, the environment underneath trees can be very different from the inter-tree areas (Vetaas, 1992). Consequently, unlike the many grassland studies reviewed earlier, for small plants growing in woodlands in Tasmania, trees must be considered as a variable which may possibly influence spatial patterns in the understorey directly, or in conjunction with a spatial pattern in the distribution of small-scale disturbance. In this case:

- Q6 *At the micro-scale of a woodland, which is a mosaic of tree and inter-tree patches, are digging and understorey plant species random in the landscape or are they associated with sub-elements that can be related to tree influence? (Chapter 4).*

Fire is a common disturbance phenomenon in Tasmania vegetation, particularly in the habitats where digging is prevalent. Therefore:

- Q7 *Do the two disturbance phenomena, fire and mechanical soil disturbance, induce different germination and/or establishment responses from plants? Do they have a cumulative or interactive effect? (Chapter 6).*

Digging by mammals mixes soil and brings sub-surface soil to the surface. Given that digging has the potential to bring buried seed to the surface:

Q8 *How much seed of different species is in the soil and how deeply buried is it?* (Chapter 7).

Exotic species have been shown to invade native vegetation in Australia, particularly after disturbance (e.g. Hobbs & Atkins, 1988; Buchanan, 1989). Consequently:

Q9 *Is mechanical soil disturbance by mammals encouraging exotic species to displace native species?* (Chapter 8).

Finally, the results of the various studies can be synthesised to answer the following questions:

Q10 *Can a guild of species be recognised which is adapted to colonise mammal diggings and do these species have common attributes (i.e. strategies)?* (Chapter 9).

Q11 *Are some plant species rare because of a dependence on a specialised regeneration niche which involves animal disturbance?* (Chapter 9).

Q12 *How important is animal disturbance for plant species in Tasmania?* (Chapter 9).

## Chapter 2

### The Distribution of Native Mammal Digging in Relation to Rare Plant Species, and Study Site Descriptions.

#### Introduction

At the time of the start of this study, some general observations on animal disturbance in the habitats of rare plant species had been made, but a more comprehensive knowledge was not available. It was therefore necessary to gain an overall impression of the extent to which mechanical soil disturbance created by mammals and rare plant species co-occur, and of any environmental correlates. This overview made possible the selection of a number of species and sites for more detailed investigation. In this chapter, a summary is given of the extent to which small-scale disturbance by small mammals is present in the habitats of rare and endangered plant species. The sites and species which were selected for further study from this survey are described.

#### Methods

A survey was undertaken, which involved the collection of distribution records of rare plant species from the Tasmanian Herbarium and a number of individuals, followed by brief examination of the habitats after populations were located. It was not intended to be an exhaustive survey of all plant species considered to be rare, but to examine as many species as possible in a reasonably short period of time to identify suitable species and sites for more detailed study. Thus, the purpose of the survey was to locate spatial juxtapositions of rare species and diggings and no causal relationships were assumed at this stage. The habitats of 22 species were examined in the survey, all in eastern Tasmania, and these species were chosen simply because of the availability of good location records. The habitats of 18 more rare or endangered plant species were examined during the course of the entire project and all 40 species are reported on here, over a total of 73 populations.

The following were noted for each population (over areas of varying size): a general description of the vegetation; the geology; a general indication

of the abundance of digging within the proximity of individuals of the rare species (i.e. within several metres); and the identity of the diggers. Digging abundance was estimated visually as the percentage of ground covered by diggings; three categories were recognised: abundant =  $\geq 5\%$ ; moderate =  $\geq 1$  but  $< 5\%$ ; and sparse =  $< 1\%$ .

The identity of the animal species digging at any one site was determined, as far as possible, by the morphology of diggings and by sightings of animal species present. Echidna diggings are readily identified because they are usually associated with ant nests (Taylor, 1992a). Bandicoot diggings are conical when shallow, although less so when deeper, but always with the excavated soil accumulated in an elliptical mound on one side. Although eastern barred bandicoot diggings are reputedly shallower than those of the southern brown bandicoot (Heinsohn, 1966), I doubt that they are distinguishable in individual cases. Bettong diggings tend to be in the form of shallow craters with excavated soil spread around most sides. Some bettong diggings are possibly similar in appearance to bandicoot diggings. I have no knowledge on the morphology of potoroo diggings, but the juxtaposition of rare species and mammal diggings was not observed in the habitat where potoroos are reputed to live.

Plant nomenclature throughout this thesis follows Kirkpatrick *et al.* (1991) for native species and Buchanan *et al.* (1989) for exotic species. Species were identified using a variety of books and papers, using the latest available literature as far as possible.

## Survey Results and Discussion

The full information from the initial survey is presented in Appendix 1, along with information which was collected on other species during the course of the project. Digging by native mammals was evident in the habitats of 21 of the 40 species, although digging was sparse in the habitats of six out of the 21.

Geology is clearly an important factor in determining the frequency of digging. Digging is far more common in the habitats of rare species which are found on sedimentary substrates than in habitats on dolerite or basalt

(Table 2.1). Most of the rare species populations which were found on sedimentary substrates which did *not* have frequent digging were either in very small, isolated or altered remnants; or else the sites were prone to waterlogging (Table 2.1). Small and isolated remnants are probably unable to sustain populations of small native mammals. Highly altered remnants are possibly less likely to have the food resource to attract digging. Mammal digging does not appear to be a feature of waterlogged or creek-side habitats. Although no rare species were examined on granite in this survey, digging by bettongs and echidnas is common on the gravelly and sandy soils formed on this substrate. On all substrates, digging is often abundant in places where no rare species are present.

The finding of very little digging in the habitats of rare plant species on dolerite or basalt has important implications, since a considerable number of rare species are confined to these igneous geologies in eastern Tasmania (16 out of 40 in this survey). Doleritic and basaltic soils are generally more fertile than soils formed on sedimentary substrates and productivity tends to be greater as a consequence (Fensham, 1989; Fensham & Kirkpatrick, 1989). In grassy vegetation on fertile sites, a dense sward of rank grasses can have very few gaps and any gap creating mechanisms such as small-scale disturbance by mammals could be expected to be very important for the regeneration of plants.

Taylor (1992a) found that digging by Tasmanian bettongs was less common on dolerite than on sedimentary substrates and suggests that this may be related to mycorrhizal growth rates, which decrease with increasing fertility (Slankis, 1974). Taylor (1992a) also noted that digging activity could be influenced by how easy it is to dig in a given substrate. Sandy soils should be far easier to dig in than the soils which form on dolerite and basalt, which usually have a high clay content and can be extremely hard, particularly when dry. There has so far been no definitive test of the relative importance of the two hypotheses for the cause of less digging on dolerite, that is: fertility/food resource availability versus ease of digging. It appears that the phenomenon of less digging on dolerite also includes digging by bandicoots (see Chapter 4). Given that hypogean fungi are only a minor component of

the diet of bandicoots (Heinsohn, 1966; Quin, 1985), it seems likely that the ease of digging influences the abundance of diggings. There is some further evidence for this hypothesis, because the soil tends to have a coarser texture on dolerite in the places where digging is locally more common (e.g. the Flagstaff Gully population of *Velleia paradoxa*, the Chimney Pot Hill population of *Gahnia rodwayi* and the Kellevie Road population of *Odixia achlaena*, Appendix 1). Sheets of Quaternary wind-blown sand may be responsible for some of this variation in soils formed on dolerite bedrock, although this process has been documented at only a few sites in the lower Derwent Valley (Sigleo & Colhoun, 1982). However, it is relevant that digging on dolerite *does* occur, if only on a localised basis.

There is sufficient knowledge on the distributions of many of the rare plant species included in Appendix 1 to make some general conclusions. Rare species which probably grow *exclusively* in frequently dug habitats in Tasmania (without considering small remnants) include *Brunonia australis*, *Caladenia caudata*, *Lepidium hyssopifolium* and *Pultenaea humilis*. Species which occur *often* in frequently dug habitats, although not *exclusively*, include *Bertya rosmarinifolia*, *Glycine latrobeana*, *Gahnia rodwayi*, *Lepidium pseudotasmanicum*, *Odixia achlaena*, *Olearia ericoides*, *Olearia hookeri*, *Stenanthemum pimeleoides* and *Velleia paradoxa*.

This survey was not intended to be exhaustive. The design does not allow the making of conclusions on the spatial association of diggings and rare species in the landscape, nor on the fidelity of rare plant species to habitats with digging disturbance, nor on causal relationships. However, this general survey suggests that there is not a strong spatial association in the landscape between diggings and rare species. The abundance of diggings appears to be strongly related to geology and the highest concentrations of rare species in eastern Tasmania are on geological substrates where digging is uncommon. This picture may have been very different prior to European occupation of Tasmania as digging patterns, particularly by humans, have changed considerably.



**Table 2.1** Summary of the survey of the digging by native mammals in the habitats of populations of rare and endangered plant species. The number of populations and number of species are shown in life form categories and in digging frequency categories.

Geology	Life form <sup>1</sup>			Digging frequency <sup>2</sup>					
	F	G	Sh	A	M	Sp	N	W	Sm
alluvial gravels & sands (Tertiary & Quaternary)	6 (5)	1 (1)	3 (3)	8 (7)	1 (1)	0	2 (2)	2 (2)	
Jurassic dolerite	15 (12)	5 (3)	15 (8)	1 (1)	5 (4)	8 (7)	20 (15)		1 (1)
Permian mudstone & siltstone	4 (3)	0	1 (1)	3 (3)	0	0	2 (1)		2 (1)
Quaternary alluvium	2 (2)	0	0	0	0	0	2 (2)	1 (1)	1 (1)
Quaternary windblown sands	2 (2)	0	0	0	0	0	2 (2)		
Tertiary basalt	3 (3)	0	0	0	0	0	3 (3)		
Triassic sandstone & mudstone	11 (6)	3 (2)	1 (1)	4 (3)	0	0	11 (8)	1 (1)	7 (5)
unknown	0	1 (1)	0	0	0	0	1 (1)	1 (1)	1 (1)
Totals	43 (22)	10 (5)	20 (13)	16 (11)	6 (5)	8 (7)	43 (27)	5 (4)	12 (5)

Number of species is indicated in brackets below the number of populations.

<sup>1</sup> F = forb; G = grass or graminoid; Sh = shrub.

<sup>2</sup> A = abundant, M = moderate; Sp = sparse; N = none; W = number of populations with no digging which are in water-logged habitats; Sm = number of populations with no digging which are in very small, isolated or highly altered remnants.

## Descriptions of rare species and study sites

The second stage of study, after the initial survey, was the setting up of permanent plots to monitor seedling emergence and survival on natural diggings. This was carried out for nearly all those rare species from the initial survey — 11 in all over nine study sites — which were identified as growing in the vicinity of such diggings. An exception was *Brunonia australis* at Westwood, for which a single sample of seedling emergence was undertaken.

Where seedling emergence was observed, the monitoring of digging rates and the examination of soil seed banks was generally undertaken. At some sites, such as Chimney Pot Hill, Kellevie Road and Powranna, no further studies were undertaken because of the lack of observable seedling germination of the target species on or near diggings.

The study sites for simulated digging experiments were chosen because little or no natural digging was occurring at those sites, but it was suspected that the rare species present would respond to mechanical soil disturbance (e.g. *Lepidium hyssopifolium* at Bagdad, *L. pseudotasmanicum* at Rosny Point, *Lasiopetalum micranthum* at the Old Coach Road and *Vittadinia muelleri* and *Stackhousia gunnii* at the Tunbridge Tier Road). Laboratory experiments were set up to test the disturbance requirements of two species for which fire was suspected to be the important agent of disturbance: *Odixia achlaena* and *L. micranthum*.

The Bellerive study site was singled out for other extra studies because of its convenient location. These studies included experiments with weeds, examination of physical and chemical soil properties and the study of spatial patterns of trees, understorey and diggings. Soil temperatures were also measured at the Old Coach Road because of the results of other data collected on *L. micranthum*.

The complete studies undertaken at each site are summarised in Table 2.2 and study site locations are indicated in Fig. 2.1. Descriptions of the rare species and study sites which were the subject of study beyond the initial survey are given below.



Table 2.2 Study sites.

Study site <sup>1</sup>	Rare plant species & status <sup>2</sup>	Digging mammals	Studies <sup>3</sup>
Annandale	<i>Lepidium hyssopifolium</i> E <i>Lepidium pseudotasmanicum</i> R (T)	bettong, bandicoot	D, Se, Sb
Bagdad	<i>Lepidium hyssopifolium</i> E	none	E
Bellerive	<i>Caladenia caudata</i> V <i>Velleia paradoxa</i> V (T)	bandicoot (2 spp.)	Sl, D, P, Se, Sb, W
Chimney Pot Hill	<i>Gahnia rodwayi</i> R <i>Olearia ericoides</i> R	bandicoot, echidna	Se
Dukes Marshes	<i>Euphrasia scabra</i> V	rabbit, ? wombat	D, Se
East Risdon	<i>Olearia hookeri</i> R	bettong, bandicoot	Se, Sb
Hospital Creek	<i>Odixia achlaena</i> R <i>Gahnia rodwayi</i> R	bettong	D, Se, Sb, E
Kellevie Road	<i>Odixia achlaena</i> R	bettong	Se
Old Coach Road	<i>Lasiopetalum micranthum</i> V	echidna, bandicoot	Sl, D, Se, E, Sb
Powranna	<i>Glycine latrobeana</i> R	bettong	Se
Rosny Point	<i>Lepidium pseudotasmanicum</i> R (T)	none	E
Tunbridge Tier Rd	<i>Stackhousia gunnii</i> E <i>Vittadinia muelleri</i> V (T)	echidna	E
Westwood	<i>Brunonia australis</i> V (T)	bettong	Se

<sup>1</sup> Full locality information given in Appendix 1.<sup>2</sup> National conservation status, or T = status applicable to Tasmania only (Kirkpatrick et al., 1991): R = rare, V = vulnerable, E = endangered.<sup>3</sup> Studies undertaken at each study site: Sl = soil physical and/or chemical measurements (Chapter 3); D = monitoring of natural digging rates (Chapter 4); P = spatial patterns of diggings and vegetation (Chapter 4); Se = seedling emergence & establishment on natural diggings (Chapter 5); E = disturbance experiments (Chapter 6); Sb = soil seedbanks (Chapter 7); W = experimental weed manipulation (Chapter 8).

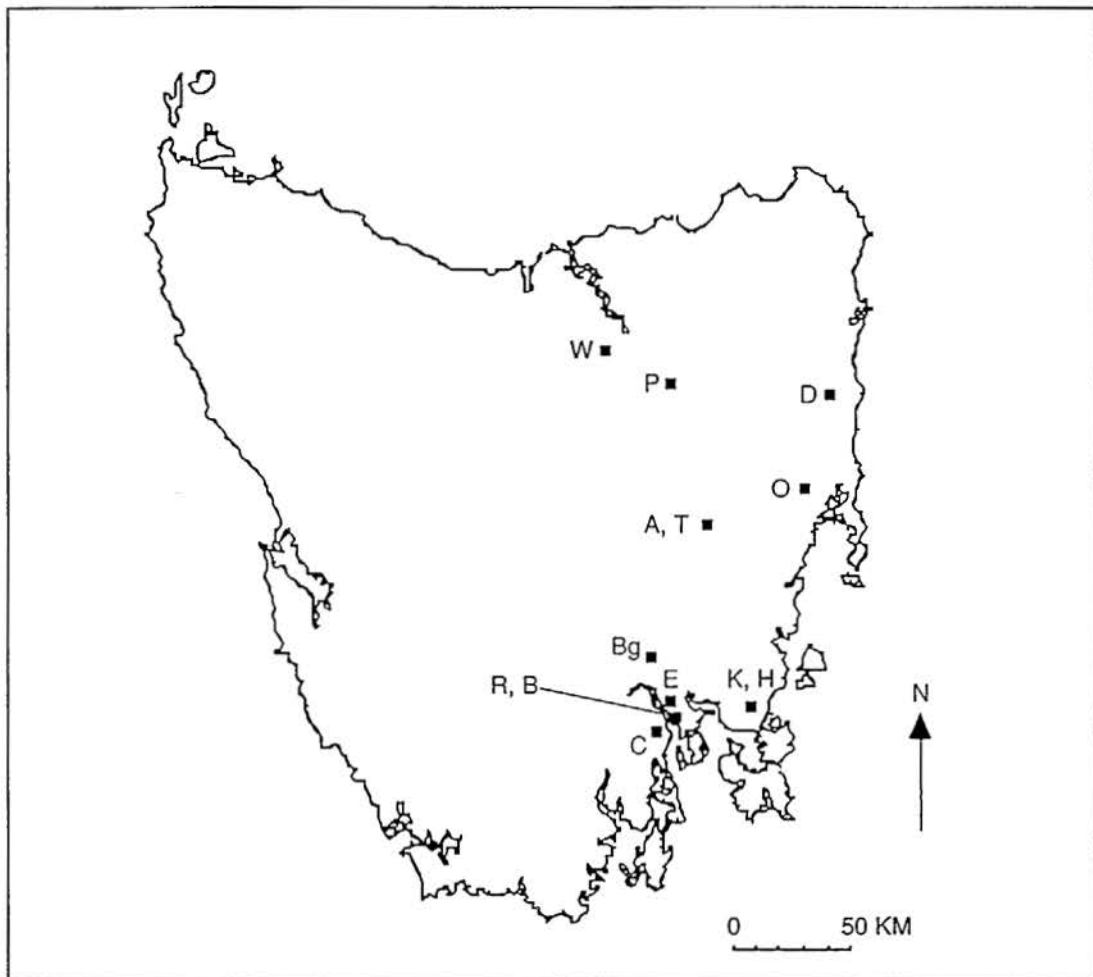


Fig. 2.1 Study sites. A = Annandale; B = Bellerive; Bg = Bagdad; C = Chimney Pot Hill; D = Dukes Marshes; E = East Risdon; H = Hospital Creek; K = Kellevie Road; O = Old Coach Road; R = Rosny Point; T = Tunbridge Tier Road; W = Westwood; P = Powranna.

### *Rare Species Descriptions*

*Brunonia australis* (Brunoniaceae) is a perennial forb with clusters of small rosettes of leaves which may die back to rootstock in summer. Each rosette produces a single inflorescence up to 30 cm tall in December. Although quite common on the mainland of Australia, it has a very restricted distribution in Tasmania. It may be found only in the few remaining remnants of grassy open-forests and woodlands on alluvial gravels and sands in the northern midlands, where it may be locally common.

*Caladenia caudata* (Orchidaceae) is a perennial, terrestrial forb which produces a single leaf in autumn or early winter and one or two flowers on a single stem up to 20 cm tall in late August or early September. Individuals die back completely to rootstock in summer and may only be identified whilst in flower. This species usually grows on sandy soils in woodlands and occurs sporadically in small populations in northern and eastern sub-coastal or coastal situations.

*Euphrasia scabra* (Scrophulariaceae) is an annual forb with brittle stems which grows up to 50 cm tall. It germinates in August, flowers from January through to March and disperses its tiny seeds till May. It has had a massive decline in abundance throughout its range in the last 80 years and is now extremely rare. In Tasmania it is currently known from only one large population at Dukes Marshes (Fig. 2.1) and another adjacent very small population. While it was formerly known in both dry and wet grassy habitats, it is now known in only wet grassy marshes in both Tasmania and Victoria.

*Gahnia rodwayi* (Cyperaceae) is a small perennial sedge which forms dense mats up to 50 cm in diameter and 15 cm high. It is endemic to Tasmania and occurs sporadically in both grassy and shrubby woodlands in eastern Tasmania, mainly on dolerite.

*Glycine latrobeana* (Fabaceae) is a small perennial forb which dies back to rootstock in April, resprouts in September, flowers in November and disperses its seed in January. It grows sporadically in grassy open-forests and woodlands in the midlands of Tasmania, mostly in very small populations.

*Lasiopetalum micranthum* (Sterculiaceae) is a prostrate shrub which spreads out over areas up to 70 cm in diameter. It flowers in September and

October and disperses its relatively large, hard seeds in December. It will resprout from rootstock after burning. It is endemic to a relatively small area in central-eastern Tasmania and is found only on very dry, rocky sites in grassy woodlands on dolerite.

*Lepidium hyssopifolium* (Brassicaceae) is a perennial forb with multiple wiry stems up to 50 cm tall. It flowers profusely and disperses its small seeds throughout most of the year, with a slight lull in August. It is now known to occur over a large geographic range in eastern Tasmania, although it is mostly found in very small, isolated populations on very disturbed sites, frequently underneath exotic trees on road verges. The Annandale population is the only one known in reasonably intact native vegetation. At this site it is evident that *L. hyssopifolium* is very sensitive to grazing because it is restricted to a small woodland remnant which is used infrequently for shelter for sheep, while it is totally absent from neighbouring woodland areas which are more intensively grazed. *Lepidium hyssopifolium* appears to avoid competition with other herbaceous species by growing in the bare area underneath a wide range of exotic and native tree species. It is rarely found in dense swards of grasses and forbs. At Annandale it grows mainly underneath *Acacia dealbata* but also under *Eucalyptus amygdalina*.

*Lepidium pseudotasmanicum* (Brassicaceae) is a wiry perennial forb which grows up to 70 cm tall. It is very similar in appearance to *L. hyssopifolium*, with which it may frequently be found growing in Tasmania. While the morphological differences between these two species are very subtle, they differ markedly in phenology. *Lepidium pseudotasmanicum* ceases flowering at the end of June, drops its leaves and dies back to rootstock. In October, new stems resprout from rootstock and produce seed prolifically until June in the following year. *Lepidium hyssopifolium* does not have this deciduous habit. Populations of *L. pseudotasmanicum* are somewhat more abundant than those of *L. hyssopifolium*, although they are mostly in habitats which are just as small, frequently disturbed and weedy. *Lepidium pseudotasmanicum* grows under *Eucalyptus amygdalina*, *E. viminalis*, *E. globulus*, *Allocasuarina verticillata*, *Acacia dealbata* and *A. mearnsii* in intact native grassy forests and woodlands, and under a wide range of exotic conifers and broad-leaved tree species on

road verges.

*Odixia achlaena* (Asteraceae) is an erect and spindly shrub which grows up to 2 m tall. It flowers in November and December and disperses its numerous small seeds, which have no pappus, in February. It is sensitive to burning, after which it does not resprout, although it appears dependent on fire as a stimulus to regenerate from seed. It is endemic to a small region in south-eastern Tasmania, where it grows exclusively on dolerite in drier grassy or shrubby eucalypt woodlands and open-forests. Despite its very limited geographic range, it can be extremely abundant in the places where it does occur.

*Olearia ericoides* (Asteraceae) is a small shrub which grows up to 1 m tall and flowers in December. It is reasonably widespread in south-east Tasmania, but populations are always small and sporadic. It grows in grassy and shrubby drier eucalypt open-forests and woodlands.

*Olearia hookeri* (Asteraceae) is a slender, wiry shrub which grows up to 1.5 m tall. It flowers in October and November and disperses seed in the summer months. It is known from only a few localities in eastern Tasmania, where it can be locally abundant. It grows on very dry and rocky north-facing slopes in woodlands which have an understorey of grasses and shrubs.

*Stackhousia gunnii* (Stackhousiaceae) is a small perennial forb which grows up to 20 cm tall. It flowers from late October until early November, disperses seed until early January and dies back to rootstock in late summer. It is endemic to a very small and extremely dry area in the vicinity of Tunbridge where it grows in grasslands and grassy woodlands on dolerite.

*Velleia paradoxa* (Goodeniaceae) is a small perennial forb which has clusters of leafy rosettes and flowering stems up to 30 cm tall. It flowers in December and disperses large, flat seeds in January and February. Many individuals have died back to sturdy rootstock by the end of summer and resprouting of new leaves occurs during winter. *Velleia paradoxa* is very rare in Tasmania and only a few populations, many of which are on roadsides, have been recorded in recent years. The study site at Bellerive has the largest of only four populations which are known to occur in vegetation remnants of more than a few metres width. *Velleia paradoxa* grows in grassy woodland on

dry sites on a variety of geologies.

*Vittadinia muelleri* (Asteraceae) is a perennial forb which grows to 15 cm tall. It has a sporadic distribution in the drier areas of the midlands and Derwent Valley, where it grows in grassy woodlands and grasslands on fertile soils.

### *Study Site Descriptions*

A number of environmental parameters are summarised for all study sites in Table 2.3. The climate data for each study site are based on the nearest or most appropriate weather station with respect to altitude and horizontal distance. The temperature data are adjusted for altitude difference between the study site and the weather station, by using the environmental lapse rates of Nunez (1988).

The Annandale property is situated 7 km north-west of Tunbridge in the midlands of Tasmania. The study site is located in a small fenced-off remnant of grassy woodland of 4 ha which is surrounded on two sides by intensively grazed and highly altered woodland and on the other two sides by exotic pasture. The site is quite flat and the sandy soil is formed on ferruginous and siliceous alluvium. *Eucalyptus amygdalina* and *Acacia dealbata* are the dominant trees and the areas beneath tree canopies are heavily invaded by exotic annual grasses and forbs, with *Lepidium* spp. being the only predominant native species. The vegetation in the inter-canopy gaps is dominated by *Themeda triandra*, *Lomandra longifolia* and *Stipa* spp. *Lepidium hyssopifolium* and *L. pseudotasmanicum* are both quite common under tree canopies throughout the fenced-off remnant, although the two species are mostly segregated.

The Bagdad study site is located on a 6 m wide road verge on the Midlands Highway. The site is quite flat and the loamy soil is formed on Quaternary alluvium. The vegetation is a dense sward of exotic grasses and forbs made up of *Agrostis capillaris*, *Plantago lanceolata*, *Trifolium subterraneum*, *Holcus lanatus* and *Dactylis glomerata*. A few *Lepidium hyssopifolium* plants grow nearby under *Cupressus* sp. in a paddock, but only one adult plant was observed in the study site.



The Bellerive study site is located in the eastern suburbs of Hobart, in an 82 ha suburban bush remnant known as the Waverley Flora Park. It straddles two geological substrates which have either a very heavy and shallow clay loam soil on Jurassic dolerite or a very sandy and shallow soil on Triassic sandstone. The vegetation is a grassy woodland dominated by *Eucalyptus viminalis*, *E. amygdalina*, *Allocasuarina verticillata* and *A. littoralis*, with an understorey dominated by *Themeda triandra*, *Stipa* spp. and *Poa* spp. The sandy soils are heavily invaded by *Briza maxima* and *Aira* spp. *Caladenia caudata* and *Velleia paradoxa* are mainly restricted to one sandstone area of approximately 2 ha. The former species is patchily scattered over this area, with less than 200 flowering individuals. The latter species is similarly scattered, but is more abundant.

The Chimney Pot Hill study site is located in a water reservoir reserve on the outskirts of western Hobart. The sandy clay loam soil is formed on Jurassic dolerite and is rocky and shallow. The vegetation is a woodland of *Eucalyptus pulchella*, with a low understorey dominated by sedges and shrubs. There are no exotic species. *Olearia ericoides* is sparsely scattered through the area, while *Gahnia rodwayi* is somewhat more common.

The Dukes Marshes study site is located 15 km south of St Marys in north-east Tasmania and is surrounded by forest which is managed for timber harvesting. The soil is formed on Quaternary alluvium, is rich in organic matter and can be waterlogged in the wetter winter months. The grassy vegetation is largely treeless as a result of clearing, although it was formerly a woodland of *Eucalyptus rodwayi*. The understorey is a dense, short turf dominated by native grasses and forbs, with some exotic species. The area had been grazed by cattle in the past. *Euphrasia scabra* is abundant throughout an area of 6 ha, with a population of flowering individuals numbering in the thousands in any one year.

The East Risdon study site it is located in the East Risdon Nature Reserve on the outskirts of Hobart. The soil, which is formed on Permian siltstone, is a shallow silty loam and is full of coarse angular gravel. The vegetation is a low shrubby woodland dominated by mallee form *Eucalyptus amygdalina*, on the edge of a hybrid zone of *E. amygdalina* and *E. risdonii*. The

understorey is extremely sparse with 95% bare soil. The area is grazed by rabbits, but weeds are uncommon. *Olearia hookeri* is reasonably abundant on the north facing dry slopes, in an area of 9 ha.

The Hospital Creek study site is located in south-east Tasmania, 3 km north of Kellevie. The sandy clay loam soil is formed on Jurassic dolerite and is rocky and shallow. The vegetation is a shrubby woodland dominated by *Eucalyptus pulchella*. Common shrubs in the understorey include *Odixia achlaena*, *Acacia genistifolia*, *Leptospermum scoparium* and *Dodonaea filiformis*; while grass and forb species form a sparse ground layer. *Gahnia rodwayi* is sparsely scattered in the study site.

The Kellevie Road study site is located 3.5 km from the Hospital Creek study site and has the same geology and rocky soil. The vegetation is a grassy woodland dominated by *Eucalyptus pulchella*, with *Poa* spp. dominating the ground layer. *Odixia achlaena* is abundant and forms a shrub layer with *Acacia dealbata*.

The Old Coach Road study site is located 12 km north of Cranbrook in central-eastern Tasmania in grassy woodland. The soil is a very shallow and very rocky clay loam formed on Jurassic dolerite. *Eucalyptus amygdalina* is the main tree species, but *E. viminalis*, *E. globulus* and *Acacia mearnsii* are also present. The ground layer is dominated by *Poa rodwayi*, *Lepidosperma laterale*, *L. inops* and *Themeda triandra*. *Lepidosperma laterale* forms intermittent dense patches, and is delimited by sharp boundaries from the generally shorter understorey. The area is intermittently grazed by sheep and more continuously by marsupial herbivores. *Lasiopetalum micranthum* is common over an area of 3 ha.

The Powranna study site is located 1.5 km west of the Midlands Highway at Powranna in the northern midlands. The sandy soil is formed on Quaternary alluvial gravels and sands. The vegetation is a grassy woodland dominated by *Eucalyptus pauciflora*. Beneath a shrubby layer of *Acacia dealbata*, the most abundant species in the ground layer are *Ehrharta stipoides*, *Stipa* spp. and *Pteridium esculentum*. Exotic annual grasses and *Hypochoeris glabra* are also common and the area is quite heavily grazed by sheep. *Glycine latrobeana* is restricted to a small area of less than 200 m<sup>2</sup> and the population numbers less



than 60 individuals. *Brunonia australis* is more widespread but patchily scattered.

The Rosny Point study site is located 30 m from the edge of the Derwent River in the eastern suburbs of Hobart, in a coastal remnant of semi-natural vegetation which is 2 km long and 50 to 100 m wide. The soil is a clay loam formed on Jurassic dolerite. The vegetation is an *Allocasuarina verticillata* low forest, with an understorey of grasses and forbs which has a large exotic component. *Lepidium pseudotasmanicum* grows mainly along the edge of an asphalt footpath which was constructed in the 1980s, and does not occur in the more undisturbed vegetation.

The Tunbridge Tier Road study site is located 3 km north-west of Tunbridge on a road verge which is 15 m wide, with exotic pasture beyond the fence. The soil is a shallow clay loam formed on Jurassic dolerite. The vegetation is a grassy woodland with very scattered trees of *Eucalyptus pauciflora*. The most visible species in the ground layer are *Themeda triandra*, *Helichrysum apiculatum*, *Schoenus apogon* and *Danthonia* spp. There is very little cover of exotic species, although *Hypochoeris radicata* and *Trifolium* spp. are common. *Stackhousia gunnii* is sparsely scattered on the road verge, but *Vittadinia muelleri* is abundant.

The Westwood study site is located 4 km north of Westwood in northern Tasmania in a relatively large and continuous remnant of grassy woodland. The sandy soil is formed on Tertiary alluvial sands. The dominant trees are *Eucalyptus amygdalina* and *E. viminalis* and the understorey is dominated by native grasses and forbs, with very few exotics. The area is not fenced off from exotic pasture and it is grazed by sheep and cattle. *Brunonia australis* is relatively abundant throughout the study site, although never dominant.

Table 2.3 Environmental parameters of study sites.

Study site	Altitude (m)	Aspect	Slope	Rainfall (mm) <sup>1</sup>			Air Temperature (°C) <sup>2</sup>			
				Annual	Wettest	Driest	Max.		Min.	
				Total	month	month	Feb	Jul	Feb	Jul
Annandale	240	-	0	457	45 Oct	15 Feb	24.5	10.8	8.8	0.2
Bagdad	150	-	0	592	56 Oct	31 Jan	23.1	10.0	10.8	1.4
Bellerive	120	S-SW	5-8	571	52 Oct	30 Feb	21.1	11.0	11.6	4.1
Chimney Pot Hill	360	NW	24	963	104 Jul	40 Jan	19.4	9.3	10.8	3.3
Dukes Marshes	500	-	0	~900	-	-	20.4	8.7	8.0	0.6
East Risdon	70	N	24	586	49 Oct	32 Feb	21.4	11.3	11.8	4.3
Hospital Creek	180	N	22	871	73 Dec	42 Feb	21.2	12.0	11.1	2.4
Kellevie Road	130	NE-SE	7-24	871	73 Dec	42 Feb	21.6	12.4	11.3	2.6
Old Coach Road	280	E	6-15	~700	-	-	19.5	11.9	11.7	5.0
Powranna	180	SE	7	668	73 Jul	31 Feb	23.0	10.6	10.2	2.2
Rosny Point	5	SE	10	571	52 Oct	30 Feb	21.9	11.8	12.1	4.6
Tunbridge Tier Rd	240	NW	2	457	45 Oct	15 Feb	24.5	10.8	8.8	0.2
Westwood	150	-	0	818	105 Jul	31 Jan	23.2	10.8	10.3	2.3

<sup>1</sup> Rainfall values are long-term medians.<sup>2</sup> Temperatures are mean daily maxima and minima for February and July, which are generally the warmest and coldest months respectively.

## Chapter 3

# The Effects of Digging on the Properties of Surface Soil

### Introduction

Digging mammals bring sub-surface soil to the surface, creating bare patches of ground and a landscape covered in holes. This process has the potential to generate heterogeneity in the microsite conditions available for the germination and establishment of plant seedlings. This chapter describes the physical and chemical changes to near-surface soil caused by bandicoot digging at Bellerive. The effects of digging on soil moisture and the quantities of some key soil nutrients are described. The effects of digging on soil temperatures at or near the surface are also described for bandicoot diggings at Bellerive and experimental soil disturbances at the Old Coach Road.

### Methods

#### *Bandicoot hole depth and disturbance area*

The relationship between the depth of bandicoot holes and the total disturbed area of the holes plus excavated soil was determined by measuring the depth and areas of 41 subjectively selected bandicoot disturbances. All disturbances were recently formed and clearly delineated.

#### *Soil moisture*

Soil moisture measurements were made at the Bellerive study site using a TRASE soil moisture measuring instrument (Soilmoisture Equipment Corp.), which operates by time domain reflectometry. The instrument gives the average volumetric soil moisture content over the length of the metal probes, expressed as a percentage. The 15 cm probes were pushed vertically into the soil. Sampling was performed on 9 April, 1992. The soil was moist, with 19.2 mm of rain recorded in the 3 days before this date, although no rainfall was recorded in the 30 hours immediately prior to sampling. Eighteen mounds of soil excavated by bandicoots were subjectively selected for

sampling. All the soil mounds were quite new, had an area of at least 400 cm<sup>2</sup> and were located on sandy soils on sandstone. The soil probes were regularly spaced on the soil mounds and in adjacent undisturbed control areas to provide three samples for each treatment (Fig. 3.1a). The control samples were randomly allocated to one side or the other of the mound by the toss of a coin. As far as practicable, control and mound samples were taken equidistant from the nearest or most influential tree. It was noted whether or not the samples were directly under the canopy of a tree.

### *Soil nutrients*

Soil samples were collected from the sandstone part of the Bellerive study site on 25 May, 1992. A total of 27.4 mm of rainfall was recorded in the 4 weeks up to and including the day of sampling, with none falling in the last 12 days of this period.

Samples were taken from 24 subjectively selected bandicoot mounds, which were all relatively recently formed from holes ranging in depth from 7-35 cm. Three sub-samples of soil were collected from each mound where possible (see below) and three from an adjacent undisturbed area. The three sub-samples were bulked within each treatment. The spatial arrangement of samples was similar to Fig. 3.1a, with the following exceptions: the distance between control and mound sampling points was 30 cm, or greater if necessary for larger mounds; and the three sub-samples were closer together and nearer the top of the mound.

Most of the soil sub-samples were 3 cm deep and were collected by scooping soil out of a plastic cylinder, 4.8 cm in diameter, which was pushed into the soil. Only excavated soil was collected from mounds, that is, soil above the original surface (Fig. 3.1b). The 18 largest mounds were greater than 3 cm high, but the 6 smallest mounds had excavated soil which was less than 3 cm deep. For these smaller mounds, as much mound soil as possible was collected as a single sample (the three control sub-samples were collected in the usual way). For all samples, care was taken to not include surface litter, or buried litter in the case of mound samples.

The depth of the hole from which each mound was formed was

measured and the mound was classified as either less than or greater than two months old.

All samples were weighed and then dried in an oven at 105°C for one week. The oven dry samples were weighed again to determine moisture content and then sieved through a 2 x 2 mm mesh. The sieved samples were analysed for organic content, total phosphorus and total nitrogen. The relevance of *total* nitrogen and phosphorus for plant growth is questionable: *available* nitrogen and phosphorus are probably more meaningful measures. However, total nitrogen and phosphorus are easily determined and provide relative measures of nutrient availability, which is all that is required in this study. Organic content was determined by loss on ignition: 1-2 g samples were weighed, heated to 550°C for 1 hr. and weighed again (Dean, 1974). Total phosphorus was determined by spectrophotometry on a vanadomolybdophosphoric colour reaction after digestion in perchloric acid. Total nitrogen was determined by the Kjeldahl method. For economy, only 24 (12 pairs) of the 48 samples were analysed for phosphorus and nitrogen. The subset of 12 pairs were selected by a stratified random method to cover the range of hole depths from which the sampled mounds were formed, using stratum units of 5 cm of hole depth.

### *Soil temperatures*

Data were collected at the Bellerive and the Old Coach Road study sites. Soil temperatures were measured with a thermocouple on areas receiving full sunlight. Temperatures for each control/digging mound pair were measured consecutively, to minimise differences due to changes in ambient air temperature. Five temperature measurements were taken at predetermined cross-points on a 5 cm grid within a 40 x 40 cm quadrat. The cover of litter, bare soil, rock and live plants was estimated, using the 5 cm grid as a guide.

At the Old Coach Road, soil temperature measurements were taken from simulated digging disturbances and adjacent control plots arranged along a short transect (see Chapter 6). The measurements were taken on 20 February, 1992, on a day with sparse cloud cover. Measurements were made at the surface and at 10 mm depth. Two of the 5 sample points in the disturbed

plots were on a shallow depression formed as a result of excavated soil (see Fig. 6.1, Chapter 6).

At Bellerive on sandstone, temperatures were measured at 5 mm soil depth on bandicoot mounds and adjacent control quadrats. Temperatures were not measured in plots while they were shaded by trees. Therefore, at any time of day and year, only a subset of the 20 pairs of quadrats could be sampled. Data are presented from one trial performed on the 10 March, 1992, with 8 pairs of quadrats. On the digging disturbances, the sampling mimicked the regular grid pattern as far as possible, although if the usual point was not over the excavated soil mound, the measurement was subjectively relocated to another grid cross-point (see methods in Chapter 5 for details on these quadrats).

On the same day at Bellerive, a small number of subjectively located soil temperature measurements were made at 5 mm depth on either side of a recent fire boundary on dolerite.

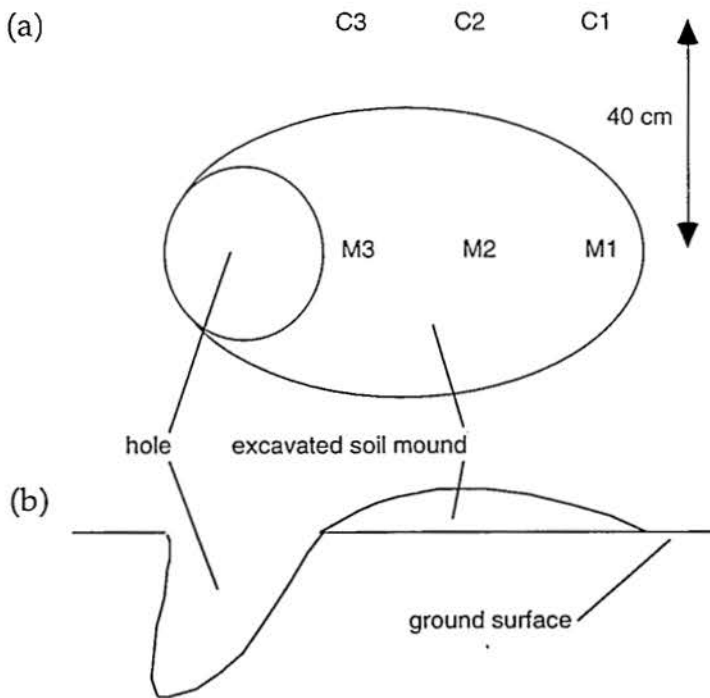
#### *Data analysis*

The field measured soil moisture data were log transformed and tested using analysis of variance for the effects of the three positions on digging mounds (Fig. 3.1a) and tree canopy, with the three control measurements being treated as sub-samples. Because of the unbalanced nature of the sampling, analysis was performed using the procedure GLM in SAS (SAS, 1988b).

Soil moisture content, organic content, total phosphorus and total nitrogen of the collected soil samples were tested for differences between control and mound quadrats by the paired sign-test. Correlations between variables were tested by Spearman rank-order correlation. The depths of the holes from which the mounds were formed and the control quadrat's nutrient status were used as predictors in stepwise multiple regressions, where the dependent variables were the mound moisture, organic content, phosphorus and nitrogen. To test for the effect of mound age on the organic content of mounds, an analysis of covariance was performed using hole depth and the organic content of control plots as covariates. The soil moisture, organic and phosphorus data were log transformed in all analyses.



The soil temperature data were tested by analysis of variance for differences between controls and disturbances, allowing for sub-sampling by specifying the block  $\times$  treatment interaction as an error term (block = a pair of control and digging plots; treatment = control or digging mound). The relationship between bare soil percentage and soil temperatures was tested by Spearman rank-order correlation on the mean of the sub-samples from each treatment.



**Figs 3.1** (a) A plan of a bandicoot digging, showing the arrangement of soil moisture measurements on soil mounds (M1, M2, M3) and control areas (C1, C2, C3), and the distance between the mound and control measuring points (e.g. C1 and M1.) (b) A profile of a bandicoot hole and excavated soil mound.

## Results

### *Bandicoot hole depth and disturbance area*

A log-linear regression best describes the relationship between hole depth and digging area ( $R^2=0.89$ ,  $n=41$ ,  $P=0.0001$ ,  $\log \text{ area} = 1.982 + \log \text{ depth}$  1.656; Fig. 3.2).

### *Soil moisture*

Volumetric soil moisture was 28.1% lower in the centre of the digging mounds than on the sides near the holes ( $P=0.03$ ), but there was no significant difference between the centres and the edges furthest from the holes ( $P=0.2$ ). The centres of the mounds had 31.3% less moisture than the control samples ( $P=0.004$ ). However, there were no significant differences between control samples and either of the other two mound locations (Fig. 3.3). Tree canopy cover reduced soil moisture by 32.9% compared with areas not under canopies ( $P=0.024$ ), with this effect operating across all control and mound samples (canopy  $\times$  control/mound interaction,  $P=0.35$ ; Fig. 3.3; Table 3.1).

### *Soil nutrients*

In the collected soil samples, moisture, organic content, total phosphorus and total nitrogen were all in greater abundance in control samples compared with digging mound samples (paired sign-test: organic content and moisture,  $n=24$ ,  $P<0.0001$ ; phosphorus and nitrogen,  $n=12$ ,  $P<0.001$ ). In the control soil samples, all variables were significantly correlated with each other, with the exception of nitrogen and phosphorus. One outlying phosphorus sample was removed in these tests (Table 3.2). In the digging mound samples, organic content was significantly correlated with phosphorus and nitrogen, but all other tests were not significant (Table 3.2).

Stepwise multiple regressions indicated that deeper holes produced mounds with lower organic content, phosphorus and nitrogen than shallower holes (organic:  $R^2=0.55$ ,  $n=24$ , hole depth  $P<0.0001$ ; phosphorus:  $R^2=0.58$ ,  $n=12$ , hole depth  $P=0.004$ ; nitrogen:  $R^2=0.39$ ,  $n=12$ , hole depth  $P=0.03$ ; Fig. 3.4). The same multiple regressions found that the organic content of the adjacent

control samples had good explanatory power for the organic content of mound soils ( $P=0.009$ ), but the controls had no explanatory power for phosphorus and nitrogen. Therefore, the nutrient status near the surface of mound soils is not only a function of the depth of the holes from which they were formed, but for organic content at least, is also a function of background spatial variation.

The analysis of covariance found no effect of mound age on the organic content of mounds ( $F_{1,20}=0.66$ ,  $P=0.4$ ), after partitioning for variation in the covariates of hole depth and control organic content ( $F_{2,20}=10.84$ ,  $P=0.001$ ).

The stepwise multiple regression for moisture found that hole depth had no explanatory power for the moisture status of mounds, although the moisture status of adjacent control plots did ( $R^2=0.37$ ,  $n=24$ ,  $P=0.001$ ; Fig. 3.5). The back-transformed means indicated that the gravimetric moisture content of the control samples was 2.0 times greater than in the mound samples at 12.4% and 6.2% respectively.

### *Soil temperatures*

The soil temperatures at 5 mm depth at Bellerive were on average 8.9°C higher on the digging mounds than in the control plots ( $F_{1,7}=66.7$ ,  $P=0.0001$ ; Fig. 3.6). At the Old Coach Road study site, soil temperatures were on average 10.8°C and 11.4°C warmer on the simulated digging mounds than in the control plots, at 10 mm depth and the surface respectively (Fig. 3.6). In the depressions formed by the soil disturbances, mean temperatures were only 2.2°C warmer than in the control plots at 10 mm depth and 3.7°C warmer at the surface (10 mm depth:  $F_{2,8}=96.58$ ,  $P=0.0001$ ; surface:  $F_{2,20}=33.05$ ,  $P=0.0001$ ; Fig. 3.6). Shade air temperature changed from 31.1°C at 1545 hours to 29.1°C during the 1 h taken for the measurements at Bellerive and declined from 26°C at 1310 hours to 25°C during 2 h at the Old Coach Road.

The soil temperatures were significantly correlated with the percentage of exposed bare soil, over the range of values found in both control and mound plots at both sites (Bellerive: Spearman  $R=0.75$ ,  $P=0.0008$ ,  $n=16$ ; Old Coach Road at 10 mm depth:  $R=0.88$ ,  $P=0.0001$ ,  $n=17$ ). At Bellerive, the response of soil temperature reached a threshold and did not show a trend in plots

with greater than 20% bare soil (Fig. 3.7a). At the Old Coach Road, the soil temperature response was different, with a dramatic increase above 65% bare soil and much lower temperatures in the range from 10-65% bare soil than at Bellerive (cf. Fig. 3.7a and Fig. 3.7b). There was more variation in soil temperatures in the control plots at Bellerive than at the Old Coach Road (cf. Fig. 3.7a and Fig. 3.7b). The cover of vegetation and litter was considerably different between the two sites, although there was little difference in bare soil. At Bellerive, most of the ground cover was litter in the control plots, while at the Old Coach Road, the control plots had a continuous cover of low grasses and herbs (Fig. 3.8).

Most of the 19.7% cover of litter on the digging plots at the Old Coach Road was located in the shallow depressions. If the digging plots are divided into 2/3 mound and 1/3 depression, the mean ( $\pm$  s.e.m.) cover values of litter were  $5.7 \pm 0.6\%$  and  $50.8 \pm 4.2\%$  respectively. These cover values were measured nine months after the creation of the experimental disturbances. At Bellerive, the cover values for which the soil temperatures were measured were recorded in October, 1992, at least 26 months after the formation of these disturbances.

On the dolerite at Bellerive, the mean ( $\pm$  s.e.m.) soil temperature at 5 mm depth on the recently burnt area, with greater than 90% bare soil, was  $51.5 \pm 1.3^{\circ}\text{C}$  ( $n=13$ , range  $44.8\text{-}61.4^{\circ}\text{C}$ ). At the same time on the unburnt area under a dense sward of native grasses, the mean ( $\pm$  s.e.m.) soil temperature at 5 mm depth was  $27.5 \pm 0.9^{\circ}\text{C}$  ( $n=10$ , range  $23.0\text{-}31.2^{\circ}\text{C}$ ).

**Table 3.1** Results of a 3-way analysis of variance on soil moisture data measured in the field at Bellerive.

Source of variation	d.f.	M.S.	F	P
Model	71	0.17	1.7	0.043
Error	36	0.10		
Canopy	1	1.66	16.1	0.0003
Block (Canopy)	16	0.27	2.6	0.009
Digging	3	0.36	3.5	0.025
Digging x Canopy	3	0.12	1.1	0.35
Block (D x C)	48	0.11	1.0	0.48

*Tests using the Type III M.S. for Block (Canopy) as an error term:*

Canopy	1	1.66	6.2	0.024
--------	---	------	-----	-------

*Tests using the Type III M.S. for Block (digging x canopy) as an error term:*

Digging	3	0.36	3.4	0.024
Digging x Canopy	3	0.12	1.1	0.35

**Table 3.2** Spearman rank-order correlations between soil sample variables collected from the Bellerive study site.

	Moisture		Organic		Phosphorus	
	Rho	n	Rho	n	Rho	n
<i>Control samples:</i>						
Organic	0.42 *	24				
Phosphorus	0.80 **	11	0.68 *	11		
Nitrogen	0.63 *	12	0.89 ***	12	0.58 ns	11
<i>Mound samples:</i>						
Organic	0.15 ns	24				
Phosphorus	-0.17 ns	12	0.69 *	12		
Nitrogen	0.39 ns	12	0.81 **	12	0.43 ns	12

\* 0.01 &lt; P &lt; 0.05; \*\* 0.001 &lt; P &lt; 0.01; \*\*\* P &lt; 0.001; ns = not significant.

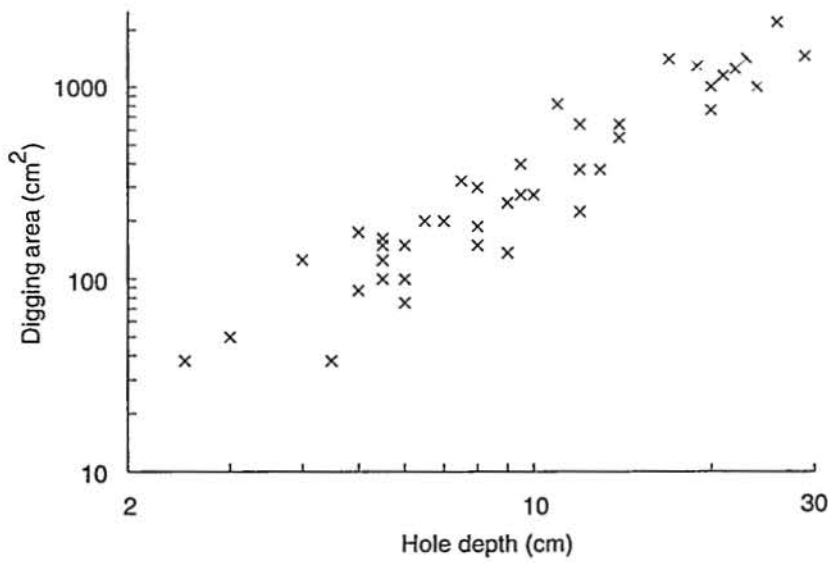


Fig. 3.2 Relationship between hole depth and the area covered by digging mound and hole on sandstone at Bellerive.

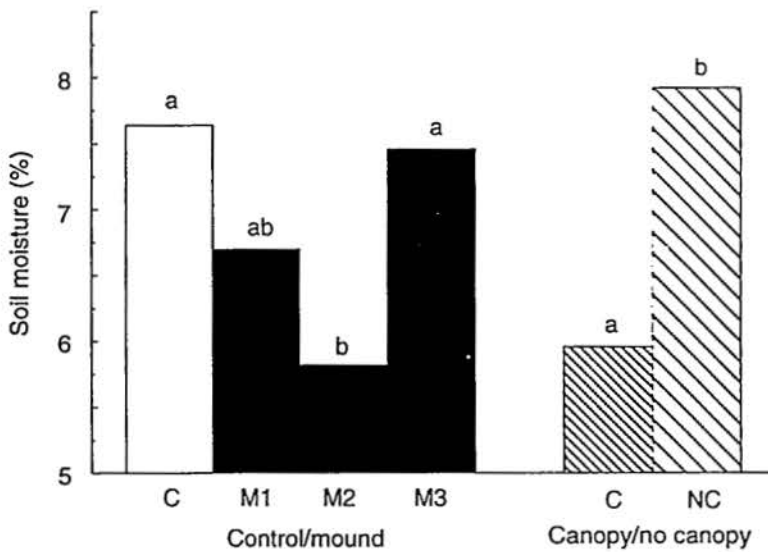
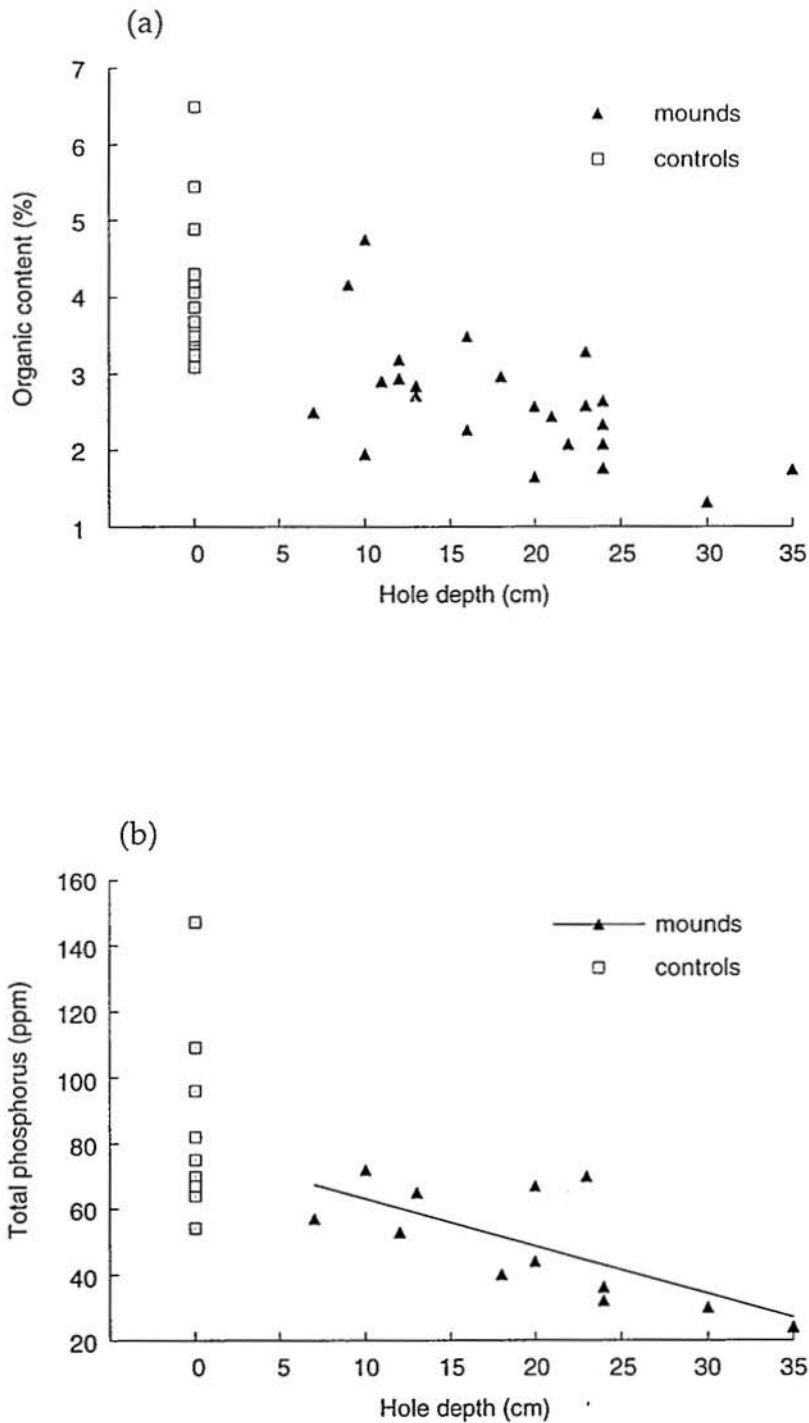
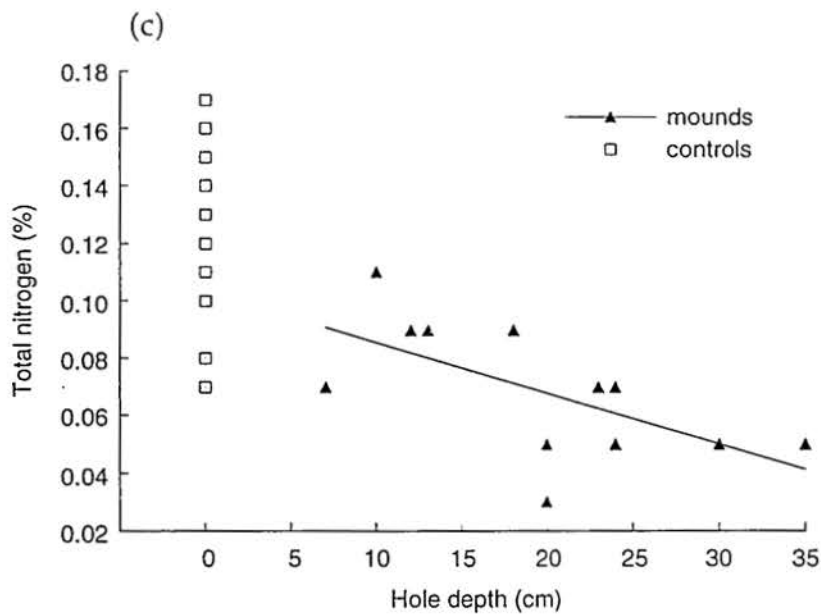


Fig. 3.3 Back-transformed least-squares means of field measured soil moisture at Bellerive. Different letters indicate significant differences ( $P < 0.05$ ) within either the control/mound factor or the canopy/no canopy factor.





**Figs 3.4** Soil nutrients of digging mounds in relation to the depth of the bandicoot holes from which they were created and in the control areas at Bellerive. (a) organic content, (b) phosphorus, (c) nitrogen.



Figs 3.4 (cont.)

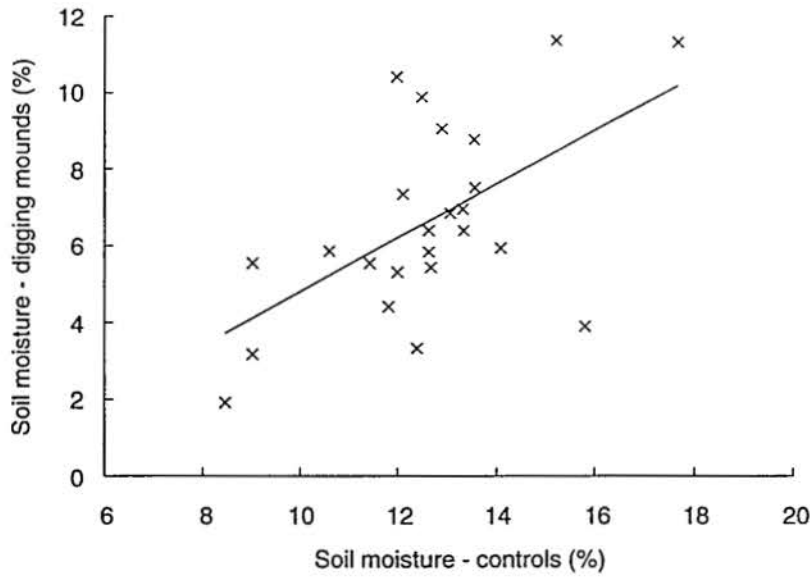


Fig. 3.5 The relationship between the soil moisture content of the digging mounds and the soil moisture content of the adjacent control areas at Bellerive.

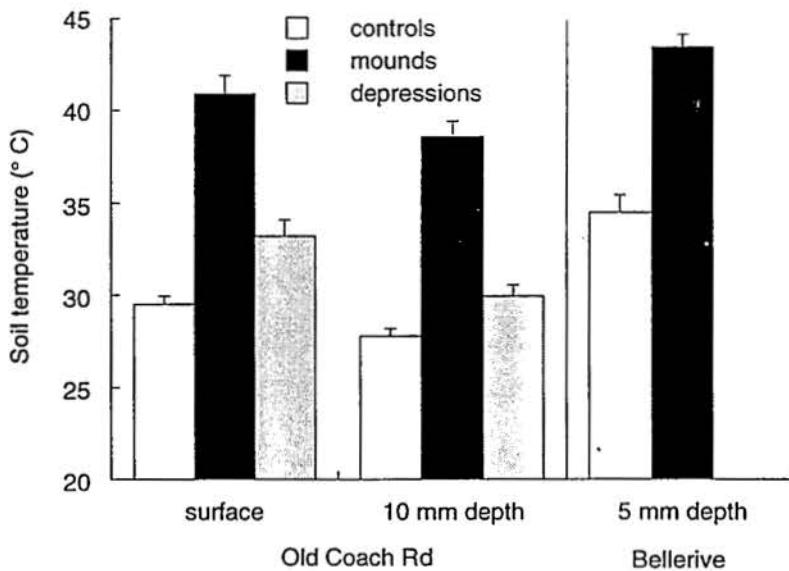


Fig. 3.6 Mean soil temperatures ( $\pm$  s.e.m.) at two study sites. All means with in each group are significantly different ( $P < 0.05$ ).

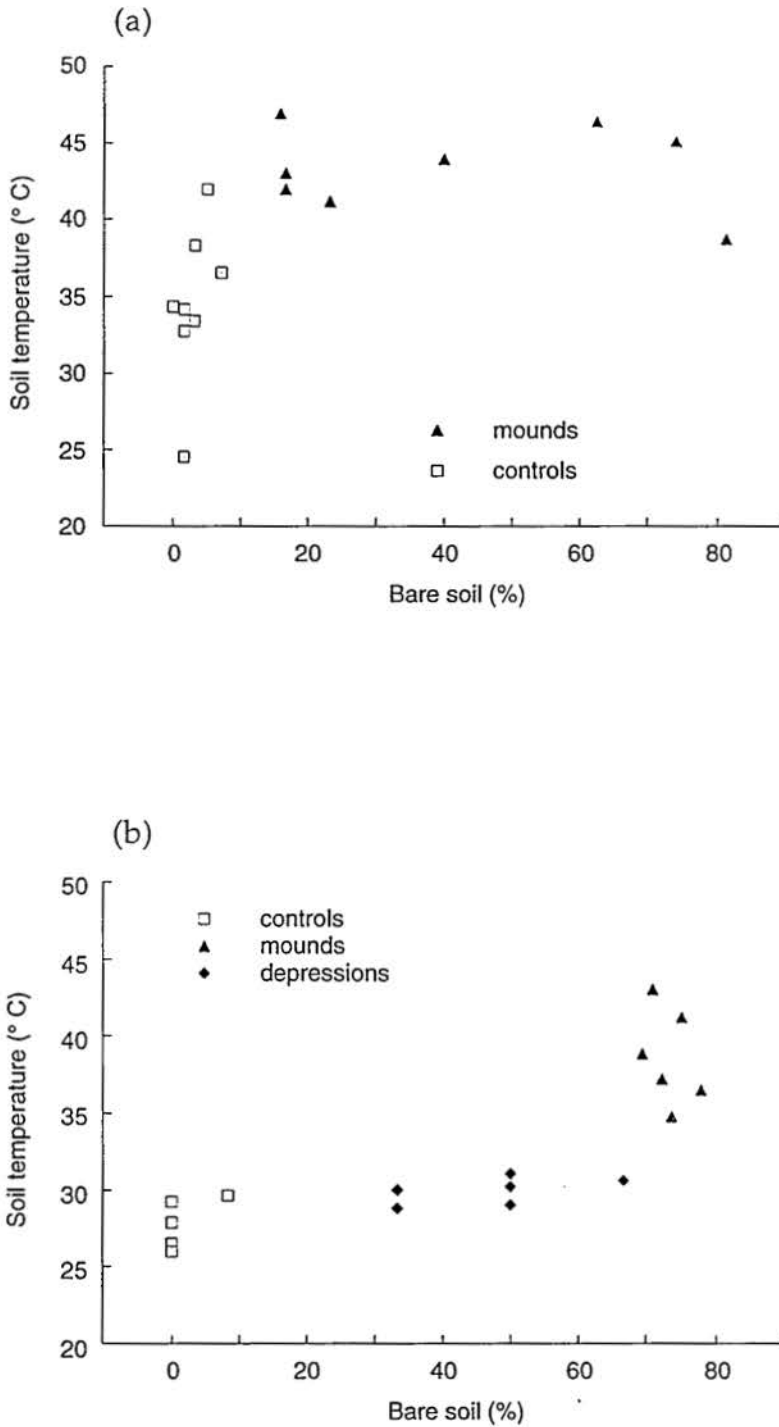


Fig. 3.7 The response of soil temperature to bare soil (%). (a) Bellerive, 5 mm depth; (b) Old Coach Road, 10 mm depth. Data points are means with  $n=5$ , all controls and Bellerive mounds;  $n=3$ , Old Coach Road mounds;  $n=2$ , Old Coach Road depressions.

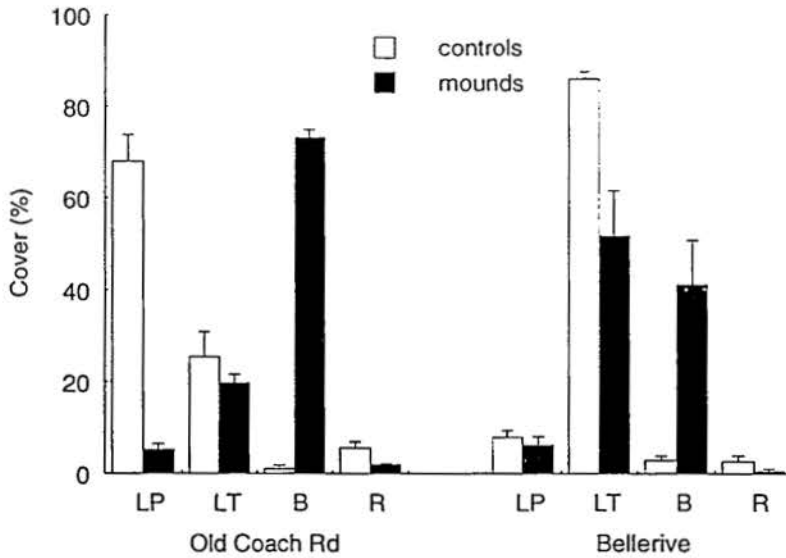


Fig. 3.8 Mean percentage cover ( $\pm$  s.e.m.) on control plots and entire simulated digging plots (Old Coach Road) or bandicoot mounds (Bellerive). LP = live plants; LT = litter; B = bare soil; R = rock.

## Discussion

### *Comparisons with other studies*

The findings here on soil moisture and fertility are congruent with other studies which have examined the physical and chemical effects of animal soil disturbances (Spencer *et al.*, 1985; Inouye *et al.*, 1987; Novoplansky, 1984, reported in Heth, 1991; Reader & Buck, 1991). The average total phosphorus and total nitrogen values for the control soil samples at Bellerive were 0.0080% and 0.124% respectively. In the edaphic scheme of Specht (1981), these levels of phosphorus and nitrogen in surface soils at Bellerive are typical of grassy communities in Australia, but are bordering on those typical of heathy communities. This is not surprising because the sandy soils that support grassy vegetation where the soil samples were collected also support heathy vegetation nearby.

The high soil temperatures on bare soil have also been reported elsewhere, although the temperatures are much lower than 80°C reported by

Williams (1992). Soil temperatures of 80°C resulting from solar heating would be extremely rare in lowland eastern Tasmania. I did not record a bare soil surface temperature over 70°C, even on soils with low albedo (i.e. dark colour), maximum angle of incidence, on very clear days of extreme temperatures, i.e. 30-33°C. In eastern Tasmania, days with higher atmospheric temperatures than this tend to have some cloud cover or haze.

### *Soil moisture*

The soil moisture values measured in the field and the soil moisture values determined from collected samples are quite different for a number of reasons. First, the values are not directly commensurable since the former are measured volumetrically and the latter are measured gravimetrically. Second, there were considerable differences in the lead up rain-free periods. The field measurements were made soon after moderately heavy rainfall, while the collected samples were collected after a long rain-free period. Third, the field measurements were based on 15 cm depth of soil profile, while the collected samples were based on 3 cm depth.

The difference between the rain-free periods reveals some useful information and the ratios of control to mound values should be directly comparable. The control:mound soil moisture ratio was 202.8% for the collected samples, while the same ratio for the field measured soils was 131.3% (for the centre of the mounds). Presumably, a large part of this difference can be attributed to evaporation and transpiration losses after many days without rain in the case of the larger ratio, with faster soil drying on digging mounds. Nonetheless, differences in soil moisture between mounds and controls are detectable very soon after rainfall. The difference in the depth over which measurements were made must be another important factor. The soil beneath the mound is protected by the same litter layer and organic matter which is probably responsible for the higher moisture content in the control samples. The 15 cm deep moisture measurements made in the field on mounds have a large contribution from the undisturbed soil profile, because mounds are at most only 6 cm high. The higher moisture values in the two measurements near the edges of the mounds, where the mound is less thick, reflect a greater



contribution from sub-mound soil (Fig. 3.3).

The soils under tree canopies were drier, presumably as a result of transpiration and the interception of rain by tree canopies. The tree canopy could be expected to reduce direct evaporation from the ground by reducing direct solar radiation, thus tending to reduce soil moisture loss. However, with only 30 hours since rainfall, this factor was not evident and could be presumed to increase in relevance with increasing time after rainfall.

Clearly, the magnitude of difference in soil moisture between digging mounds and undisturbed areas is going to be strongly related to time over various scales. After a saturating rain, there will initially be no difference in soil moisture, but a differential will appear presumably as a result of faster soil drying rates and/or lower moisture retention ability on digging mounds. These drying rates could be expected to be rapid in the warmer summer months, thus leading to equally dry soils on all microsites after long rain-free periods. Conversely, in the winter months, which is the crucial time for early seedling growth (see Chapter 5), the differential may be more long lived. It was readily observable, without the need for measurements, that the soil surface stays moister for longer in winter compared to summer. The dynamics of this situation and the questions of when and for how long the soil moisture differential is present were not explored in this study.

### *Soil nutrients on diggings*

One interpretation of the relationship between hole depth and nutrient status is that while digging holes, bandicoots amass soil on mounds as a direct inversion of the original soil profile of the hole, with very little mixing of soil on mounds. Alternatively, if soil mixing does occur on mounds, then the nutrient status could simply reflect the average nutrient content of a greater range of depth of soil profile. In either case, the soil profile could be expected to have decreasing nutrient status with increasing depth, because input from litter fall and soil biological activity concentrates nutrients near the surface (Leeper, 1964). The samples collected were 3 cm deep and covered nearly the full range of depth of mound soil, except for the biggest mounds. Very fresh mounds had no appearance of having been secondarily mixed by

bandicoot foraging or scratching. Therefore, the mounds probably are a direct inversion of the original profile, with important implications for the role that seed from the soil seed bank may play in colonising these bare mounds (see Chapter 7).

The soil on mounds has a lower nutrient status compared with neighbouring undisturbed areas and this does not change in the short term interval of two months to a year (the probable age range of the 'old' category of mounds). Return of nutrients to the soil of the mounds from litter fall is therefore a slow process. The bare soil areas created by bandicoots become covered by litter and vegetation at a relatively slow rate, exposing the soil to greater solar heating and surface evaporation than undisturbed areas for several years, at least in the case of bigger mounds. Smaller mounds tend to become obscure in the landscape much faster (pers. observ.).

#### *Soil temperatures*

The different temperature/bare soil responses at the two sites reflect the difference in total cover of live plants, which is higher at the Old Coach Road and imposes a greater and more even insulating effect on the soil compared with Bellerive. The deeper litter in the depressions at the Old Coach Road also maintained lower soil temperatures. Differences in albedo of different types of soil will have some influence on soil temperatures in direct sunlight. The bare dolerite soils measured at Bellerive and at the Old Coach Road were darker in colour than the bare sandstone soil. Temperatures at Bellerive were higher on the burnt dolerite than those on the sandstone mound plots (means 51.5°C and 43.4°C respectively), although differences in aspect and litter cover may be responsible for some of this temperature difference.

As mentioned in regard to soil moisture, the dynamics of the soil temperature differential of different microsites through time was not explored in this study. This time factor could be expected to have particular relevance in regards to providing sufficient or excessive warmth for physiological processes and therefore plant growth. Both climatic and seasonal factors could be expected to contribute to changes in the differential through time, by

influencing the extent of periods of direct and diffuse light, the ambient air temperature and the angle of incidence of the sun.

### *Conclusion*

Digging mounds at Bellerive are a harsh environment for newly emerged seedlings with very shallow roots. However, once roots have penetrated below the mound into the normal soil profile, the difference from undisturbed areas would be considerably less. On the other hand, the warmer soil may increase growth rates and the lack of litter cover may have an advantage for germination. Root competition from established plants would probably be reduced as well. Therefore, despite the fact that digging mounds are drier and less fertile than undisturbed areas, they may confer some advantages for seedlings (e.g. greater warmth and light penetration) and the disadvantages should only be relevant to very newly emerged seedlings. However, soil temperatures may sometimes be too high on digging mounds for plant physiological processes, although this is more likely to occur in the summer months when drought is preventing plant growth in any case.

Therefore, there may be a complex interaction of factors leading to periods of better growth conditions on mounds compared to undisturbed areas and vice versa. The conditions favouring a particular microsite over another may switch at various times of the year. Where the effective balance lies, both on an annual and longer-term basis, was not determined.

In conclusion, bandicoot digging mounds are drier and more infertile than the soil in surrounding undisturbed areas and get considerably hotter in direct sunlight. The nutrient status decreases with increasing size of the disturbance patch. Consequently, bandicoots create a soil landscape of various sized patches of varying fertility and moisture status.

## Chapter 4

# The Frequency of Diggings and the Spatial Pattern of Diggings in Relation to Trees and Understorey

### Introduction

To be a relevant factor for the seedling establishment of a given plant species, digging by native mammals must be frequent enough to provide an appropriate availability of bare ground, it must occur at the right times to coincide with the availability of seed and it must occur in the right places so as to be within the dispersal distance of adult plants. The first and third of these factors were considered in a very general sense for rare species in Chapter 2, where frequency was assessed on the basis of the static abundance of diggings. I now consider the frequency of diggings in more detail, comparing annual and seasonal variation in the rate of digging by different mammals in a number of habitats.

Most of the sites under investigation are woodlands where mesoscale variation in understorey might be expected to be caused by or at least be coincident with the presence or absence of tree canopies. Some of these floristic patterns are quite visible in the field, particularly for some of the more conspicuous understorey species, or where changes are very pronounced.

The Tasmanian bettong is known to dig along tree roots for sporocarps of hypogean fungi and the mesoscale spatial pattern of digging by this species has been described at one site (Chris Johnson pers. comm.). The mesoscale spatial pattern of diggings by bandicoots have not been described, but they are known to eat at least some hypogean fungi (Quin, 1985). In this chapter, therefore, the hypothesis that bandicoot diggings are distributed in association with trees is tested. The mesoscale spatial pattern of bandicoot diggings, trees and understorey are examined at one site, to determine which understorey species are growing in the vicinity of diggings, which species are responding to tree influences and how these factors combine.

## Methods

### *Rates and season of diggings*

Diggings were mapped on various sized belt transects at the following study sites (size given in brackets): Annandale (6 x 28 m), Hospital Creek (10 x 50 m), Old Coach Road (30 x 50 m) and Bellerive (10 x 50 m; 0.8 x 150 m). The size of the area was adjusted to suit the apparent overall density of diggings, with a bigger area where digging seemed less frequent to reduce the random error factor, and smaller areas where digging appeared to be more frequent and thus maximise sampling efficiency. At Bellerive on the 10 x 50 m transect, only larger sized diggings were mapped: i.e. diggings with holes greater than or equal to 10 cm at the widest point.

At each sample date, newly created diggings were mapped by recording Cartesian coordinates, after reference to a map of holes recorded on previous sample dates. The area of ground covered by each new digging was measured by a 40 x 40 cm grid with 5 x 5 cm cells. On the 0.8 x 150 m transect at Bellerive, diggings were mapped on a 5 x 5 cm coordinate system within 0.4 x 0.8 m quadrats spaced 0.5 m apart. All transects were located over populations of the rare plant species under investigation. However, the 0.8 x 150 m transect at Bellerive straddled two geological substrates, dolerite and sandstone, with rare plant species only on the sandstone. Sampling was undertaken for each transect at 2-4 monthly intervals for 1-2 years.

The species of mammal responsible for individual diggings was determined as far as possible on the basis of the morphology of the diggings, as described in Chapter 2.

### *Spatial pattern of diggings in relation to trees and vegetation*

Three separate sets of sampling were undertaken. In the first set, to examine the relationship between the spatial position of diggings and tree species, all plants which were at least 1.5 m tall were mapped on the 10 x 50 m transect at Bellerive, using the same Cartesian coordinate system used for the diggings. Additionally, all plants of the same minimum height were mapped in a 2 m zone around the 10 x 50 m area. The height and species of



all plants was recorded. A total of 9 species was thus recorded, with 3 species contributing only 4 individuals out of a total of 257. The remaining 6 species are all trees at least 6 m tall at maturity, although many young individuals of much lower stature were present.

In the second set of sampling, to examine the relationship between the floristic composition of the vegetation and the frequency of digging, a list was made in early December 1991 of all the vascular plant species present in a subset of the quadrats on the 0.8 x 150 m transect at Bellerive. The subset consisted of every second quadrat along the first 72 m of the transect on sandstone, giving a data set of 72 quadrats. The projected foliage cover of each species was estimated within the following 6 classes: <1%; 1-5%; 5-25%; 25-50%; 50-75%; and 75-100%. The abundance of each species was recorded in the following four classes: 1-2 individuals; 3-10 individuals; 11-50 individuals; and >50 individuals. For both cover and abundance, only plant species rooted in the quadrats were recorded. The percentage of exposed mineral soil in the quadrat was also noted, using the 5 x 5 cm grid cells of the grid as a guide.

In the third set of sampling, to examine the spatial relationship between diggings, trees and understorey vegetation, 1 x 1 m quadrats were located 4 m apart along four transects at Bellerive. The transects were spaced 8 m apart, were 140 m long, and all were underlain by sandstone. Sampling took place in May 1992 and all vascular plants with at least some vertical projection over the quadrats were recorded. Projected foliage cover and abundance were recorded separately as described above. The distance from the centre of each quadrat was measured to the trunks of what were considered the two most influential trees. These were the two trees with the closest canopy edges, or with canopy actually over the quadrats, or the two largest trees if three or more had a canopy over or at the same distance from the quadrat. The stem diameter of the two trees was measured at 1.3 m above ground and all had a diameter of at least 1 cm. The projected foliage cover of trees over the quadrats was estimated using a 13 class scale: 0, 1%, 5%, 10%, 20%.....100%.

The percentage cover of the following variables was estimated in the 140 quadrats, using the 13 classes from above: (a) two size categories of



diggings: those less than 150 cm<sup>2</sup> and those greater than 150 cm<sup>2</sup>; (b) ground with exposed mineral soil; (c) four categories of plant litter: *Eucalyptus*, *Acacia*, *Allocasuarina* and other (including herbaceous); and (d) exposed rock. The soil depth to a maximum of 36 cm was measured by pushing a probe into the soil once in the centre and 4 times near each of the corners. Measurements were repeated if they were considered to have been affected by rock floaters.

Some taxa could not be identified to species level because they did not have fertile material at the time of sampling. Knowledge from previous seasons reveals the identity of these unresolved taxa as follows: *Dichelachne* spp. = *D. inaequiglumis*, *D. rara*; *Pterostylis* spp. = *P. concinna*, *P. alata*; *Aira* spp. = *A. caryophyllea*, *A. elegantissima*; *Diuris* spp. = *D. sulphurea*, *D. maculata*; *Caladenia* spp. = *C. caudata*, *C. dilatata*, *C. clavigera*; and *Stipa* spp. = mostly *S. semibarbata*, *S. mollis*, *S. pubinodis*, *S. rudis*.

To identify which species of bandicoots were digging at Bellerive, trapping was undertaken for 6 nights between 30 September and 6 October 1992. Eleven steel mesh traps were spread out along one of the 140 m transects of the 1 x 1 m quadrat study. The traps were opened each night shortly before dusk and checked shortly after dawn. The traps were removed each day, because of the likelihood of theft, and returned to the same place in the evening. The traps were baited with bread and peanut butter.

### Data Analysis

The variation by season in the size of individual diggings was tested by one-way analysis of variance on log transformed data. Multiple comparisons between sample times were performed by the least significant difference test.

The spatial association between bandicoot diggings and tree species was tested by Monte Carlo simulations using random translations of the tree points as represented on a toroid (Lotwick & Silverman, 1982; Harkness & Isham, 1983; Upton & Fingleton, 1985). The idea of this method is that the complete spatial pattern of the two series (i.e. diggings and trees) is preserved intact, while one series is moved in entirety by a random distance in a random direction. Points which are thus moved outside of the original area 'reappear' on the opposite side because of the representation of the data on a toroid. By

not altering the spatial pattern of each series, the test makes no assumptions about the spatial structure of points within a series (i.e. clumped, regular, random). However, there is one implicit assumption which is unavoidable: the pattern of both series is assumed to be stationary, that is, to be unchanging between different parts of the total area. The translated series of points on the toroid has a 'cross-shaped seam' of points lying close together which were not so originally. If this 'seam' has an effect on the outcome of the test, it should be to favour the null hypothesis of independence for the two series (Lotwick & Silverman, 1982).

The test statistic was the mean of the nearest neighbour distances from each digging to the nearest tree. The significance was determined from the number of random translations out of 200 which resulted in a mean nearest neighbour distance equal to or less than the real mean nearest neighbour distance. In other words, the test examines the likelihood of diggings being closer to trees than would be expected by chance alone. All diggings were excluded which were closer to the boundary of the area than the nearest tree, for both the random translations and the original data. The boundary edge effect was reduced by the mapping of trees in a larger area than the area used for the diggings (Upton & Fingleton, 1985). As well as digging/tree comparisons, tests of association were made between two series of diggings made at different time intervals. The simulations were performed using SAS (SAS Institute Inc.).

All floristic data were entered into the ecological database DECODA (ANUTECH Pty. Ltd., Australian National University, Canberra). The floristic data from the 0.8 x 150 m transect were ordinated by global non-metric multidimensional scaling (GNMDS) using the programme MDS (ANUTECH Pty. Ltd., Australian National University, Canberra). The Bray-Curtis dissimilarity coefficient was used on data with species cover or abundances standardised to equal maxima (Faith *et al.*, 1987; Jongman *et al.*, 1987). The analyses were performed in 1 to 5 dimensions with 50 random starting configurations. One set of analyses was based on the midpoints of the projected foliage cover classes and another on the midpoints of the abundance classes (log transformed to down-weight high values), treating the >50 class as 50-100.

A vector fitting algorithm in DECODA was used to find the maximum correlation between the digging data (and other variables) and the floristic trends revealed by GNMDS solutions, and to apply a Monte Carlo significance test based on 999 random permutations. The response of individual species to the intensity of bandicoot digging was tested by Spearman rank-order correlation. For these individual species tests, only quadrats within the total range of a species along the transect were included.

The 1 x 1 m quadrat data were classified by agglomerative cluster analysis using the CLUSTER procedure in SAS (SAS, 1988b), on a dissimilarity matrix calculated by DECODA. The distance measure was the quantitative symmetric (Faith *et al.*, 1987). The fusion strategy employed was Ward's method (Jongman *et al.*, 1987) with 10% of the samples trimmed to reduce the likelihood of distortion being caused by outliers (SAS, 1988b). The midpoints of the abundance classes (i.e. number of individuals) were log transformed, treating the >50 class as 50-100, and species were standardised to equal maximum abundance. To make possible the testing of hypotheses on the influence of overstorey on understorey, the five common tree species (*Allocasuarina littoralis*, *A. verticillata*, *Eucalyptus amygdalina*, *E. viminalis*, *Dodonaea viscosa*) were omitted from the classification of the floristic data.

Soil depth, rockiness, digging and a number of tree-related parameters of the floristic cluster groups were tested in pairwise comparisons by the Wilcoxon 2-sample test. Data are presented in the form of 'box plots', which indicate the 25th and 75th percentiles (the box), the median (the bar inside the box) and the range of values (lines with bars beyond the box, with circles indicating outliers). Each tree species was treated as a separate variable for the calculation of an 'influence' index, which was the inverse of the distance to the nearest tree. In this index, a species gained a score of zero if it was not one of the two most influential trees for a given quadrat.

A subset of the 1 x 1 m quadrats was ordinated by GNMDS, using the same distance measure and transformations as in the cluster analysis. The analyses were performed in 1 to 5 dimensions with 50 random starting configurations. The vector fitting procedure was used to find the maximum correlation between the understorey composition and environmental variables,

including eight tree influence indices calculated from stem diameter and distance (after Lorimer, 1983; see Table 4.9).

## Results

### *Rates and season of digging*

#### *Bellerive*

The highest annual rate of digging out of all study sites was found at Bellerive on sandstone (Table 4.1). Most of the diggings in this area were from bandicoots, although a very small percentage (which are not considered here) were dug by echidnas and rabbits. The digging rates on sandstone were an order of magnitude greater than on dolerite (Table 4.1; Figs 4.1, 4.2). The rates for larger diggings ( $\geq 100 \text{ cm}^2$  in area) were very similar for both the  $0.8 \times 150 \text{ m}$  transect on sandstone and the  $10 \times 50 \text{ m}$  transect (Table 4.1).

The rate of digging was greatest in late autumn and in the winter months, both in terms of the number of holes dug and the total ground surface that the diggings covered (Figs 4.2). Very few holes were dug in summer and early autumn (Fig. 4.2b). The frequency of appearance of larger diggings peaked in late winter/early spring, although larger holes were dug all year round (Figs 4.3).

The size distribution of bandicoot diggings was negatively skewed (Fig. 4.4). There was considerable seasonal variation in the mean size of diggings ( $F_{9,918}=8.51, P=0.0001$ ). Smaller diggings appeared in late autumn or winter and the size increased and became maximal in summer (Fig. 4.5a). (This analysis included diggings whose size is under-estimated because they lie partially outside the quadrat. However, 97.5% of diggings are less than 5% of the size of the quadrat and the tendency would be to truncate the size of larger diggings more severely than smaller diggings, which would favour the null hypothesis of no seasonal variation in individual digging size). When only larger diggings are examined (on the  $10 \times 50 \text{ m}$  transect), there is very little seasonal difference in the size of diggings, with only the July 1991 sample having a mean digging size smaller than most of the other sample

intervals ( $F_{5,227}=2.86$ ,  $P=0.016$ ; Fig. 4.5b).

On a seasonal basis, there was an inverse relationship between the mean size and the rate of appearance of diggings on the 0.8 x 150 m transect (cf. Figs 4.2b and 4.5a). The mean rank of the size of diggings on the sandstone was not significantly different from the dolerite (Wilcoxon 2-sample test,  $P=0.2$ , dolerite  $n=108$ , sandstone  $n=820$ ), but the largest digging on the dolerite was 137.5 cm<sup>2</sup> compared with 900 cm<sup>2</sup> on the sandstone (cf. Figs 4.4a and 4.4b).

### *Annandale*

The annual rate of digging at Annandale was slightly more than half that found at Bellerive on sandstone (Table 4.1). Diggings at Annandale were dug by bandicoots and bettongs. Diggings and scrapings created by rabbits and possibly fallow deer were also present, but these are not considered here. Diggings were most prolific in the winter and spring in terms of total area disturbed (Fig. 4.6a), although the most holes were dug in spring (Fig. 4.6b). Most of these spring diggings were smaller and located around the bases of tussocks of *Lomandra longifolia*, but many diggings were associated with tree roots at other times of the year. The transect was located mostly under the canopies of trees of *Acacia dealbata* and *Eucalyptus amygdalina*.

### *Hospital Creek*

The annual digging rate at Hospital Creek was similar to the rate at Bellerive on dolerite, although diggings were created by echidnas and bettongs as well as bandicoots (Table 4.1). In terms of ground area disturbed, the proportion of disturbance created by different species was as follows: Tasmanian bettong, 32.0%; bandicoot, 36.9%; echidna, 30.1%; and unknown, 1.0%. The maximum disturbance occurred in summer in terms of total area (Fig. 4.6c), but this can be attributed to a few large echidna and bettong diggings. A larger number of smaller bandicoot diggings was recorded in winter (Fig. 4.6d).



*Old Coach Road*

Diggings were formed by echidnas and bandicoots at the Old Coach Road and the annual digging rate was extremely low (Table 4.1). Some very small bandicoot diggings were observed in winter and were not recorded (these were negligible in terms of total area). Many ant nests are located underneath dolerite boulders. To gain access to these nests, echidnas frequently overturn and dig under large boulders which may weigh more than 10 kg. More ground area is disturbed in late autumn and winter compared with other times of the year (Fig. 4.6e) although there is no clear trend in the number of individual diggings (Fig. 4.6f).

*Dukes Marshes*

No diggings were recorded on the transect at this study site.

*Spatial pattern of diggings and trees: 10 x 50 m transect at Bellerive*

While the assumption of stationary patterns in both series of points is difficult to validate quantitatively (see Methods), there appears to be no strong trend along the transect in either the pattern of diggings or trees (Figs 4.7).

The toroidal random translations suggested that larger bandicoot diggings were closer to tree species ( $\geq 1.5$  m) than might be expected by chance alone, when all diggings which appeared over two years were included ( $P=0.035$ , Table 4.2; Fig. 4.7a). The degree of association with trees appears to have a seasonal basis. In tests based on diggings from individual sample periods, which covered time intervals of three to four months, a significant association with trees was only detected for two sample periods: one ending in October 1990 ( $P<0.005$ ) and the other ending in April 1991 ( $P=0.015$ ; Table 4.2). The combination of diggings for the periods ending in October 1990 and October 1991 was also highly significantly associated with individuals of tree species ( $\geq 1.5$  m tall) ( $P=0.005$ , Table 4.2; Fig. 4.7b). The details of sample periods, numbers of diggings and trees are given in Table 4.3.

Tests of association were performed where individual tree species were excluded one at a time and also included one at a time. These tests were performed using the diggings from the combination of the two sample periods



ending in October, because these diggings appear to have the strongest association with trees. All tree species except *Acacia dealbata* and *Allocasuarina verticillata* could be removed individually and still produce a significant association at the  $P=0.05$  level (Table 4.2). No tree species on its own was significantly associated with diggings (Table 4.2). A highly significant association was found for the combination of *A. dealbata* and *A. verticillata* with all other species excluded ( $P<0.005$ , Table 4.2).

Tests were significant with only trees greater than 2 m tall, with all diggings included ( $P=0.01$ ) and the combined October samples alone ( $P=0.02$ ). Tests with trees greater than 2.5 m tall were highly significant with all diggings included ( $P=0.005$ ), but were not significant for the combined October samples ( $P=0.09$ ; Table 4.2).

The diggings from the two sample periods ending in October 1990 and 1991 were significantly associated with each other ( $P=0.005$ ), but the diggings from the rests of these two 12 month periods were not significantly associated when tested against each other ( $P=0.59$ ). The total diggings for the first year were not significantly associated with the total diggings from the second year ( $P=0.09$ ; Table 4.2).

#### *Digging in relation to understorey and trees: 0.4 x 0.8 m quadrats*

One method of determining the appropriate number of dimensions for multidimensional scaling is to examine a plot of the stress values and the number of dimensions. An 'elbow' is taken to indicate the correct dimensionality, because an increase to a higher number of dimensions returns a considerably smaller stress reduction compared with the previous increase in dimensions (Kruskal & Wish, 1978). By this method, two dimensions would appear to be appropriate for the 0.4 x 0.8 m quadrat data analysed using counts of individual plants as an abundance measure (Fig. 4.8). For the data analysed with projected foliage cover, three dimensions might be appropriate (Fig. 4.8). Despite these stress plots, the results from the vector fitting in four dimensional ordinations are presented here because both abundance measures in 4 dimensions produced higher and more significant correlations for most variables.

Overall, both abundance measures produced similar results. There were highly significant correlations between trends in the floristic composition and the intensity of digging over two years (expressed as a proportion of the total quadrat area); the distance along the transect; the percentage of bare soil; and the total cover of forbs (Table 4.4). Tree cover was only significantly correlated in the ordination based on counts of individuals (Table 4.4). The breakdown of digging intensity into two separate one year components, and individual sample intervals, also produced some significant correlations with trends in floristic composition (Table 4.4).

The angles between fitted vectors for distance along the transect and the two year total of diggings were close to  $90^\circ$  in both 4 dimensional ordinations in Table 4.4, indicating that the trend in species composition that is related to total digging is quite distinct from the trend in changing species composition along the transect. Although digging appeared to be clumped at a more local scale, the total digging over two years was not correlated with distance along the transect (Spearman  $R=0.06$ ,  $P=0.6$ ,  $n=70$ ; see Fig. 4.1). Similarly, vectors for the two separate one year totals of digging were both at angles close to  $90^\circ$  to the vectors for distance along the transect (Table 4.4).

The angle between the vectors for the two consecutive yearly totals of digging was  $18.6^\circ$  in the ordination based on counts of individuals (Table 4.4). This low angle indicates that the intensity of digging in the separate years was correlated with a similar trend in floristic composition. This result is not so evident in the ordination based on cover (Table 4.4). The angles between vectors for comparable individual sample intervals from consecutive years were quite variable, except that the angles between vectors for the April samples were quite small (Table 4.4).

The angle between the vector for total forb cover and the vector for the total digging over two years was approaching  $180^\circ$  in both ordinations, indicating that digging intensity and forb cover were related to the same trend in floristic composition, although with one increasing and the other decreasing (Table 4.4). A significant negative correlation is obtained when the total abundance of native forbs (lilies, orchids and herbaceous dicotyledons) is summed and compared directly with the total 2 years digging ( $P=0.0005$ ,

Table 4.7). Several individual native herb species were clearly less abundant in the quadrats with more intense digging (Table 4.5) and some of these were also significantly and negatively correlated with the total digging intensity (Table 4.7).

In contrast to the response by native forbs and some native grasses, many exotic species were more abundant in quadrats with more intense digging (Tables 4.5). This positive relationship was significant for some exotic species individually, and for all exotic species as a group (Table 4.7). The abundance of native forbs was negatively correlated with the abundance of exotic plants (Spearman  $R=-0.45$ ,  $P=0.0001$ ,  $n=70$ ) and with *Aira* spp. separately ( $R=-0.37$ ,  $P=0.002$ ,  $n=70$ ). With the exception of *Aira* spp. and *Briza maxima*, most weeds were concentrated in the first 25 m of the transect (Table 4.6). The correlation between exotic weeds and native forbs is highly significant for the first 25 m ( $R=-0.74$ ,  $P=0.0001$ ,  $n=24$ ), but not significant for the rest of the transect ( $R=-0.20$ ,  $P=0.2$ ,  $n=46$ ). No native species was significantly correlated with digging in a positive direction (Table 4.5).

#### *Digging in relation to trees and understorey: 1 x 1 m quadrats*

The cluster analysis of 1 x 1 m quadrats identified six major floristic groups on the basis of understorey (Fig. 4.9; Table 4.8; Appendix 2). The distributions of these groups overlap to varying extents within the area covered by the four transects. Groups 1 and 2 occupy a largely separate part at the western end of the transects and have little overlap with each other or other groups. Group 6 occupies a largely separate region between these two groups and the others. Groups 3, 4 and 5 are interspersed with each other at the eastern end of the transects (Fig. 4.10).

Group 1 is floristically most similar to group 2 and shares with it the characteristics of lower surface rockiness, a dense sward of *Themeda triandra* (and other native perennial grasses), and a thick cover of litter composed mainly of grass material (Figs 4.11e, 4.14d; Table 4.8). Tree cover is low in these two groups and the distance to the most influential tree is higher than in other groups (Figs 4.12f, 4.13f). Some species of daisies, lilies and orchids, including *Velleia paradoxa* and *Caladenia* spp., tend to be common in the other

groups but are largely absent from groups 1 and 2 (Table 4.8). Group 1 occurs on shallower soils than group 2, has less tree litter and lower alpha diversity (Figs 4.11f, 4.14c, 4.11a). Group 1 is distinguished from all other groups by having the lowest cover of eucalypt litter and total tree litter (Figs 4.14a,c). Group 2 is distinguished from all other groups by occurring on the deepest soil (Fig. 4.11f).

Group 6 is most similar floristically to groups 4 and 5 (Fig. 4.9). It is intermediate in relation to other groups in terms of total tree cover and the proximity to trees, but has quite high cover of tree litter (Figs 4.12f, 4.13f, 4.14c). It is distinguished from all other groups by having the highest rate of digging by bandicoots, by being closer to *Allocasuarina littoralis* and well away from *A. verticillata* (Figs 4.11b,c; 4.13c,d). Group 6 lacks the dense sward of *Themeda triandra* found in groups 1 and 2. It has no distinctive species of its own in the understorey and is defined by absences of species in comparison with other groups (Table 4.8).

Groups 3, 4 and 5 occur on sites of similar rockiness (Fig. 4.11e). They do not differ significantly in soil depth, although group 4 has a higher median, which may have been reduced by the fact that depths were measured to a maximum of 36 cm (Fig. 4.11f). Groups 3, 4 and 5 differ in the degree of tree canopy cover and tree litter as follows: group 3 > group 5 > group 4 (Figs 4.14f; 4.14d). Similarly, the median distance to the most influential tree is in the same order, although only group 3 and 4 are significantly different (Fig. 4.13f). *Allocasuarina verticillata*, *Eucalyptus viminalis* and *Dodonaea viscosa* are all either in the vicinity of or within quadrats of groups 3, 4 and 5, although group 4 has no cover of the latter species (Figs 4.13b, c, e; 4.12e). Group 3 has considerably less bare soil than the other two groups (Fig. 4.11d). Group 5 has a higher number of species per quadrat than any other floristic group (Fig. 4.11a).

The quadrats from cluster groups 3, 4 and 5 were ordinated by multidimensional scaling (GNMDS). The 4 dimensional solution (stress=0.16) is considered here because it had higher correlations for most variables. The fitted vectors for total tree canopy cover and total tree litter were highly significant and the angle between these two vectors was only 2.4° (Table 4.9).

Significant vectors were fitted for cover of *Allocasuarina verticillata* and *Eucalyptus amygdalina* individually, and a vector fitted for the combined cover of these two species has a higher correlation than for total tree cover. Other tree influence indices gave similar results (Table 4.9). Vectors for *A. verticillata* and *E. amygdalina* are separated slightly in the third dimension of the ordination space (as it is presented here), although the rank ordering of the quadrats along these two vectors is still highly correlated (Spearman  $R=0.82$ ,  $n=67$ ,  $P=0.0001$ ). Therefore, it appears that the change in species composition in the understorey which relates to tree influences is similar for both *A. verticillata* and *E. amygdalina*.

A two-way table of these quadrats and species, sorted on the basis of the fitted vector for canopy cover of *Eucalyptus amygdalina* and *Allocasuarina verticillata*, illustrates the trend in species composition which correlates with tree influences (Table 4.10). The three cluster groups are largely segregated along this floristic gradient, in the order 4, 5, 3. A number of species are absent from the quadrats with higher tree cover. In contrast, a few species are only found where tree cover tends to be greater. There were also a few species with a slight tendency to fade out at each end of this floristic gradient. Those species with a preference for one or other end of the gradient fade out at varying points along the continuum. More species are to be found in the middle region, which accounts for the greater alpha diversity of cluster group 5 (Table 4.10).

The mean total cover of bandicoot diggings appears to peak at the middle of this floristic gradient, as it does in response to other tree indicators such as the distance to the most influential tree (over all quadrats) (Figs 4.15a,b). The ends of the tree gradients in these graphs are characterised by fewer samples and the variability is greater and quite considerable in the middle.

Two x 2 contingency table analyses on the presence or absence of diggings and tree cover in quadrats gave results consistent with the toroidal tests. Larger diggings are weakly associated with tree cover (but only for the combination of *Allocasuarina verticillata* and *A. littoralis*), while smaller diggings are not. There are significant, but weak associations between smaller diggings and either *Aira* spp. or *Briza maxima* (on the basis of low or high abundance).



Larger diggings show no association with either of these two exotic species (Table 4.11).

### *Mammal trapping*

Two brown bandicoots were trapped in a total of 66 trap-nights over six nights, one female with pouch young and one male. The female was re-captured twice and the male was recaptured once. The only other trappings were two common brush tail possums (*Trichosurus vulpecula*). Large diggings were abundant in the immediate vicinity of the traps where the brown bandicoots were captured.

**Table 4.1** Digging rates in five study sites over one or two year periods.

Site	Digging <sup>1</sup> species	Transect area (m <sup>2</sup> )	No. Days	Digging <sup>2</sup> Rate A	Digging <sup>3</sup> Rate B	Re-dug <sup>4</sup> area (%)
Annandale	bg, bt	168.00	407	42.30	1.54	15.2
Bellerive:						
0.8 x 150 dolerite	bt	44.16	741	7.68	0.28	0.0
0.8 x 150 sandstone <sup>5</sup>	bt	49.92	741	78.47	2.86	7.8
0.8 x 150 sandstone <sup>6</sup>	bt	49.92	741	34.22	1.25	14.5
10 x 50 <sup>6</sup>	bt	500.00	390	32.65	1.19	2.8
Hospital Creek	bg, bt, e	500.00	360	5.72	0.21	15.8
Old Coach Road	e, bt	1500.00	391	1.56	0.06	13.1

<sup>1</sup> Digging species: bg = Tasmanian bettong, bt = eastern barred bandicoot or brown bandicoot, e = echidna.

<sup>2</sup> Digging rate A = cm<sup>2</sup>.100 m<sup>2</sup>.day<sup>-1</sup>.

<sup>3</sup> Digging rate B = % of total transect area disturbed per annum.

<sup>4</sup> % of total disturbed area arising from diggings which at least partially cover previous diggings.

<sup>5</sup> All diggings.

<sup>6</sup> Diggings ≥ 100 cm<sup>2</sup>.



Table 4.2 Results from toroidal translation tests of association between bandicoot diggings and trees, and bandicoot diggings from different time periods on the 10 x 50 m transect at Bellerive.

Group 1	Group 2	Original no. points		No. gp 1 points used		Mean nearest neigh. dist. (m)		Prob. <sup>5</sup>
		Gp1	Gp2	Untran. <sup>1</sup>	Min. <sup>2</sup> Rand.	Untran. <sup>3</sup>	Mean <sup>4</sup> Rand.	
Diggings	Trees							
all	all	309	253	303	296	0.90	1.02	0.035
Oct 90	all	72	253	72	69	0.79	1.02	<0.005
Jan 91	all	43	253	43	40	0.93	1.02	0.175
Apr 91	all	43	253	43	42	0.82	1.01	0.015
Jul 91	all	22	253	22	19	0.85	1.02	0.12
Oct 91	all	64	253	64	62	0.89	1.03	0.08
Mar 92	all	27	253	27	25	1.09	1.01	0.755
Jul 92	all	38	253	38	36	1.07	1.01	0.795
Oct 90/91	all	136	253	136	133	0.84	1.02	0.005
Oct 90/91	all excl. Ad	136	128	136	139	1.10	1.22	0.06
Oct 90/91	all excl. Av	136	164	126	112	1.28	1.47	0.11
Oct 90/91	all excl. Al	136	242	136	129	0.88	1.08	0.01
Oct 90/91	all excl. Dv	136	239	133	126	0.89	1.09	0.01
Oct 90/91	all excl. Ev	136	246	136	131	0.84	1.04	0.005
Oct 90/91	all excl. Ea	136	246	136	131	0.87	1.05	0.01
Oct 90/91	all excl. eucs	136	239	136	131	0.87	1.06	0.015
Oct 90/91	Av	136	89	122	113	1.32	1.56	0.05
Oct 90/91	Ad	136	125	104	82	1.46	1.91	0.07
Oct 90/91	Ev	136	7	53	34	3.16	3.01	0.71
Oct 90/91	Ea	136	7	58	22	2.77	2.88	0.45
Oct 90/91	Al	136	11	55	27	2.37	2.54	0.34
Oct 90/91	Dv	136	14	92	53	2.46	2.71	0.195
Oct 90/91	eucs	136	14	97	68	2.64	2.62	0.54
Oct 90/91	Av + Ad	136	214	129	121	0.94	1.23	<0.005
all	> 2m	309	114	301	288	1.19	1.34	0.01
all	> 2.5m	309	58	280	262	1.50	1.69	0.005
Oct 90/91	> 2m	136	114	135	127	1.12	1.34	0.02
Oct 90/91	> 2.5m	136	58	123	114	1.50	1.67	0.09
Diggings	Diggings							
Oct 90	Oct 91	72	64	43	30	0.88	1.24	0.005
yr1 excl. Oct	yr2 excl. Oct	108	65	81	62	1.28	1.26	0.59
year 1	year 2	180	129	137	111	0.85	0.94	0.09

<sup>1</sup> In the original untranslated data, the number of group 1 points with a group 2 point closer than or equal to the distance to the boundary of the area (i.e. the actual no. of points used in the tests).

<sup>2</sup> The random translation (out of 200) which had the minimum number of group 1 points, as defined above.

<sup>3</sup> In the original untranslated data, the mean of the nearest neighbour distances from each group 1 point to a group 2 point.

<sup>4</sup> The mean of the mean nearest neighbour distances from the 200 random translations.

<sup>5</sup> All significance tests are based on 200 random translations.

Ad = *Acacia dealbata*, Av = *Allocasuarina verticillata*, Al = *A. littoralis*, Dv = *Dodonaea viscosa*, Ea = *Eucalyptus amygdalina*, Ev = *E. viminalis*, eucs = *E. amygdalina* + *E. viminalis*.

**Table 4.3** Sample dates, number of bandicoot diggings and trees on the 10 x 50 m transect at Bellerive.

Sample dates	No. days	No. new diggings	No. re-dug	Total dug area (m <sup>2</sup> )
13 Jul 1990	-	-	-	-
4 Oct 1990	83	72	5	-
11 Jan 1991	99	43	0	1.575
17 Apr 1991	96	43	5	1.438
4 Jul 1991	78	22	1	0.533
29 Oct 91	117	64	2	2.643
5 Mar 1992	128	27	1	0.913
23 Jul 1992	140	38	4	1.493

Tree species (54 x 14 m area)	No. $\geq$ 1.5 m	No. > 2 m	No. > 2.5 m
<i>Acacia dealbata</i>	125	32	6
<i>Allocasuarina littoralis</i>	11	6	4
<i>A. verticillata</i>	89	53	30
<i>Bursaria spinosa</i>	2	1	1
<i>Dodonaea viscosa</i>	14	9	7
<i>Eucalyptus amygdalina</i>	7	6	4
<i>E. viminalis</i>	7	7	6

Table 4.4 Maximum correlation coefficients ( $R_{\max}$ ) and angles between vectors for the intensity of bandicoot diggings and other variables in 4 dimensional GNMDS ordinations of floristic data on the 0.8 x 150 m transect at Bellerive.

Variables	No. individuals <sup>1</sup>	Cover % <sup>1</sup>
$R_{\max}$ :		
Diggings:		
2 years	0.52 ***	0.50 ***
Year 1	0.48 **	0.42 **
Year 2	0.36 *	0.47 ***
Diggings in period ending:		
14 Jun 90	0.42 **	0.38 *
27 Aug 90	0.39 *	0.46 ***
20 Nov 90	0.16	0.24
29 Jan 91	0.34	0.28
4 Apr 91	0.29	0.43 **
5 Jun 91	0.13	0.09
9 Aug 91	0.27	0.40 *
23 Oct 91	0.31	0.39 *
16 Jan 92	0.24	0.3
30 Apr 92	0.21	0.29
Transect distance	0.90 ***	0.88 ***
% bare soil	0.45 **	0.59 ***
Grasses	0.41 *	0.34
Forbs	0.59 ***	0.64 ***
Tree canopy cover	0.46 ***	0.32
<i>Angles between fitted vectors:</i>		
2 years diggings & transect distance	91.8	89.9
Year 1 diggings & transect distance	93.9	99.7
Year 2 diggings & transect distance	89.4	82.2
2 years diggings & forbs	161.5	146.6
Year 1 & year 2 diggings	18.6	61.1
Jun 90 & Jun 91 diggings	47	72.6
Aug 90 & Aug 91 diggings	50.8	67.9
Nov 90 & Oct 91 diggings	81	114.5
Jan 91 & Jan 92 diggings	70.7	77.6
Apr 91 & Apr 92 diggings	32.8	12.1

<sup>1</sup> The abundance measure used in the GNMDS ordinations.

\* 0.01 < P < 0.05; \*\* 0.001 < P < 0.01; \*\*\* P < 0.001.



**Table 4.6** The distribution of exotic species along 72 m of the 0.8 x 150 m transect at Bellerive.

DISTANCE ALONG TRANSECT (m)	1111111111222222233333333333444444444455555555556666666666777	1234567890123456789023457890123456789012345678901234567890123456789012
<i>Centaureum erythra.</i>	1 11 11 1	1
<i>Hypochoeris radica.</i>	2 211 111211	121 2 1
<i>Briza maxima</i>	333332211 11 111 12343334311 33322344444432432-33233 3334443443333333	
<i>Aira spp.</i>	3443332331 2 3 3222444 1	33323 1 1 1213232 121 12 33
<i>Vulpia myuros</i>	1	2 2
<i>Rumex acetosella</i>	1 11111 111	
<i>Briza minor</i>	2232212	
<i>Holcus lanatus</i>	12233 212132323321	1 1
<i>Agrostis capillaris</i>		2123
<i>Silene gallica</i>	21 1 1111 11 1	

Full names are given in Appendix 4.

1 = 1 or 2 individuals; 2 = 3 to 10 individuals; 3 = 11 to 50 individuals; 4 = > 50 individuals.



**UTAS**

**Table 4.7** Spearman rank correlation coefficients between the abundance (no. individual plants) of individual species and the total area dug by bandicoots over 2 years on the 0.8 x 150 m transect at Bellerive.

Species	Rho	No. <sup>1</sup> quadrats	No. quadrats <sup>2</sup> (non-zero)
<i>Leptorhynchus squamatus</i>	-0.49 *	23	10
<i>Thelymitra pauciflora</i>	-0.17	64	7
<i>Poa sieberiana</i>	-0.41 **	46	29
<i>Microtis unifolia</i>	-0.40	13	8
<i>Craspedia glauca</i>	-0.20	30	11
<i>Diuris</i> spp.	-0.24	67	23
<i>Cynoglossum suaveolens</i>	-0.03	29	9
<i>Gonocarpus tetragynus</i>	-0.40 **	62	22
<i>Lepidosperma concavum</i>	-0.33 *	41	17
<i>Helichrysum apiculatum</i>	-0.24	63	29
<i>Carex breviculmis</i>	-0.08	32	17
<i>Danthonia pilosa</i>	-0.09	67	32
<i>Plantago varia</i>	-0.30	27	14
<i>Hibbertia riparia</i>	-0.22	26	13
<i>Wahlenbergia stricta</i>	-0.38 **	48	18
# <i>Centaurium erythraea</i>	-0.14	43	7
<i>Elymus scabrus</i>	-0.47 *	22	19
<i>Pimelea humilis</i>	-0.10	65	27
# <i>Aira</i> spp.	0.34 **	69	42
<i>Velleia paradoxa</i>	0.13	33	9
# <i>Rumex acetosella</i>	0.35	15	9
# <i>Briza minor</i>	0.67	7	7
# <i>Holcus lanatus</i>	0.11	66	19
# <i>Silene gallica</i>	0.58 **	20	10
native herbaceous dicots	-0.39 ***	70	67
native orchids	-0.27 *	70	27
native lilies	-0.14	70	60
native forbs <sup>3</sup>	-0.41 ***	70	68
native grasses	-0.20	70	70
exotic grasses & forbs	0.33 **	70	68

<sup>1</sup> Number of quadrats in test, also indicates range along transect (m).

<sup>2</sup> Number of quadrats with at least 1 individual of test species.

<sup>3</sup> Herbaceous dicots+lilies+orchids.

# denotes exotic species.

\* 0.01 < P < 0.05; \*\* 0.001 < P < 0.01; \*\*\* P < 0.001.



**Table 4.8** The mean projected foliage cover, mean abundance and percentage frequency of species in the six floristic groups defined by cluster analysis of 1 x 1 m quadrat data at Bellerive.

Species	Mean Cover						Mean Abundance						Percentage frequency					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
<i>Acacia dealbata</i>	1	2	2	2	2	2	1	1	1	1	1	1	6	30	21	24	21	13
<i>Agrostis aemula</i>	1	1	1	0	1	1	1	1	1	0	1	1	31	19	21	0	11	6
* <i>Aira</i> spp.	1	2	1	1	1	1	2	3	2	3	3	3	13	74	36	84	68	94
<i>Allocasuarina littoralis</i>	1	2	2	2	1	3	1	1	1	1	1	1	6	30	7	8	4	50
<i>Allocasuarina verticillata</i>	3	2	4	2	3	2	1	1	1	1	1	1	69	59	64	44	71	31
<i>Arthropodium milleflorum</i>	1	1	2	1	1	1	2	2	3	2	3	2	69	48	71	48	93	56
<i>Astroloma humifusum</i>	1	1	1	1	1	0	1	1	1	1	1	0	6	22	29	16	21	0
<i>Bossiaea cinerea</i>	0	1	1	1	0	1	0	1	1	1	0	1	0	4	14	4	0	6
<i>Bossiaea prostrata</i>	2	1	1	2	1	1	2	2	1	1	1	1	100	56	14	28	39	13
<i>Brachyscome spathulata</i>	0	1	1	0	1	1	0	1	1	0	1	1	0	11	21	0	7	6
* <i>Briza maxima</i>	0	1	1	1	1	1	0	2	3	3	4	3	0	26	93	80	100	100
<i>Bulbine glauca</i>	0	1	1	1	1	0	0	1	2	2	2	0	0	11	79	56	89	0
<i>Bursaria spinosa</i>	1	1	0	1	1	1	1	1	0	1	1	1	31	11	0	8	7	19
<i>Caladenia</i> spp.	0	0	1	1	1	1	0	0	1	1	1	1	0	0	14	28	39	25
<i>Carex breviculmis</i>	1	1	1	1	1	0	1	2	1	2	1	0	50	41	7	20	25	0
* <i>Centaurium erythraea</i>	2	1	1	1	1	1	3	3	1	1	1	1	81	67	7	24	11	25
<i>Craspedia glauca</i>	0	0	1	1	1	1	0	0	1	1	1	1	0	0	21	24	50	38
<i>Danthonia pilosa</i>	1	2	1	2	2	1	2	2	2	2	2	1	50	74	57	76	79	38
<i>Danthonia setacea</i>	1	2	1	1	1	1	1	2	1	2	2	2	19	44	29	60	46	56
<i>Deyeuxia quadriseta</i>	1	1	1	1	1	1	1	1	1	1	1	1	31	26	29	8	14	6
<i>Dianella revoluta</i>	2	2	2	2	2	2	2	2	2	3	2	2	50	56	64	80	68	94
<i>Dichelachne crinita</i>	0	1	2	1	1	1	0	1	2	1	1	1	0	4	50	28	25	6
<i>Dichelachne rara</i>	1	1	1	1	1	1	1	2	2	2	1	2	44	70	71	52	39	56
<i>Dichelachne</i> spp.	1	1	0	1	0	0	1	1	0	1	0	0	19	7	0	8	0	0
<i>Dillwynia cinerascens</i>	1	1	0	1	1	1	1	1	0	1	1	1	44	11	0	8	7	38
<i>Diplarrena moraea</i>	1	1	0	0	0	1	1	1	0	0	0	1	6	19	0	0	0	6
<i>Diuris</i> spp.	0	1	1	1	1	1	0	1	2	2	2	2	0	19	79	80	75	88
<i>Dodonaea viscosa</i>	1	1	2	1	3	1	2	1	2	1	2	1	63	41	71	48	64	63
<i>Drosera peltata</i>	1	1	0	0	0	0	1	1	0	0	0	0	69	19	0	0	0	0
<i>Ehrharta distichophylla</i>	1	3	1	1	1	2	1	3	1	1	1	2	19	78	7	8	7	44
<i>Ehrharta stipoides</i>	1	2	1	2	1	2	2	3	2	3	2	2	44	93	64	96	54	81
<i>Elymus scabrus</i>	1	1	1	1	1	0	1	1	1	1	1	0	6	4	43	8	4	0
<i>Eucalyptus amygdalina</i>	0	2	3	0	2	3	0	1	1	0	1	1	0	15	21	0	14	31
<i>Eucalyptus viminalis</i>	1	2	3	2	3	1	1	1	1	1	1	1	6	15	43	28	32	6
<i>Gahnia radula</i>	2	3	0	2	1	3	3	3	0	2	2	3	69	89	0	44	21	94
<i>Gonocarpus tetragynus</i>	1	1	1	1	1	2	1	2	1	2	2	2	38	52	36	48	82	88
<i>Helichrysum apiculatum</i>	2	2	1	2	2	1	2	2	1	2	2	2	63	41	36	72	68	31
<i>Helichrysum scorpioides</i>	0	0	1	1	1	1	0	0	1	1	1	1	0	0	29	4	14	25
<i>Hibbertia riparia</i>	2	2	2	2	2	2	2	2	1	1	2	1	94	63	36	64	71	50
<i>Hovea linearis</i>	1	1	1	1	1	1	1	1	1	1	1	1	25	26	14	24	54	50
* <i>Hypochoeris radicata</i>	1	1	1	1	1	1	1	1	1	1	2	1	50	56	43	48	68	19
<i>Kennedia prostrata</i>	1	1	1	1	1	0	1	1	1	1	1	0	13	4	36	4	14	0
<i>Laxmannia orientalis</i>	0	1	0	0	1	1	0	1	0	0	1	1	0	19	0	0	4	13
<i>Lepidosperma concavum</i>	0	0	2	1	2	1	0	0	1	1	2	1	0	0	43	16	50	6
<i>Lepidosperma lineare</i>	1	1	0	1	1	0	2	1	0	2	1	0	75	52	0	56	32	0
<i>Leptorhynchus squamatus</i>	1	1	1	1	1	0	1	1	1	1	1	0	44	4	14	16	11	0
<i>Leucopogon virgatus</i>	3	2	2	2	2	2	2	2	1	2	1	2	69	63	14	76	54	63
<i>Lomandra longifolia</i>	2	2	3	2	3	2	1	1	2	1	1	1	25	67	57	40	61	44
<i>Luzula meridionalis</i>	1	1	1	1	2	1	3	3	2	3	3	3	94	100	64	92	100	100
<i>Microtis unifolia</i>	0	1	0	1	1	1	0	1	0	1	1	1	0	4	0	4	11	6
<i>Opercularia varia</i>	2	1	2	1	2	2	2	2	1	1	1	2	69	74	36	44	61	81
<i>Oxalis perennans</i>	1	1	1	1	1	0	1	1	1	2	1	0	13	33	36	28	29	0

(cont. next page)

Table 4.8 (cont.)

Species	Mean Cover						Mean Abundance						Percentage frequency					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
<i>Pimelea humilis</i>	1	1	1	1	1	1	2	2	1	1	2	2	88	85	43	72	82	56
<i>Plantago varia</i>	0	0	1	1	1	0	0	0	2	1	2	0	0	0	43	20	25	0
<i>Poa rodwayi</i>	3	2	3	2	2	1	3	2	3	3	2	1	94	85	71	80	57	13
<i>Poa sieberiana</i>	0	2	1	1	2	2	0	2	2	1	2	2	0	26	57	24	79	75
<i>Podolcis jaceoides</i>	0	1	1	1	1	1	0	1	1	1	2	1	0	15	7	44	57	19
<i>Poranthera microphylla</i>	1	1	0	1	0	1	1	1	0	1	0	1	6	11	0	4	0	13
<i>Pterostylis concinna</i>	0	0	1	1	1	1	0	0	1	1	2	1	0	0	36	16	29	6
<i>Schoenus apogon</i>	1	1	1	1	1	1	3	2	1	1	1	1	88	74	7	36	25	31
* <i>Silene gallica</i>	0	1	1	0	1	1	0	1	1	0	1	1	0	4	7	0	14	6
<i>Stackhousia monogyna</i>	1	1	1	1	1	1	1	1	1	1	1	1	6	26	36	8	29	38
<i>Stipa</i> spp.	3	3	2	2	2	2	3	3	3	3	3	3	100	100	100	96	100	100
<i>Stylidium graminifolium</i>	1	1	0	1	1	1	1	1	0	1	1	1	25	33	0	8	11	38
<i>Thelymitra pauciflora</i>	1	1	1	1	1	1	1	2	1	1	2	2	50	81	14	56	71	75
<i>Themeda triandra</i>	3	3	1	3	1	2	3	3	1	3	2	1	94	100	14	88	50	13
<i>Thysanotus patersonii</i>	1	1	1	1	1	1	1	1	1	2	1	1	13	7	50	76	79	38
<i>Velleia paradoxa</i>	0	0	2	1	1	1	0	0	2	2	2	1	0	0	29	24	32	6
<i>Wahlenbergia stricta</i>	0	1	1	1	1	1	0	1	2	1	2	1	0	11	64	8	36	13

Means are based on the midpoints of classes on the original scale. Only species occurring in at least 5% of the quadrats are shown.

Projected foliage cover classes: 1=<1%; 2=1-5%; 3= 5-25%; 4=25-50%; 5=50-75%; 6=75-100%.

Abundance classes: 1=1-2 individuals; 2=3-10 individuals; 4=11-50 individuals; 5=>50 individuals.

\* denotes exotic species.

**Table 4.9** Maximum correlation coefficients ( $R_{\max}$ ) and angles between fitted vectors and configuration axes, for variables and the GNMDS 4 dimensional ordination of the understorey vegetation at Bellerive. The 1 x 1 m quadrats are from cluster groups 3, 4 and 5.

Variable	N	$R_{\max}$	Angles to axes			
			1	2	3	4
Rock	64	0.16	92	16	89	106
Soil depth	67	0.57 ***	113	134	127	94
Bare soil	67	0.55 ***	162	102	77	87
Bandicoot diggings:						
$\leq 150 \text{ cm}^2$	67	0.42 *	125	85	51	121
$> 150 \text{ cm}^2$	67	0.11	75	114	30	85
Total	67	0.27	115	92	37	115
Tree cover:						
<i>Allocasuarina littoralis</i>	67	0.32	110	59	69	134
<i>A. verticillata</i>	67	0.40 *	24	108	103	82
<i>Eucalyptus amygdalina</i>	67	0.51 ***	31	99	62	81
<i>E. viminalis</i>	67	0.28	73	64	125	52
<i>Dodonaea viscosa</i>	67	0.32	58	82	46	118
<i>A. vert.</i> + <i>E. amyg.</i>	67	0.64 ***	19	104	82	81
Total	67	0.55 ***	12	88	82	82
Distance to most influential tree	67	0.44 **	148	106	98	65
Litter:						
<i>Eucalyptus</i>	67	0.39 *	31	105	71	73
<i>Allocasuarina</i>	67	0.36	23	68	93	94
Total tree	67	0.54 ***	12	86	81	83
Herb & shrub	67	0.13	104	76	118	145
Tree influence indices (all spp.):						
$\sum \text{dia}/(\text{dist}+1)$	67	0.59 ***	24	73	84	74
$\sum \text{dia}/(\text{dist}+1)^2$	67	0.62 ***	24	80	89	69
$\sum \text{dia}/\sqrt{(\text{dist}+1)}$	67	0.53 ***	26	70	81	77
$\sum \text{dia}$	67	0.44 **	29	67	76	79
Tree infl. ind. ( <i>A. vert.</i> + <i>E. amyg.</i> ):						
$\sum \text{dia}/(\text{dist}+1)$	57	0.58 ***	18	81	76	85
$\sum \text{dia}/(\text{dist}+1)^2$	57	0.59 ***	15	91	83	76
$\sum \text{dia}/\sqrt{(\text{dist}+1)}$	57	0.56 ***	23	76	73	88
$\sum \text{dia}$	57	0.51 **	29	71	70	91

\* 0.01 < P < 0.05; \*\* 0.001 < P < 0.01; \*\*\* P < 0.001.



**Table 4.11** Selected results of 2 x 2 contingency tests of association (continuity adjusted  $\chi^2_1$ ) between diggings and tree cover, and diggings and exotic species. Data are from the 1 x 1 m quadrats at Bellerive.

Diggings	Tree cover or exotic abundance	$\chi^2$	+ / + frequency <sup>1</sup>	
			Obs.	Exp.
Diggings & trees (presence/absence):				
all diggings	Al + Av	1.79	37	33.6
all diggings	all trees	0.22	56	54.4
diggings > 150 cm <sup>2</sup>	Al + Av	4.48 *	21	15.0
diggings > 150 cm <sup>2</sup>	all trees	0.61	27	24.3
diggings ≤ 150 cm <sup>2</sup>	Al + Av	0.71	32	29.4
diggings ≤ 150 cm <sup>2</sup>	all trees	0.49	50	47.6
Diggings & exotic species (low/high abundance):				
all diggings	<i>Aira</i> spp.	3.11	50	44.4
all diggings	<i>Briza maxima</i>	2.93	54	48.6
diggings > 150 cm <sup>2</sup>	<i>Aira</i> spp.	0.35	27	24.8
diggings > 150 cm <sup>2</sup>	<i>Briza maxima</i>	0.22	29	27.2
diggings ≤ 150 cm <sup>2</sup>	<i>Aira</i> spp.	5.39 *	39	31.7
diggings ≤ 150 cm <sup>2</sup>	<i>Briza maxima</i>	4.00 *	41	34.7

<sup>1</sup> Total frequency = 140.

Low/high abundance of exotic species defined as < or ≥ 11 individuals per quadrat; for diggings defined as < or ≥ 5% cover. Al = *Allocasuarina littoralis*; Av = *A. verticillata*.

\* 0.01 < P < 0.05.

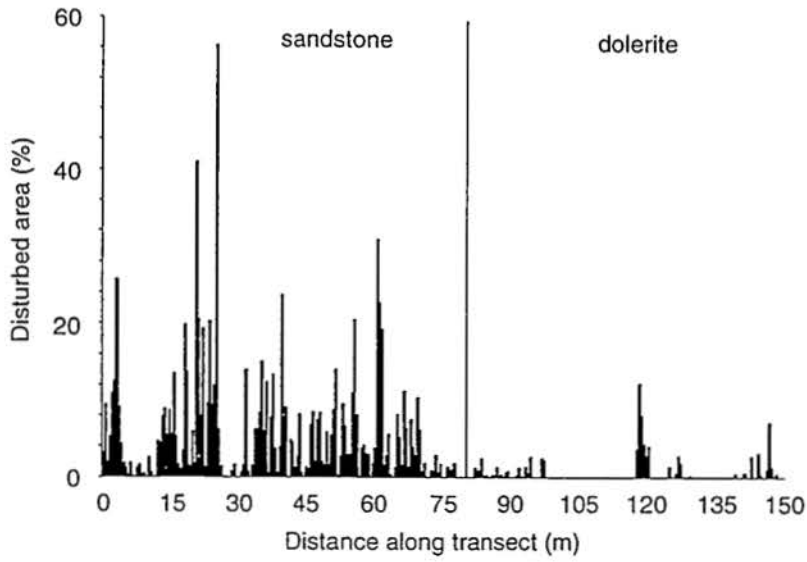
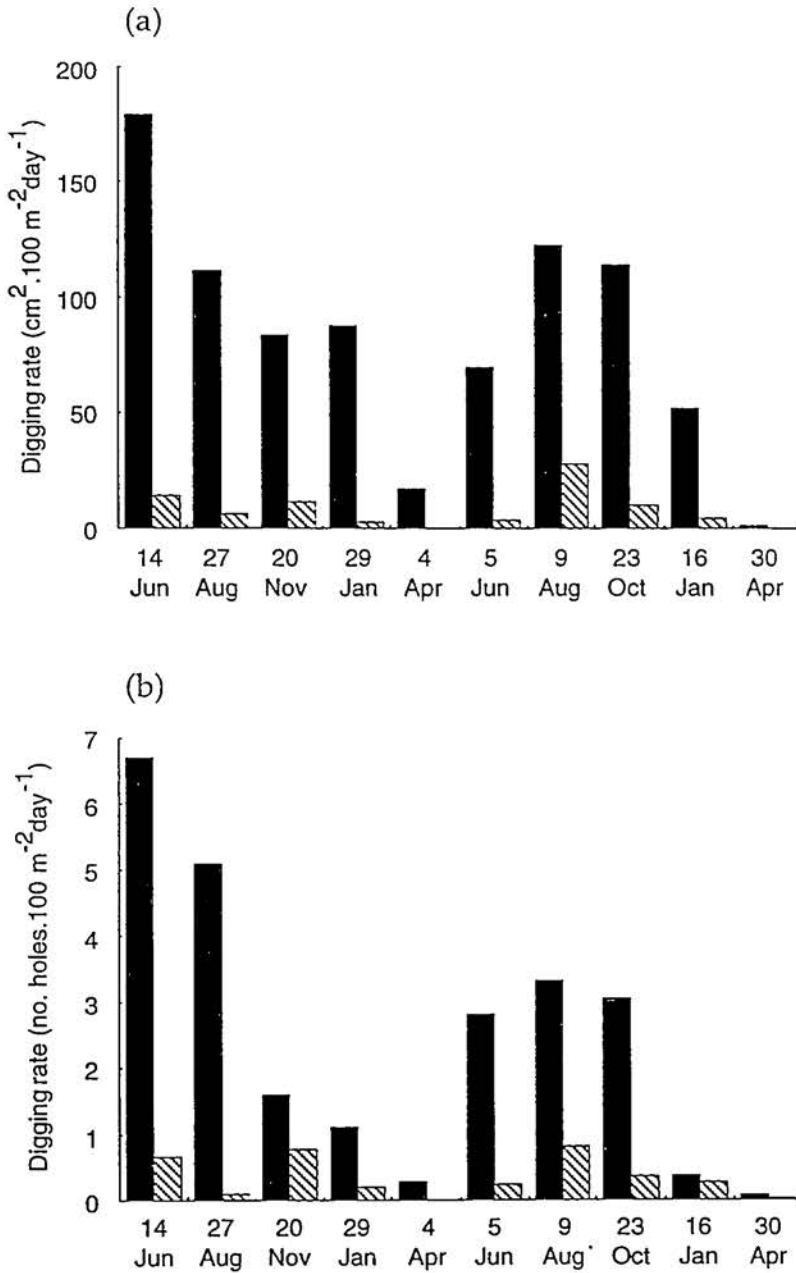
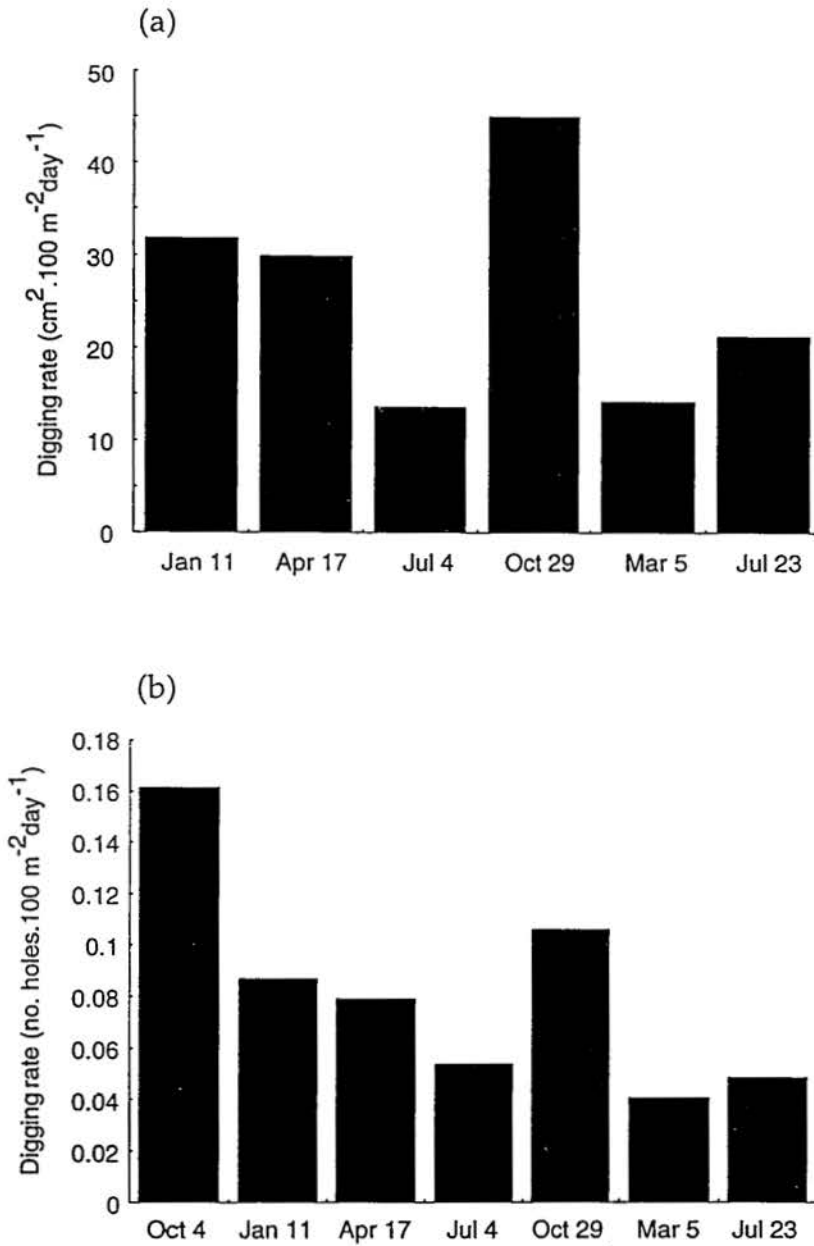


Fig. 4.1 The distribution of the total bandicoot diggings for 2 years along the 0.8 x 150 m transect at Bellerive, expressed as a percentage of the total quadrat area disturbed.

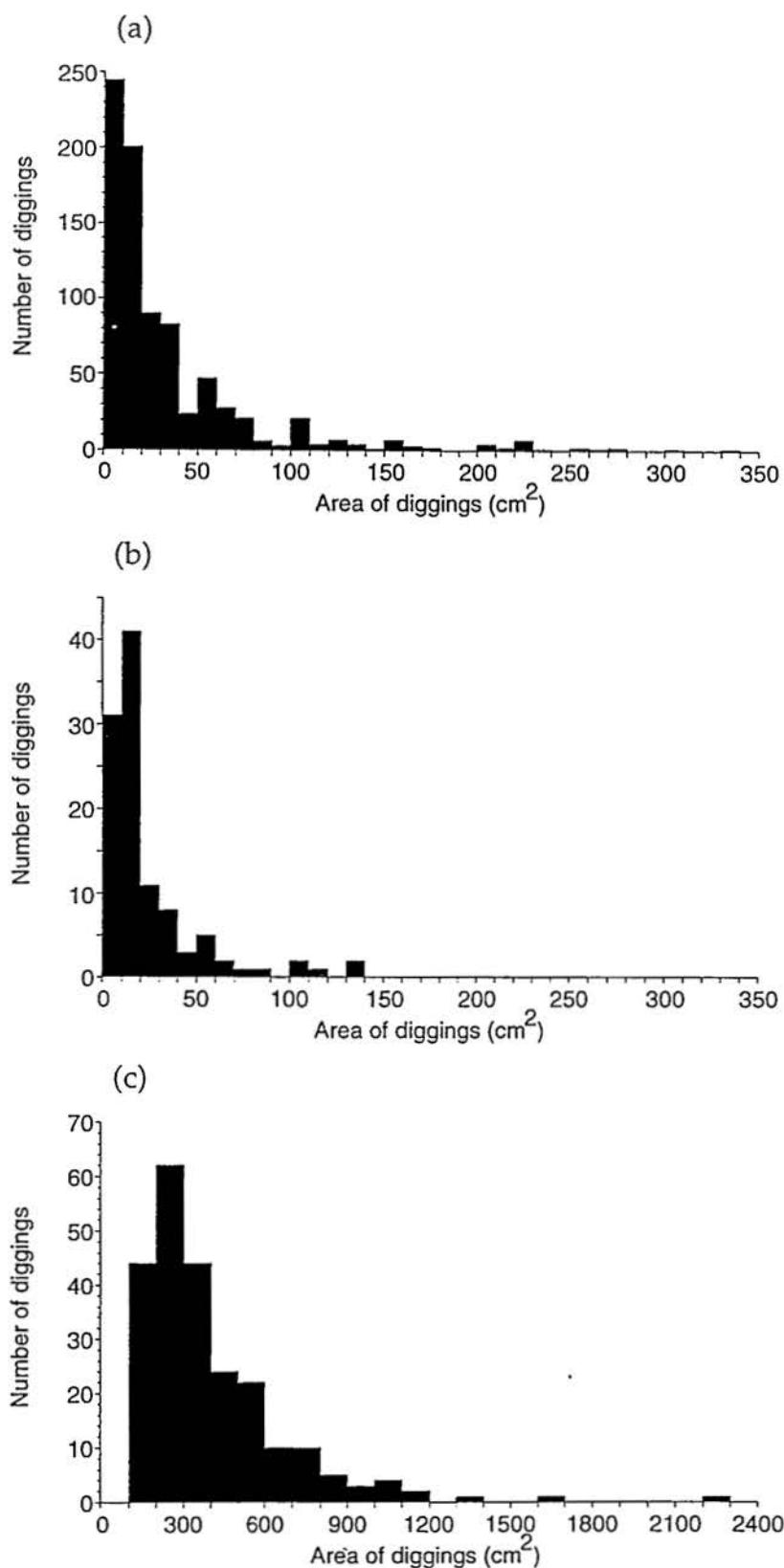




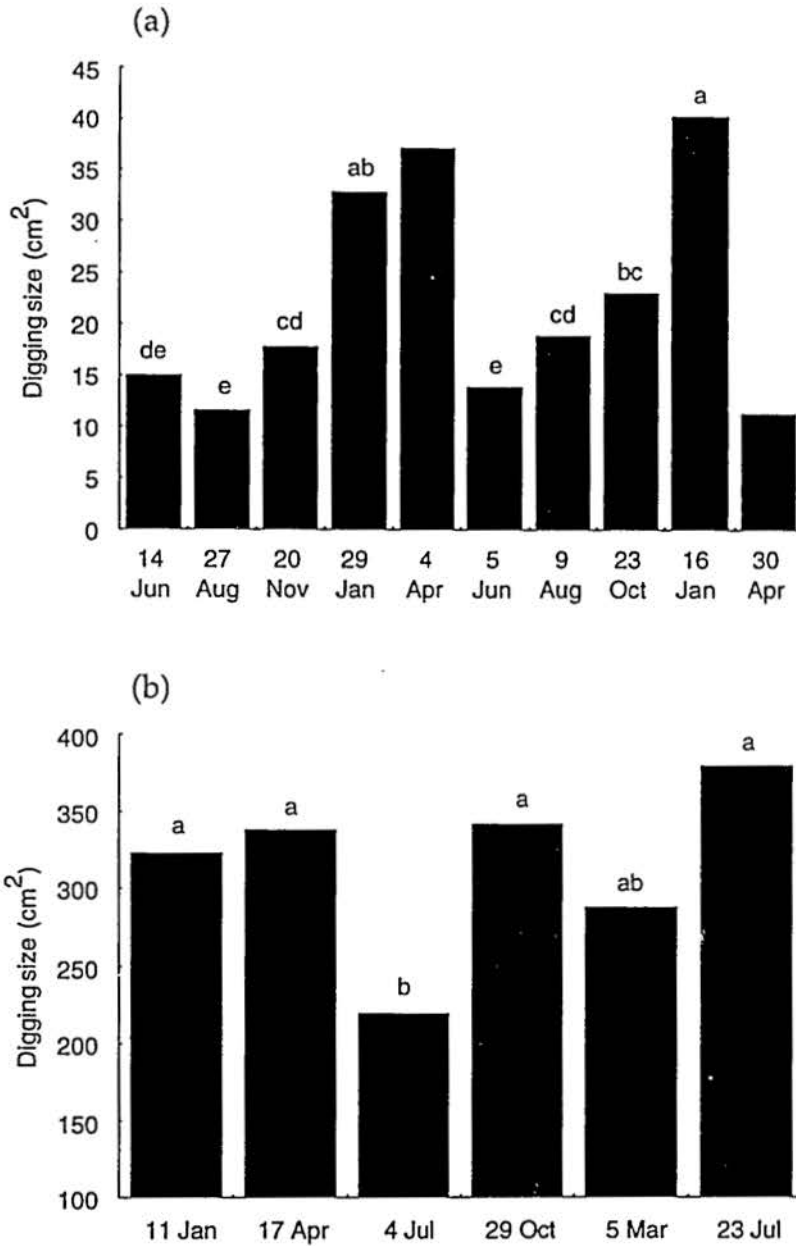
**Figs 4.2** Seasonal variation in the rate of digging at Bellerive over two years on a 0.8 x 150 m transect, in terms of (a) total area disturbed and (b) number of new individual diggings. Dates indicate the end of each time interval. Observations commenced on 20 April 1990. (■) = sandstone, (▨) = dolerite.



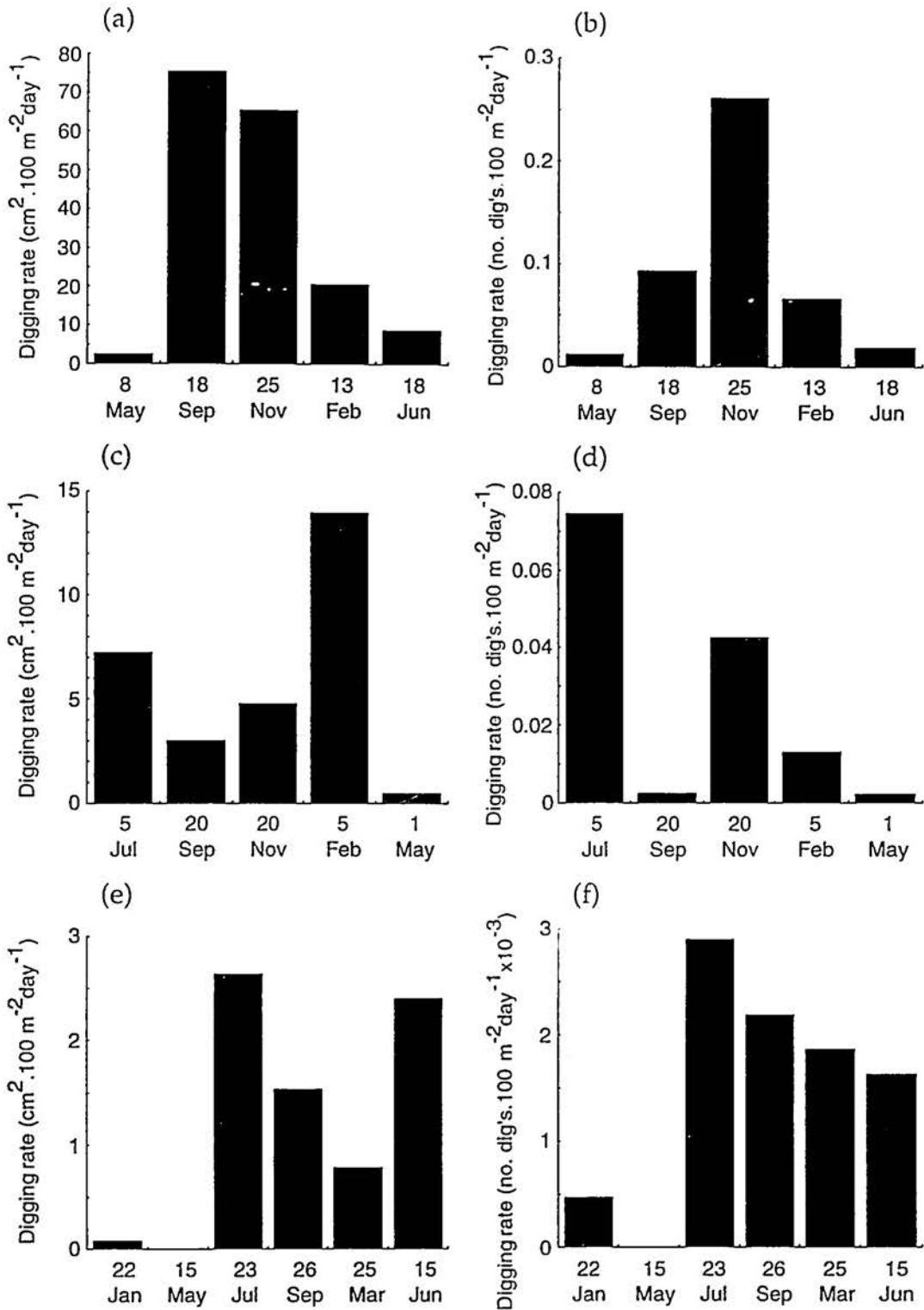
**Figs 4.3** Seasonal variation in the rate of appearance of larger diggings ( $\geq 100 \text{ cm}^2$ ) at Bellerive on a  $10 \times 50 \text{ m}$  transect, in terms of (a) total area disturbed and (b) number of new individual diggings. Dates indicate the end of each time interval. Observations commenced on (a) 4 October 1990, and (b) 13 July 1990.



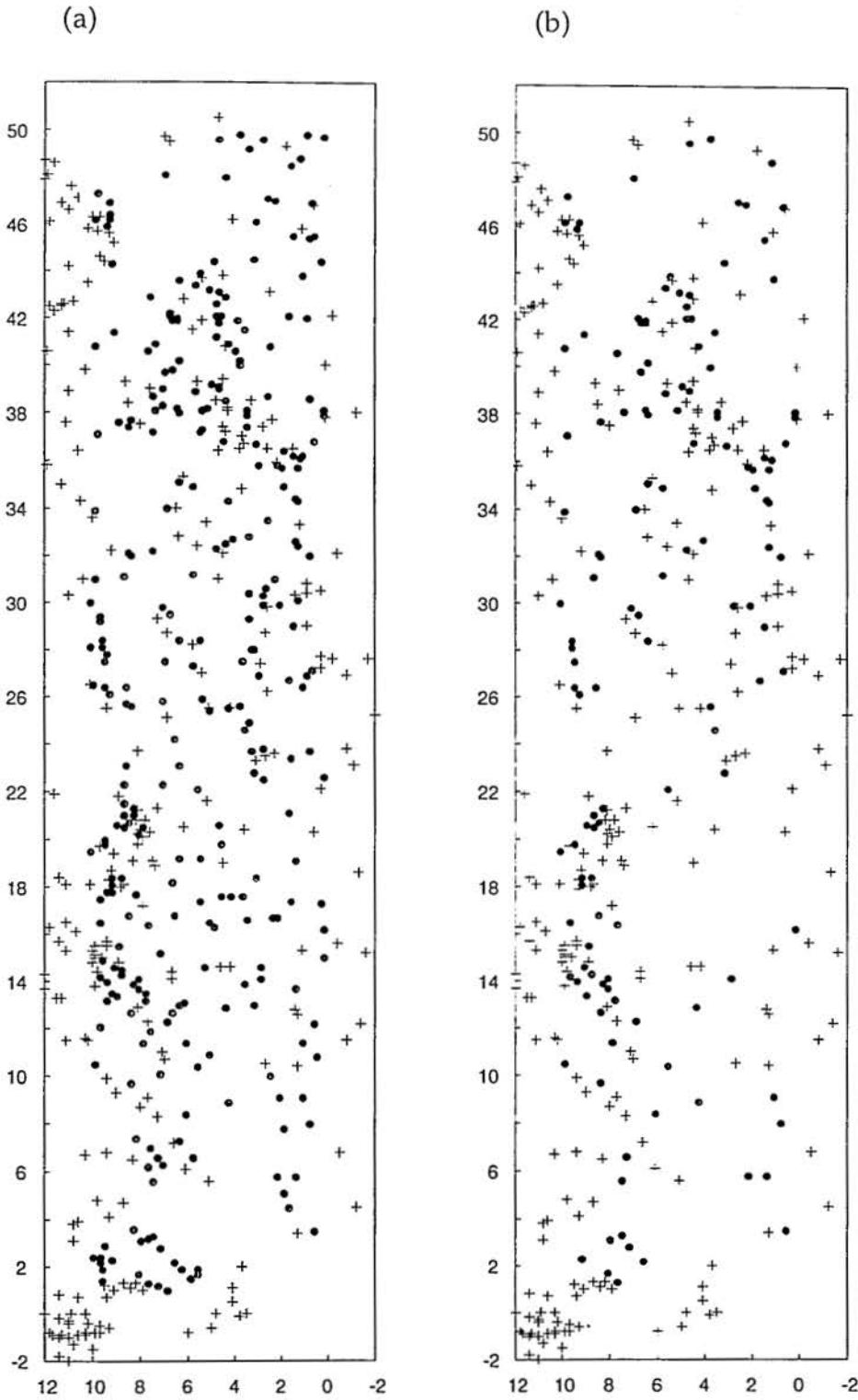
**Figs 4.4** Frequency distribution of the size of individual diggings on the 0.8 x 150 m transect on (a) sandstone (2 diggings omitted: 750 cm<sup>2</sup> and 900 cm<sup>2</sup>); (b) dolerite; and (c) the 10 x 50 m transect. The class intervals are (a) and (b) 10 cm<sup>2</sup>; and (c) 100 cm<sup>2</sup>.



Figs 4.5 Seasonal variation in the mean size (back-transformed) of bandicoot diggings at Bellerive. Dates indicate the end of each sample period. Means with the same letter are not significantly different ( $P < 0.05$ ). (a) 0.8 x 150 m transect (April samples not included in multiple-comparisons due to small sample sizes); (b) 10 x 50 m transect (all diggings  $\geq 100$  cm<sup>2</sup>).



Figs 4.6 Seasonal variation in digging rates at (a) and (b) Annandale (initial sample 18 March 91); (c) and (d) Hospital Creek (initial sample 7 May 91); (e) and (f) Old Coach Road (initial sample 4 September 90). The rate is in terms of total area disturbed (a), (c) and (e); and number of individual diggings (b), (d) and (f). Dates indicate the end of each time interval. Each graph has a different scale.



**Figs 4.7** The spatial distribution of all trees  $\geq 1.5$  m tall (+), and larger bandicoot diggings (•) on the 10 x 50 m transect at Bellerive. The map scales are in metres. (a) 2 years diggings ending 23 July 1992, (b) diggings for 13 July-4 Oct. 1990 and 4 July-29 Oct. 1991.



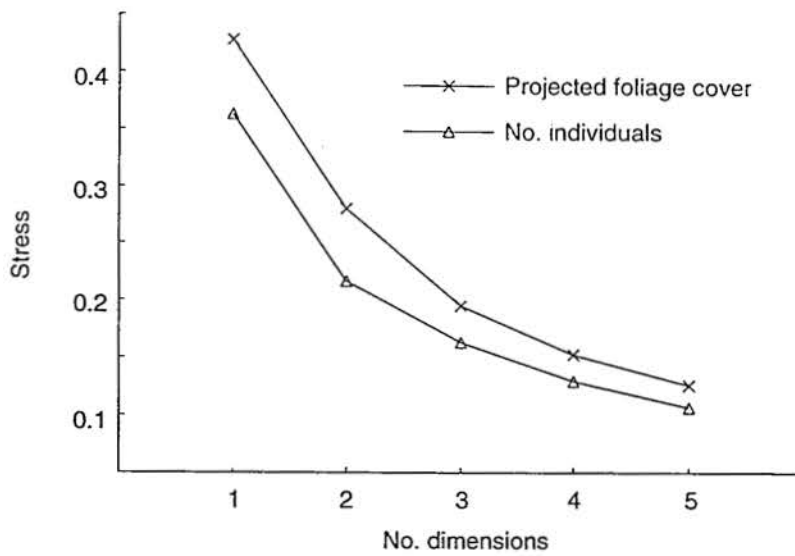


Fig. 4.8 The minimum stress values in GNMDS ordinations on floristic data on the 0.8 x 150 m transect at Bellerive.

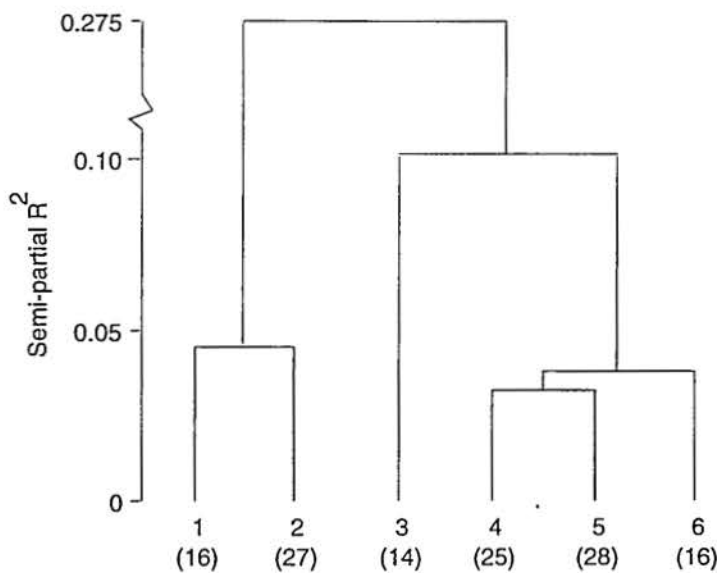


Fig. 4.9 Dendrogram of the groups defined by the cluster analysis of the 1 x 1 m quadrats at Bellerive. The number of quadrats in each cluster is indicated in brackets. Fourteen quadrats (10%) were removed from the analysis and were thus not classified (see Data Analysis section).

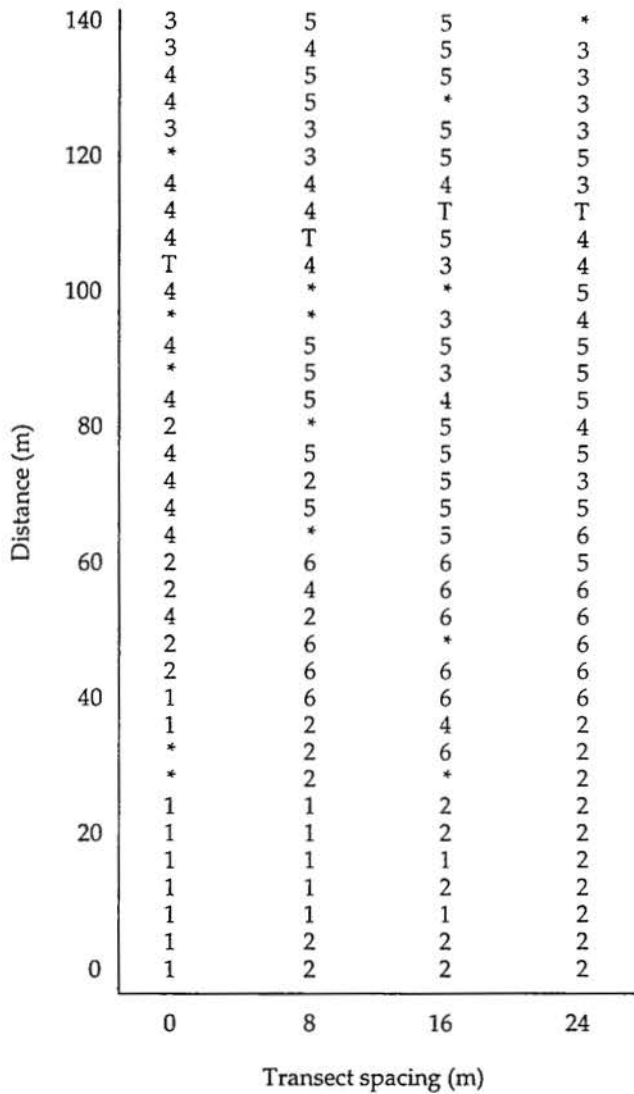
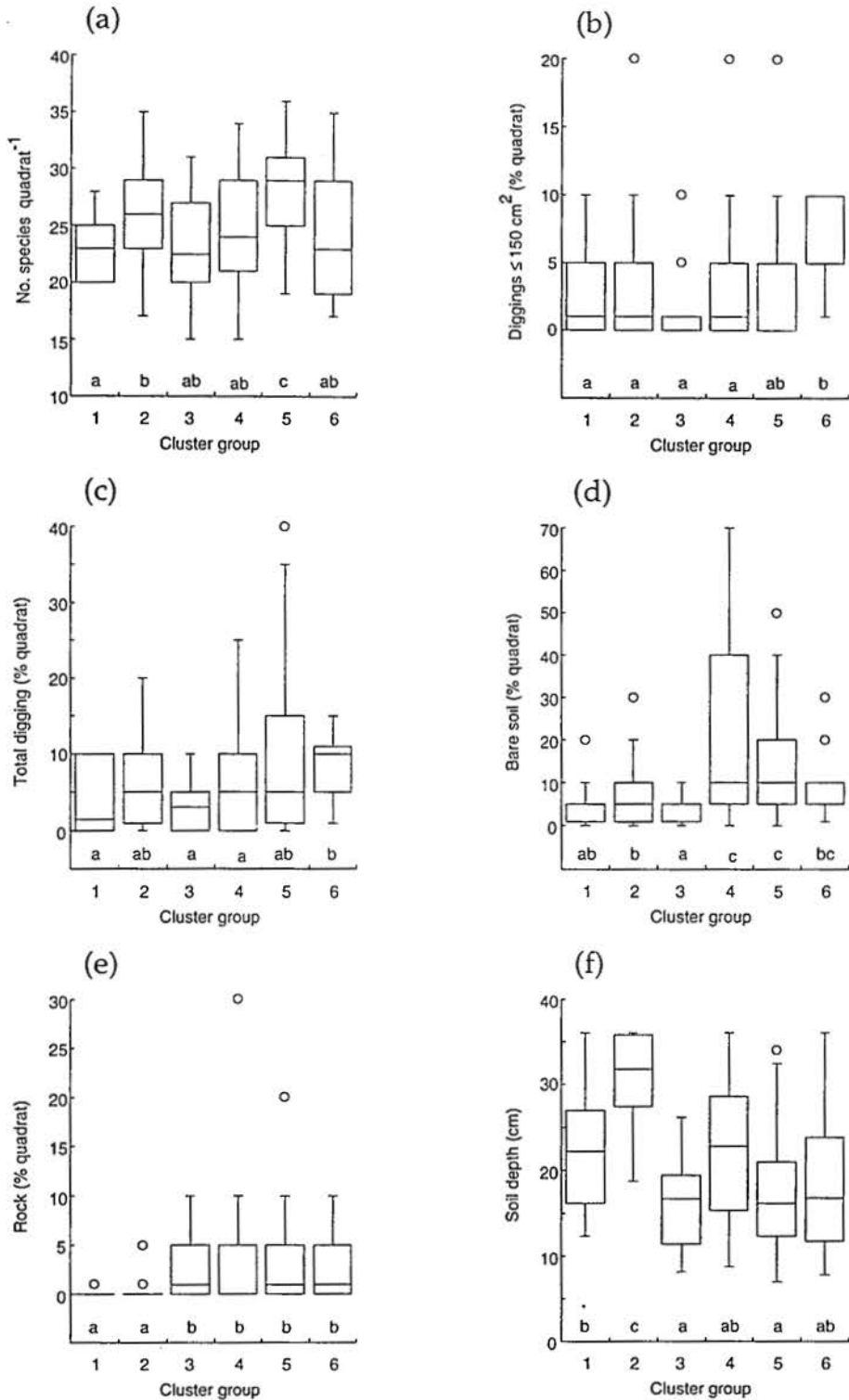
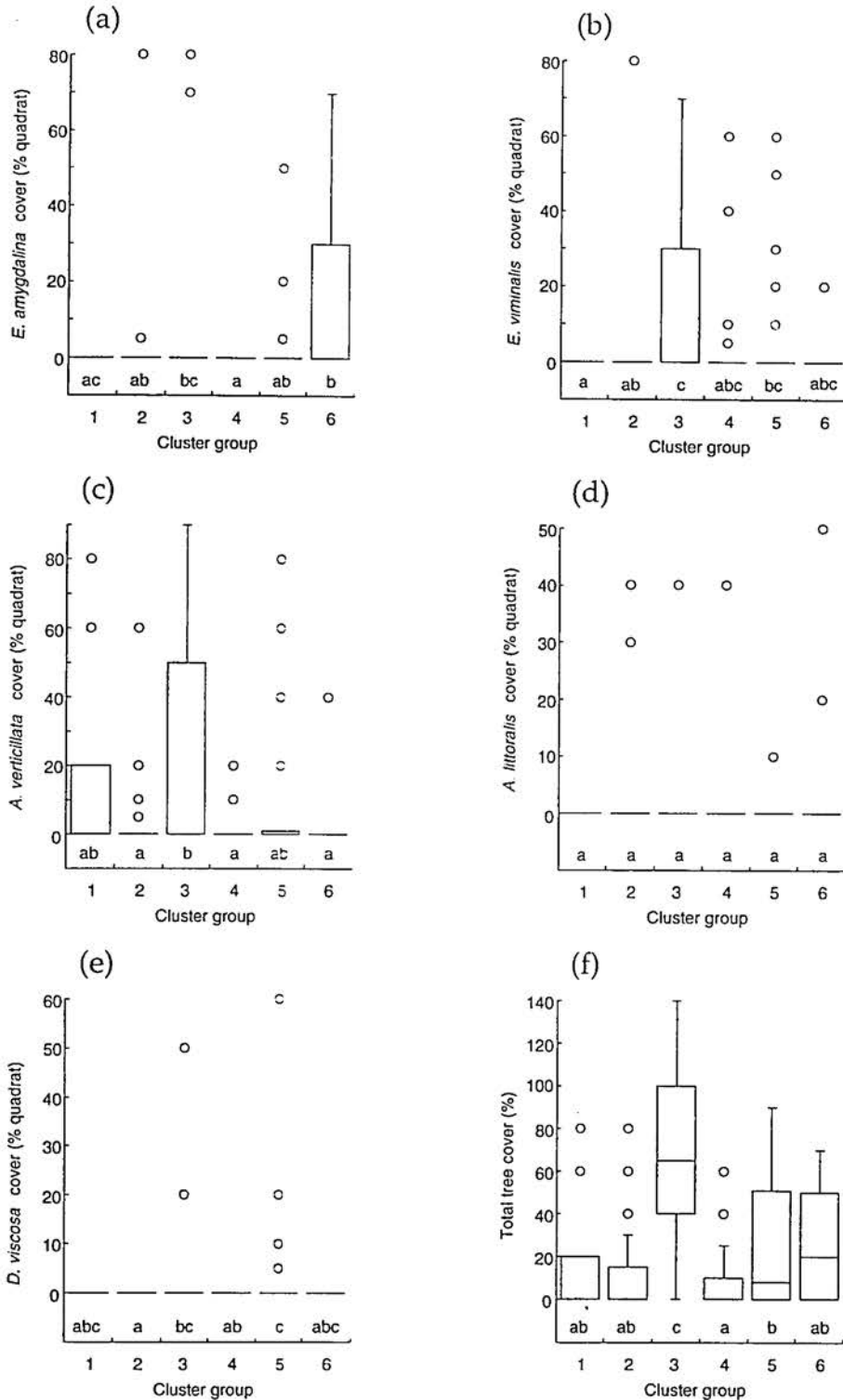


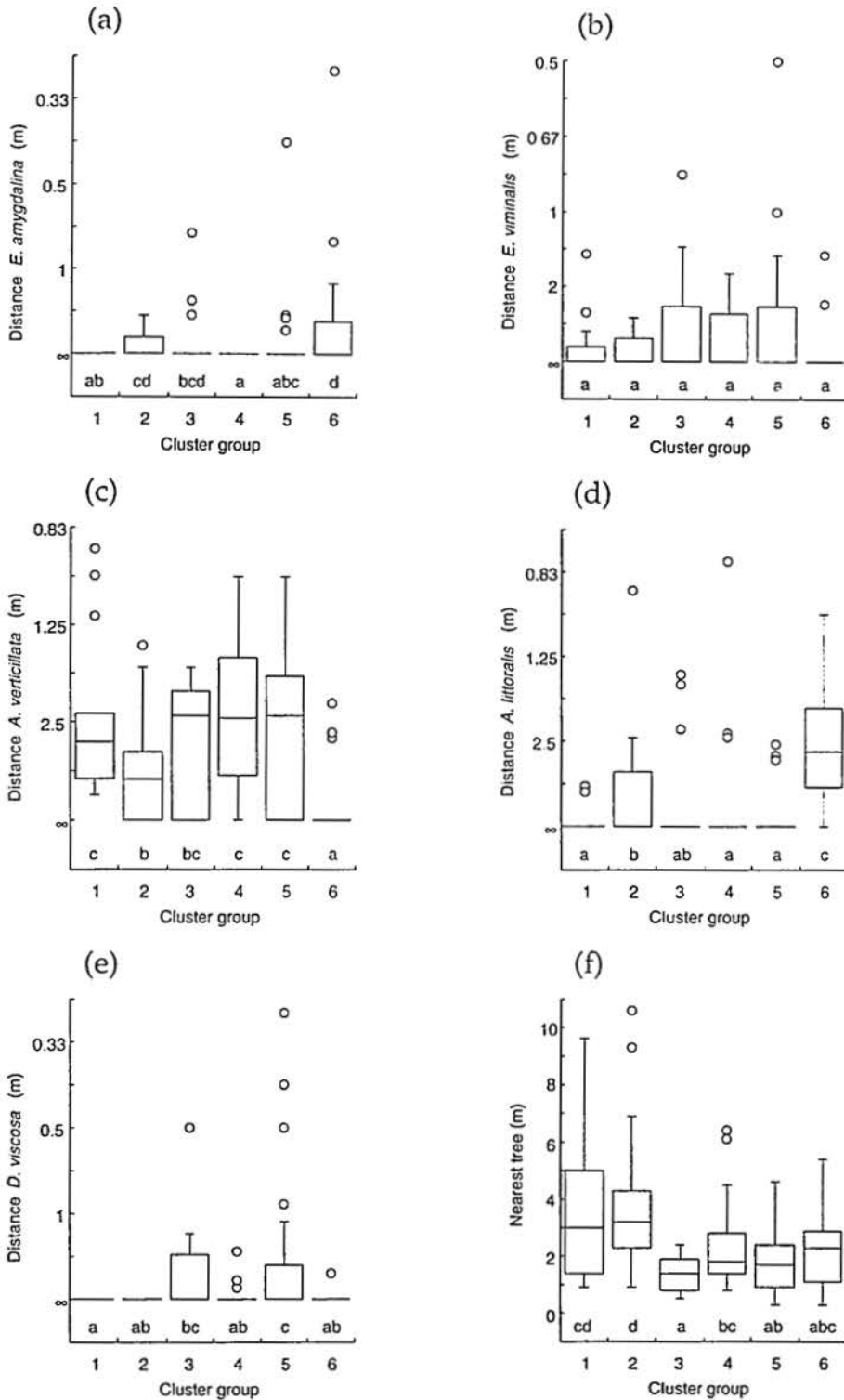
Fig. 4.10 A schematic map of the spatial distribution of the floristic groups defined by cluster analysis of the 1 x 1 m quadrats at Bellerive. \* = unclassified; T = vehicular track.



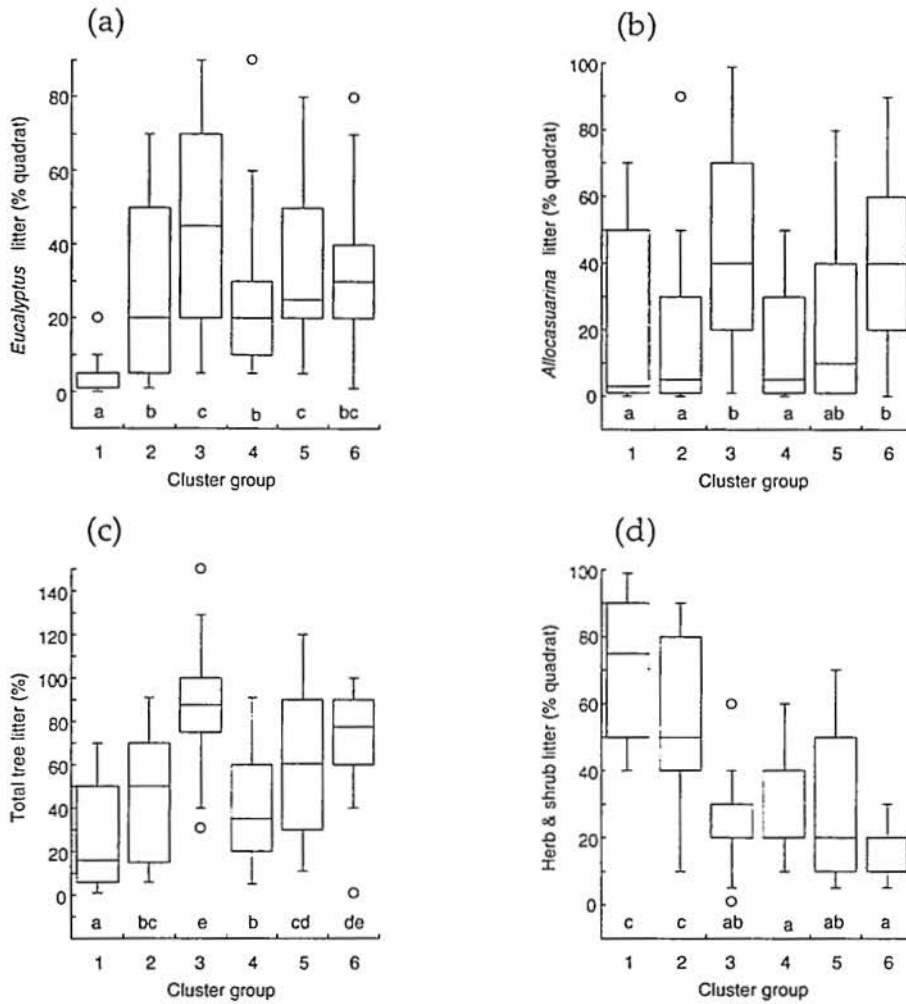
**Figs 4.11** Attributes of floristic groups defined by cluster analysis on the 1 x 1 m quadrats at Bellerive. (a) total number of species per quadrat; (b) bandicoot diggings ≤ 150 cm<sup>2</sup> in size; (c) total bandicoot diggings; (d) exposed mineral soil; (e) exposed rock; (f) soil depth. Groups with the same letter are not significantly different ( $P < 0.05$ ).



**Figs 4.12** The projected foliage cover of trees for floristic groups defined by cluster analysis on the 1 x 1 m quadrats at Bellerive. (a) *Eucalyptus amygdalina*; (b) *E. viminalis*; (c) *Allocasuarina verticillata*; (d) *A. littoralis*; (e) *Dodonaea viscosa*; (f) total overlapping tree cover. Groups with the same letter are not significantly different ( $P < 0.05$ ).

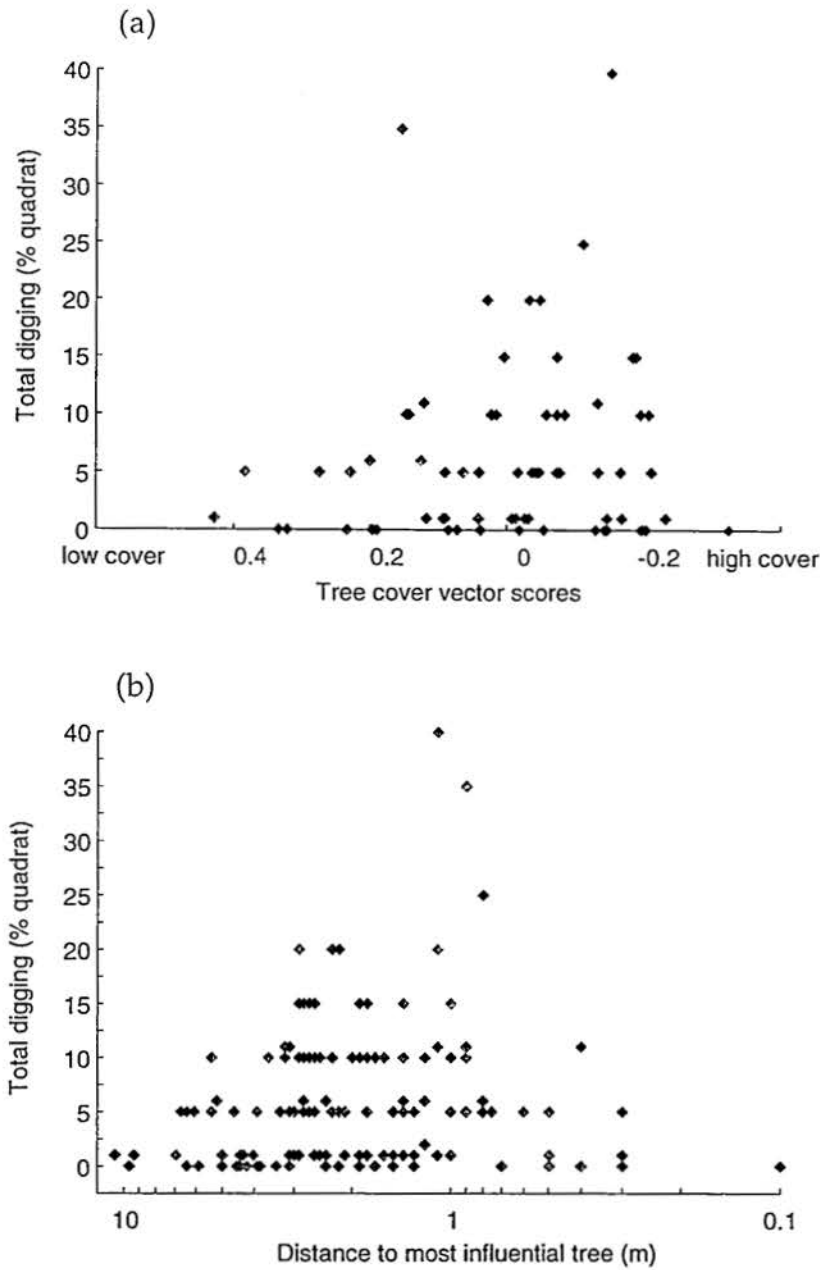


**Figs 4.13** Distance to the most influential trees for floristic groups defined by cluster analysis on the 1 x 1 m quadrats at Bellerive. (a) *Eucalyptus amygdalina*; (b) *E. viminalis*; (c) *Allocasuarina verticillata*; (d) *A. littoralis*; (e) *Dodonaea viscosa*; (f) all species. Note that (a)-(e) have different scales from (f). On the distance scales,  $\infty$  indicates that the species was not one of the two most influential trees for a quadrat. Groups with the same letter are not significantly different ( $P < 0.05$ ).



**Figs 4.14** The cover of tree litter for floristic groups defined by cluster analysis on the 1 x 1 m quadrats at Bellerive. (a) *Eucalyptus* spp.; (b) *Allocasuarina* spp.; (c) *Eucalyptus* + *Allocasuarina*; (d) Herb & shrub (mostly grass). Groups with the same letter are not significantly different ( $P < 0.05$ ).





**Figs 4.15** The percentage of ground covered by total bandicoot diggings in the 1 x 1 m quadrats at Bellerive, in relation to (a) the ordination scores for the vector fitted for combined cover of *Eucalyptus amygdalina* and *Allocasuarina verticillata*; and (b) the distance to the most influential tree (distance is shown on a log scale).

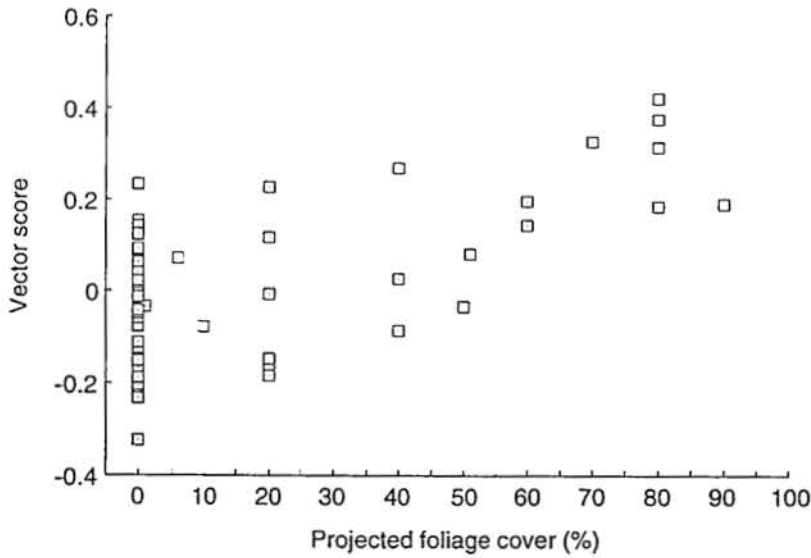


Fig. 4.16 The ordination scores for a vector fitted for the combined cover of *Eucalyptus amygdalina* and *Allocasuarina verticillata* in relation to the projected foliage cover of the same species.

## Discussion

### *Rates and season of digging*

Digging at all sites was considerably less in the summer and autumn than in the winter and spring. At Hospital Creek and the Old Coach Road, even though the sample areas were large, they may not have been large enough to give reliable seasonal trends because the overall rates of digging were so low. With such low rates at these sites, it is not worth considering the diggings of different animal species separately.

The rate of digging at Annandale is relatively high, but the sample area was located mostly under the canopies of trees, to coincide with the location of *Lepidium hyssopifolium*. The overall digging rate over a larger area, which included inter-canopy gaps, would probably be much lower. The seasonal trend in the digging rate at Annandale, expressed as the total area of disturbance per 100 m<sup>2</sup>, is consistent with that found by Taylor (1992a) for

a rate based on the number of holes per time interval. The difference in the winter and spring peaks in digging rate for the two different measures at Annandale (Fig. 4.6a), is probably confounded by the combining of data on bandicoot and bettong diggings. Individual diggings could not reliably be attributed to either bandicoots or bettongs.

Digging by bettongs and bandicoots was markedly more frequent at the sites with sandy soils on sedimentary substrates (Annandale, Bellerive on sandstone) than at the sites with heavier soils on dolerite (Bellerive on dolerite, Hospital Creek, Old Coach Road). This fact has been reported elsewhere for bettongs (Taylor, 1992a), but has not been recorded before for bandicoots. The diet of the two bandicoot species is considerably different from that of bettongs (cf. Heinsohn, 1966; Quin, 1985; Taylor, 1992c), but they all appear to dig infrequently on dolerite, possibly for different reasons. Availability of suitable food and the ease with which the soil may be dug could both be factors (Taylor, 1992a). As mentioned in Chapter 2, moderately intense digging on dolerite has been observed at some localities.

The many large diggings and the results of the trapping suggest that brown bandicoots were probably responsible for most of the diggings at Bellerive, although eastern barred bandicoots may have contributed some of the smaller ones. Brown bandicoots are reported to dig deeper holes (Heinsohn, 1966) and therefore larger diggings (see Chapter 3). Brown bandicoots were frequently sighted, both dead and alive, and eastern barred bandicoots were sighted on two nights with a spotlight. The morphology and size of larger diggings are certainly consistent with the description of brown bandicoot diggings on sandy soils by Heinsohn (1966).

The dolerite part of the 0.8 x 150 m transect at Bellerive faces north while the sandstone part faces south, with the boundary at the top of the hill. The dramatic difference in digging rate on these geologies is consistent with other sites, but the lie of the land may have had some influence. The largest diggings on the sandstone were much larger than those on the dolerite. It is possible that both bandicoot species were responsible for digging on the sandstone, but that brown bandicoots did not venture far on to the dolerite area. No brown bandicoots were observed on the northern slope, and when

the trapped brown bandicoots were released they ran south for cover into thicker heathy vegetation. The vegetation on the dolerite, which was a very dense sward of *Poa rodwayi*, *Themeda triandra* and *Stipa* spp. with very few trees, was possibly more suitable for eastern barred bandicoots than brown bandicoots (Heinsohn, 1966).

Although individual diggings at Bellerive are on average smaller in winter, the higher rate of digging of new holes means that the total area of disturbance is much greater (Fig. 4.2a). The diggings which are less than 10 cm<sup>2</sup> tend to fade away and be unrecognisable after several months, being covered in litter or washed away by rain. The largest diggings remain quite conspicuous, with considerable bare soil, for up to several years (see Chapters 3 and 5). For diggings larger than 100 cm<sup>2</sup>, there is little seasonal variation in size (Fig. 4.5b), but there is still a greater number of holes being dug in the late winter and spring (Fig. 4.3b). These larger diggings are probably a more ecologically important modification of the soil environment than the many smaller winter diggings, which probably contribute very little in terms of a modified soil resource for plants.

The Hospital Creek study site was burnt in early September 1990 by the logging company which owns the land (Peter Kent, Triabunna, pers. comm.). Although detailed records of digging activity were not commenced until eight months after the fire, there was no evidence of recent bettong diggings when the site was visited in January 1991. Individual diggings remain visible for more than a year, and the approximate age can be determined by the degree of infilling and the amount of litter covering the hole. Similarly, very few bettong diggings were noted during the detailed record period which ended on 1 May 1992. An increase in bettong digging soon after fire has been reported for sedimentary substrates in Tasmania, where it coincided with an increase in the production of sporocarps of hypogean fungi (Taylor, 1991; Chris Johnson, pers. comm.). The findings at Hospital Creek suggest that either the fire/fungi relationship is different on dolerite, or alternatively that bettong digging is less predictable as well as being less frequent on dolerite.

*Spatial pattern of diggings and trees*

The toroidal translation tests suggest that larger bandicoot diggings at Bellerive are not random in the landscape but are on average located closer to at least some tree species than would be expected by chance, at least at certain times of the year. The difference between the mean of the mean nearest tree distances for the random translations and the real mean distance ranged from 0.1 to 0.3 m (Table 4.2). This difference is not very large, suggesting that either the strength of the association between diggings and trees is not very strong, or alternatively that trees are so close together that the sub-regions inside the mapped area which are less favoured for digging are only a small proportion of the total area. It is also possible that diggings are associated with trees, but tend not to occur at very small distances from trees (Fig. 4.15b).

Diggings are associated with trees at certain times of the year, but not at others times, although the results are apparently not consistent from year to year (Table 4.2). Diggings appear to be most strongly associated with trees in the sample intervals that cover the months from July to October. The second sample period of these particular months was in fact much longer than the first (Table 4.3), and may have not shown a significant association between diggings and trees because of the inclusion of diggings which were unrelated to tree location. For these seasonal tests (and others), the test used the distance *from* diggings *to* the nearest tree of any species. Thus, the tests should not be affected if diggings were in fact closer to different tree species at different times of the year.

The various tests suggest that no single tree species is responsible for the distribution of diggings. *Allocasuarina verticillata* and *Acacia dealbata* appear to be particularly important, but they are also by far the most abundant species (Table 4.3). Diggings are still significantly associated with trees even after the elimination of virtually all *A. dealbata* individuals (Tables 4.2, 4.3). However, *A. dealbata* was highly clumped in the mapped area and probably never far from the numerous individuals of younger *A. verticillata*.

It is beyond the scope of this study to determine the cause of the relationship between bandicoot diggings and trees, because no investigation of the diet of bandicoots was undertaken. It would be interesting to know

what food the bandicoots are hunting, particularly in relation to deeper holes. Given the extremely varied diet of the southern brown bandicoot (Quin, 1985), it is quite possible that trees are determining the spatial pattern of a variety of very different foodstuffs. Some bandicoot digging could be in pursuit of sporocarps of hypogean fungi. These fungi grow along the roots of trees (Claridge *et al.*, 1993a) and could therefore be responsible for the tendency of diggings to be associated with the general area of trees, rather than the actual trunk itself. Some unidentified tubers of either lilies or orchids were observed at the surface of fresh diggings at Bellerive. Some lily and orchid species grow where tree influence is greater (Table 4.10). Insect larvae from the family Scarabaeidae may be present in the soil in greater numbers beneath trees, because of the practice of hypsotaxis (Peter McQuillan, pers. comm.). These larvae are eaten by southern brown bandicoots (Quin, 1985).

#### *Digging in relation to understorey and trees*

The digging and floristic data from the 0.8 x 150 m transect indicate that the abundances of native understorey species are lower in the quadrats which have both a greater percentage of dug ground and a greater abundance of exotic species. The negative response of native species to total digging does not appear to be simply a result of burial by diggings, because the total quadrat area disturbed in two years was less than 26% in all quadrats, which could not account for the degree of depletion of native species (Table 4.5). It could be hypothesised that digging is encouraging the invasion of weeds, which are in turn displacing native species. Digging could well be a direct cause of a greater abundance of annual weeds such as *Aira* spp. and *Silene gallica*. The abundance of *Aira* spp. and native forbs was negatively correlated, but the projected foliage cover of *Aira* spp. was always very small. Additionally, the distribution of most weed species was confined to the first part of the transect, which limits the degree of confidence that can be placed on the influence of exotics. The weeds certainly have displaced native species in the first part of the transect, but the cause of this very weedy patch was possibly a human disturbance such as the dumping of lawn clippings.



The indices of tree influence which were used in the analysis of the 1 x 1 m quadrats are only an approximate index of the many factors which possibly affect the understorey. Percentage of tree canopy cover can only be directly related to the through-fall and stem-flow of leachates from the leaves, branches and trunk of trees. In a woodland situation at this latitude, the degree of shading will depend on the sky view factor, which will in turn depend on which side of the tree is being considered, as well as the locations of other trees. For example, a 1 x 1 m plot on the north side of a taller tree, but just beyond the canopy edge, will receive very nearly as much direct insolation as a plot of the same size one metre closer but underneath the canopy. The influence of trees will be exerted beyond the canopy edge—these influences could involve competition in the root zone for nutrients and water and/or various effects contributed by tree litter (see review in Vetaas, 1992). Photographs taken with a fish-eye lens could have provided another index of tree influence.

Another problem involves the definition of the zone of influence in relation to the size of a tree. If the zone of influence extends beyond the canopy edge, then for any one tree species, presumably there is some fixed relationship between the diameter of the canopy and/or trunk, the height, the age and the diameter of the zone of influence. Without making detailed measurements of soil parameters such as moisture and nutrients at varying distances away from the trees in all directions, such a relationship is difficult to establish. The sampling strategy of the 1 x 1 m quadrat data was not based upon individual trees because the canopies frequently overlapped, often between different species.

The 1 x 1 m quadrat data identify the relationship between trees and understorey, but for the reasons outlined above, the indices of tree influence are very crude. The percentage cover of tree litter might have been more revealing, had it been recorded on an individual species basis. The distances to the most influential trees would probably give more powerful indices, if a relationship between tree size and the zone of influence could be established. The relationship between tree canopy cover and the floristic variation of the understorey, as shown by ordination scores, has a truncated appearance

because of quadrats with zero tree cover, thus indicating the limitation of tree cover as an index of tree influence (Fig. 4.16).

Despite these problems, it is possible to identify a strong trend in the floristic composition of the understorey which can be related to overall tree influence. The influence of different tree species does not appear to give rise to distinctive floristic groups, at least not in the analysis presented here for cluster groups 3, 4 and 5. There is a suggestion that this does happen to some extent in group 6, although *Allocasuarina littoralis* may not be the direct cause of the different assemblage of understorey species with which it is associated.

Analagous patterns in understorey and overstorey have been found by other workers in grassy woodlands in south-eastern Australia (Robertson, 1985; Ian Lunt, pers. comm.). In a piedmont woodland in North Carolina, where tree influence indices were similarly tested, the understorey/overstorey relationship was found to be very weak. This was possibly because of the overriding influence of soil and topographic variables (Reed *et al.*, 1993).

Intermediate levels of tree influence appear to favour the highest alpha diversity of understorey species, possibly because competition from dominant species reduces diversity at both ends of this gradient. At the treeless end of the gradient, *Themeda triandra* is a dominant grass which is known for its ability to form a dense sward and is believed to eliminate many 'interstitial' forbs (Stuwe & Parsons, 1977; Robertson, 1985). *Themeda triandra* is less abundant under trees, so at the very shaded end of the gradient, tree-related factors appear to reduce alpha diversity and the total cover of understorey (Table 4.10). At intermediate levels of tree influence, trees are able to suppress the dominant grasses but not the other understorey species. This hypothesis seems plausible and higher species richness at intermediate levels of tree influence has also been described in Victoria (Robertson, 1985).

Bandicoots appear to dig across the full spectrum of tree influence in cluster groups 3, 4 and 5 (Figs 4.11b, c). Although the trend is inconclusive from the 1 x 1 m quadrat data, it appears that they may dig most intensely at intermediate distances from trees (Fig. 4.15). Further evidence for this supposition comes from the mapped data on the 10 x 50 m belt transect (see earlier discussion). Twelve of the 1 x 1 m quadrats are within the mapped

belt transect area, and all but one of these quadrats were classified in cluster groups 3, 4 or 5.

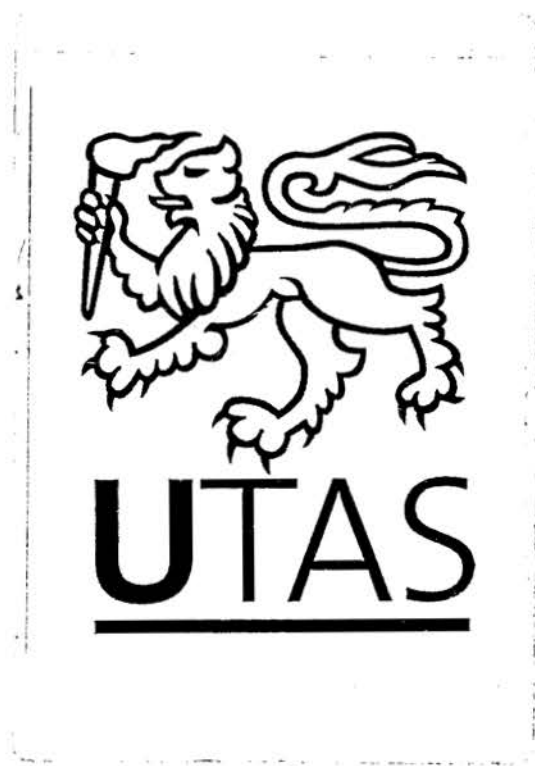
Tests based on fully-mapped data (e.g. the 10 x 50 m belt transect) are more powerful at detecting spatial patterns than those based on quadrat data (e.g. the 1 x 1 m quadrats) (Upton & Fingleton, 1985). There is very much a 'hit or miss' problem with recording the cover of diggings in the 1 x 1 m quadrats, so the lack of resolution of spatial pattern from that data set is more likely to be a type II error than a genuine support of the null hypothesis of no difference in digging intensity between the cluster groups. Additionally, sample sizes may have been limiting the power of these analyses.

If gaps created by digging facilitate the regeneration of herbaceous species, digging might be expected to be most beneficial where competition from dominants is greater, such as where there is a dense sward of grasses. Digging does occur in these areas and may well be important. However, there is a suggestion in the data that digging may be more intense in the areas where the alpha diversity of the understorey is greatest; these areas are also where competition from understorey dominants is possibly lower. Therefore, if digging is having some influence on regeneration, does this influence become more important where competition is greater, or is it simply proportional to the frequency of digging? On the basis of the trend in alpha diversity in relation to tree influence, it could be hypothesised that the latter is true and the importance of digging is simply proportional to the digging rate. However, no causal relationship between digging frequency and alpha diversity can be assumed at this stage: there may be two quite independent processes occurring. The question of whether or not digging does facilitate the regeneration of plants is the subject of the next chapter.

### *Conclusion*

Diggings are more common on sedimentary substrates compared with dolerite areas. Up to 2.9% of the ground surface area is disturbed per annum on sandstone at Bellerive. Seasonal trends in digging frequency exist at several sites, with a general trend towards greater digging in the months of winter and early spring. At Bellerive, bandicoot diggings are smaller in winter, but

both the number and total area disturbed are greater in winter. The larger diggings at Bellerive are associated with trees in August and September, when the rate of appearance of these holes is greater, but they are not consistently associated with trees at other times of the year. The intensity of bandicoot digging is correlated at least to some extent with trends in the floristic composition of the understorey. Trends in the floristic composition of the understorey are strongly correlated with the degree of influence of trees.



## Chapter 5

### The Germination and Establishment of Seedlings on Diggings

#### Introduction

The diggings of small native mammals create microsites which differ from surrounding areas in a number of measurable physical characteristics, as described in Chapter 3. In this chapter I investigate the effect that these differences have on the germination and survivorship of seedlings.

While the emphasis of this thesis is on rare and endangered species, data are also presented for some common species. There are several reasons for this. Firstly, it is conceivable that if only rare and endangered species were considered, some important responses may not have been recorded. These observations may be relevant to the conservation and management of both rare and common species throughout the range of similar plant communities in Australia. Secondly, it has enabled a comparison between the responses of rare species and common species to be made; discussion of this will be left to Chapter 9. Thirdly, it was time efficient to collect data on other species in the same plots.

In a number of places in Tasmania, the success of rare or threatened plant species at establishing on disturbances associated with road works has been observed. To gain insight into this process, observations on the germination and establishment of *Lasiopetalum micranthum* on an area disturbed during road works were made at the Old Coach Road. The aim was to compare the results with those for natural mechanical disturbances created by mammals and with undisturbed areas.

#### Methods

Data on species other than those recognised as rare or threatened at either the state or national level were collected mainly at Bellerive, but also at Hospital Creek and East Risdon.

*Annandale*

Twenty-three 40 x 40 cm permanent quadrats were established over recent bettong and bandicoot diggings, 21 on 25 May 1990 and the other two on 8 May 1991. The quadrats were marked with 250 mm nails in two opposing corners. The quadrats were located so that all were within 2 m of adult *Lepidium hyssopifolium*, to be certain that diggings were within the range of potential dispersal of seed (see Chapter 6). The quadrats were spread over an area of approximately 200 m<sup>2</sup>. Within each quadrat there was a proportion of undisturbed ground, a proportion of ground which was the hole formed by the digging, and a proportion of ground covered by soil excavated from the hole. These three categories will be referred to as 'undisturbed', 'holes' and 'mounds' throughout this chapter. The boundaries of the hole and mound were carefully drawn on to a graphical representation of the quadrat. The boundary between hole and mound was drawn along the original ground level (see Chapter 3, Fig. 3.1).

All seedlings and mature plants of *L. hyssopifolium* within the quadrats were mapped on to the graph paper, using a grid with 25 cm<sup>2</sup> cells as a guide. The grid had a double layer of string to reduce parallax error (Mueller-Dombois & Ellenberg, 1974). The location of seedlings was carefully determined to be certain that they were mapped on the correct category of ground (i.e. undisturbed, hole, mound). At each subsequent visit, the seedlings mapped in the previous visit were located to determine whether they were still alive, and new germinants were mapped, using a different colour for each visit so that the time of germination and death of each individual could be distinguished. The projected foliage cover of each vascular plant species over the whole quadrat was estimated using the 25 cm<sup>2</sup> grid cells as guide. The visits were spaced at one to four monthly intervals.

*Bellerive*

Twenty 40 x 40 cm permanent quadrats were located over larger bandicoot diggings in July 1990 and new seedlings (i.e. with cotyledons) and adult plants (i.e. older plants) were mapped as described above. After most



of the large nails had been stolen they were replaced by thin metal rods. These quadrats were all subjectively chosen to be within the vicinity of mature *Velleia paradoxa* and were spread over an area of approximately 1000 m<sup>2</sup>. A second quadrat was established next to each of the dug quadrats on undisturbed ground to serve as a control. The centres of the pairs of quadrats were one metre apart and the direction to the centre of the control plots was determined by random numbers between 0 and 360 to establish a compass direction. A control plot was rejected if more than 15% was disturbed by animal diggings and a new random number was drawn. This process was repeated until a suitable control area was found. Although the location of diggings is determined by the food requirements of bandicoots (see Chapter 4), differences in vegetation between mound quadrats and adjacent controls would only be due to random variation at that spatial scale.

The species mapped included all dicotyledons and all monocotyledons with the exception of Poaceae spp. For *Briza maxima*, which is an exotic annual grass, separate counts were made of all individuals occurring on holes, mounds and controls (results in Chapter 8).

Samples were mostly made at two monthly intervals, with the final sample in December 1992. Although sampling commenced in July 1990, data are only presented for seedling emergence and survivorship from 1991 and 1992. The sampling in 1990 was dedicated to the identification of seedlings of the many species and to the mapping of already established plants, some of which did not resprout from perennating underground organs until well into the winter; many species at this site are deciduous and retreat underground over summer.

At the conclusion of the study in December 1992, the total projected foliage cover of all living vascular plants over the treatment portion of the quadrats was recorded, using the 25 cm<sup>2</sup> grid cells as a guide. The cover of litter and bare mineral soil was similarly recorded in October 1992. One digging quadrat was demolished by the removal of a large stone by suburban bush raiders and this pair of quadrats was excluded from analyses where necessary.



Two areas with a spatial juxtaposition of adult *Velleia paradoxa* and abundant bandicoot diggings were marked out for long term sampling in April 1991. The two areas, which were 7.2 x 4.8 m and 2.4 x 4.8 m, were 4.4 m apart. This method of sampling was chosen because of the extremely patchy distribution of *V. paradoxa* in the study site. All recent germinants and adults of *V. paradoxa* within these areas were mapped on to graph paper as described earlier, along with the boundaries of diggings. The diggings were subjectively classified as 'new' or 'old', that is, either less or greater than an approximate age of 12 months. At a subsequent visit in July 1991, all seedlings were mapped, and deaths of previous germinants were noted. At two subsequent samples on 21 November 1991 and 23 March 1992, the fate of seedlings mapped in the two previous samples was noted, but no more seedlings were mapped. This saved considerable time and no new seedlings were observed in the course of searching for previously mapped ones.

A once-only sample of *V. paradoxa* seedlings was carried out on another 6 x 12 m area in May 1992. A tally was made of the number of new seedlings occurring on 'old', 'new', or 'undisturbed' ground, and the area of ground covered by each of the three categories was recorded using a grid with 25 cm<sup>2</sup> cells as a guide.

### *Chimney Pot Hill*

Twenty-seven 40 x 40 cm permanent quadrats were established over bandicoot diggings in May 1990 and mapped as described for Annandale. All quadrats were located in the vicinity of *Gahnia rodwayi* and *Olearia ericoides* and were spread over an area of approximately 2500 m<sup>2</sup>. The site was visited at approximately six month intervals, with the final visit in December 1991.

### *Dukes Marshes*

*Euphrasia scabra* and diggings were recorded along two transects in March 1990. One transect was 33 m long and had 40 x 40 cm quadrats, while the other was 100 m long with 40 x 80 cm quadrats. Quadrats were spaced 0.5 m apart along both transects. In all quadrats, a count was made of

individuals of *E. scabra* on and off diggings and the proportions of dug and undisturbed ground were recorded.

#### *East Risdon*

Twenty-eight 40 x 40 cm permanent quadrats were established over recent bettong and bandicoot diggings in April 1990 and individuals of all vascular plant species were mapped using the methods described for Annandale. The quadrats were spread over an area of approximately 1000 m<sup>2</sup> and all were located within 1.5 m of mature *Olearia hookeri* plants. The quadrats were recorded until March 1992 at intervals of around five months.

#### *Hospital Creek*

Thirty-one 40 x 40 cm permanent quadrats were established over subjectively chosen bettong diggings in April 1990 and mapped as described for Annandale. The quadrats were spread over an area of 1400 m<sup>2</sup> and all were within a few metres of adult *Odixia achlaena* plants. No seedlings or adults of *O. achlaena* were observed in these plots in April or July 1990. The entire site was burnt in September 1990 and many new germinants of *O. achlaena* were observed in May 1991. On this date, a count was made of new germinants of *O. achlaena*, *Dodonaea filiformis* and *Acacia genistifolia* in a series of 51 pairs of 40 x 40 cm quadrats, with one of each pair located over a bettong digging and the other serving as a control. The control plots were located as described for Bellerive. This series of quadrats consisted of the following: 15 of the original quadrats which still had clearly delineated diggings; all recognisable diggings within the vicinity of the original quadrats; and all such diggings in an adjacent 700 m<sup>2</sup> area. The location of seedlings on undisturbed ground, holes and mounds was determined for the dug quadrats. A subset of 25 pairs of these quadrats was established as permanent plots and all seedlings of the three species were mapped. These plots were chosen on the basis of having at least one seedling of *O. achlaena* on either the hole or mound, to have sufficient numbers for analysis of survivorship. To further this objective, three extra quadrats were established over diggings.

*Kellevie Road*

Sixteen 40 x 40 cm permanent quadrats were established over recent bettong diggings in April 1990, and mapped as described for Annandale. The quadrats were spread over an area of 1000 m<sup>2</sup> and all were within 2 m of adult *Odixia achlaena* plants. The site was subsequently visited in September 1990 and April 1991. The areas between permanent quadrats were also searched for seedlings of *O. achlaena* on each visit.

*Old Coach Road*

Seven 40 x 40 cm permanent quadrats were established over recent echidna diggings in March 1990, plus two more in September 1990. These were mapped as described for Annandale and all were within a few metres of mature *Lasiopetalum micranthum* plants. All animal diggings within the 50 x 30 m area (see Chapter 4) were also inspected at each visit for the presence of seedlings of *L. micranthum*. Additionally, two permanent belt transects were established in March 1990. One of these transects was 28 x 2 m and was located entirely on ground that was bulldozed in August 1987, during maintenance of the unsealed Old Coach Road. The second transect was 50 x 2 m and was located nearby on undisturbed native vegetation. All individuals of *L. micranthum* in these two areas were mapped (including adults, seedlings and recent germinants), and the maximum diameter of each individual plant was measured to the nearest centimetre, or half centimetre for seedlings less than one centimetre in diameter. *Lasiopetalum micranthum* is a prostrate shrub with radiating branches forming an approximately circular outline. Subsequent records were made at 2 to 6 monthly intervals until March 1992.

*Powranna*

All individuals of *Glycine latrobeana* in a 5 x 11 m area were mapped in March 1990. Subsequent records were made in May and December 1990, and in January and December 1991.

### Westwood

The occurrence both on and off bettong diggings of recently germinated seedlings of *Brunonia australis* was recorded in two sets of once-only sampling in August 1991. In the first set, 3 areas with a spatial juxtaposition of adult *B. australis* and abundant bettong diggings were identified and a 5 x 10 m plot was marked out on each. All diggings within the plot had a 40 x 40 cm quadrat placed over them and a control plot located 0.7 m away (centre to centre) using the method described earlier, but with a 25% disturbance threshold for rejection. The area of the treatment portions of the quadrats was calculated using the 25 cm<sup>2</sup> grid as a guide. Diggings were classified as 'very old', 'old' or 'new'; with the approximate age of these categories being: greater than 12 months, 3-12 months and less than 3 months respectively. All recently germinated seedlings and adults of *B. australis* were counted.

In the second set of sampling, 40 x 80 cm quadrats were placed along 50 m transects using a stratified random method, which involved the random placement of two quadrats in each 10 m segment. The transects were parallel, spaced 5 m apart and a total of 15 transects were sampled. In each quadrat the following was recorded: (a) the number of recent germinants of *B. australis* on each of the three age categories of diggings mentioned above and on undisturbed ground; (b) the same for adults; (c) the area covered by diggings in the three age categories; (d) the minimum distance from recent germinants to the nearest digging; (e) the same for adults; (f) for each individual germinant, the distance to the nearest inflorescence of adult *B. australis*. These were dead inflorescences from the previous flowering season and were still quite visible, even if broken off near the rosette.

### Data Analysis

The seedling density data on paired quadrats were not amenable to testing by parametric analysis of variance because of numerous zero counts, the need to standardise densities to the same unit area and the need to log transform the data to meet the assumptions of ANOVA. All paired comparisons

of seedling densities were tested by the Wilcoxon signed-rank test, which was also used to compare other parameters such as litter, bare soil and total plant cover. Data are presented in the form of 'box plots', which indicate the 25th and 75th percentiles (the box), the median (the bar inside the box) and the range of values (lines with bars beyond the box, with circles indicating outliers). The densities are presented per 1000 cm<sup>2</sup>, because this unit is at the same approximate scale of the quadrats (1600 cm<sup>2</sup>) and the actual treatment areas were mostly less than the full quadrat size. The seedling density data from unpaired sampling were tested by the  $\chi^2$  one-sample test. For the Bellerive data, the correlation between the percentage of exposed bare soil and seedling densities in control quadrats was tested using Spearman rank-order correlation.

At Bellerive, seedlings of the following taxa were combined in analyses: *Eucalyptus amygdalina*, *E. viminalis*; and *Senecio quadridentatus*, *S. glomeratus*, *S. hispidulus*. New rosettes and leaves were observed for a number of orchid species. Some of these species are colonial and reproduce clonally by underground root extensions which give rise to new tuberoids and rosettes (Jones, 1988). It is possible that other species reproduce clonally and a means of distinguishing genets and ramets was not pursued. Therefore these have been treated as one in the analyses and only new individuals which were at least 1 cm inside the edge of the mapped area were counted, to avoid confusion with resprouting old rosettes and leaves. Data were pooled for the following orchid species which could not be distinguished vegetatively: *Pterostylis alata*, *P. concinna*; *Diuris maculata*, *D. sulphurea*; *Caladenia caudata*, *C. dilatata*, *C. clavigera*.

The seedling emergence data for mounds and controls from Bellerive were analysed by global non-metric multidimensional scaling (GNMDS) using the programmes MDS and DECODA (ANUTECH Pty. Ltd., Australian National University, Canberra). The dissimilarity matrix used the Kulczynski dissimilarity coefficient on log transformed densities, with species standardised to equal maximum abundances. Species that occurred in less than 3 quadrats were excluded. The analyses were performed in 1 to 5 dimensions with 50 random starting configurations. A vector fitting algorithm in DECODA was used to find the maximum correlation between quadrat



variables and the GNMDS solutions, and to apply a Monte Carlo significance test based on 999 random permutations.

Spatial association between seedlings and adults of *Velleia paradoxa* was tested for the 7.2 x 4.8 m mapped area, by measuring the distance to the nearest seedling and adult plant from 50 random points. The degree of association was then tested by Spearman rank-order correlation of the paired distances (Upton & Fingleton, 1985). The index of dispersion test was used to determine whether the spatial distribution of individuals of *Brunonia australis* in the transect quadrats was clumped, regular or random (Upton & Fingleton, 1985). These tests were performed for adults and seedlings separately. The degree of spatial association between plants of *Brunonia australis* and bettong diggings was tested by a 2 x 2 contingency test on the presence or absence of diggings and plants in transect quadrats, using the continuity-adjusted  $\chi^2$ . The same method was used to test for association between adults and seedlings (Upton & Fingleton, 1985).

The survivorship curves of seedlings were examined using the LIFETEST procedure in SAS (SAS, 1989). In these analyses, a survivorship function is calculated and the homogeneity of survivorship curves from different microsites (i.e. mounds, holes, undisturbed) was tested using the Wilcoxon test and the Log-rank test. The Wilcoxon test is more strongly influenced by early deaths than the Log-rank test (SAS, 1989; Cox & Oakes, 1984). The undisturbed category included seedlings from control quadrats and the undisturbed portion of dug quadrats. The limited number of sample intervals meant that the real survival times of seedlings were estimated to varying degrees and effectively treated as a small number of groups in the analyses. This kind of data has been described by discrete failure time models (Kalbfleisch & Prentice, 1980). To examine the effect that the discrete sampling intervals may have on the significance of tests for homogeneity, some analyses were performed where the survival times were made continuous by assigning the time at death for each seedling as a random number within the range of the interval in which it was known to die.

Where insufficient data were available for the comparison of survival curves, the proportions of seedlings surviving on different microsite areas

were compared using Fisher's exact probability test (2-tailed) on 2 x 2 or 2 x 3 contingency tables.

For *Lasiopetalum micranthum* at the Old Coach Road, comparisons of changes in plant radii from the first measurement of March 1990 were tested between the bulldozed transect and two categories of microsite on the undisturbed transect, either with or without dense cover of the sedge *Lepidosperma laterale*. The data were stratified in intervals of 5 cm of original diameter to remove the grazing/plant size effect (see Results section), and only live plants with original diameters from 5-44 cm were included, to cover the range of sizes that were present on all three transect categories. This was considered preferable to analysis of covariance because the slopes of the grazing response in relation to plant size were not constant across the three transect categories. The data were analysed using the GLM procedure in SAS (SAS, 1988b), with tests for differences between the transect categories being made against the plant size x microsite interaction.

Comparisons of the growth rates of newly emerged seedlings were made between disturbed and undisturbed microsites by analysis of variance and *t* tests on log transformed data. The growth rate calculations used the mid-points of the sample intervals as the emergence date for each seedling.

## Results

### *Annandale*

Germination of *Lepidium hyssopifolium* was observed in the late autumn through to early spring (May to September), with little or no germination occurring in the other months (Fig. 5.1a). In 1991, the onset of germination in June was coincident with the breaking of a short drought in May (Fig. 5.1b), but this was an atypical rainfall pattern (Fig. 5.2). The many seedlings observed in June 1992 were well advanced compared with the seedlings observed at the same time in the previous year. Therefore, germination appears to commence in late autumn or early winter and can be delayed by lack of rainfall.



There were no significant differences for 1990 or 1991 between the densities of newly emerged seedlings recorded on the three categories of microsite, holes, mounds or undisturbed (all 1990 comparisons:  $n=15$ ,  $P>0.4$ ; all 1991 comparisons:  $n=18$ ,  $P>0.17$ ; Fig. 5.3). In June 1992, the density of newly emerged seedlings was significantly greater on the digging mounds in comparison to both holes and undisturbed ground (both comparisons:  $n=18$ ,  $P<0.01$ ; Fig. 5.3). The relationship between the density on mounds and the density on undisturbed ground was linear for the paired samples, but with nearly four times as many seedlings on mounds (Fig. 5.4). Based on the total standing count of seedlings, including those mapped in June 1991 that were still alive, the density of seedlings was significantly greater on mounds than on undisturbed ground in September 1991 ( $n=17$ ,  $P<0.05$ ; Fig. 5.3; this comparison excluded one outlying quadrat which had a very small mound area with no seedlings).

The mortality of seedlings of *L. hyssopifolium* which were first mapped in June 1991 was not homogeneous across the three categories of microsites. The Wilcoxon and Log-rank tests were significant using the actual sample intervals and 20 replications of the same tests with random allocation of the time at death within the sample intervals (Table 5.1). The survivorship curves indicate that mortality in the first 90 days was higher on undisturbed ground and holes compared with mounds, although there was only one seedling still alive on a mound at the conclusion of the study in June 1992 (Fig. 5.5a). There was no difference in the survivorship of seedlings between microsite categories for the seedlings first mapped in September 1991 (Wilcoxon test  $\chi^2_2=1.0$ ,  $P=0.6$ ; Log-rank test  $\chi^2_2=2.0$ ,  $P=0.4$ ; Fig. 5.5b). All survivorship curves indicate that the mortality of *L. hyssopifolium* seedlings in the first few months is extremely high (Fig. 5.5). All seedlings which were mapped in either May or September 1990 were dead by January 1991. Of all the seedlings that emerged from May 1990 until February 1992, 4.0% (5 seedlings) were still alive in June 1992 on the mounds, none on the holes and 0.6% (1 seedling) on the undisturbed areas (Fisher's exact 2-tailed  $P=0.098$ ).

The majority of the ground cover in the quadrats consisted of the exotic annual grasses and forbs: *Bromus diandrus*, *B. hordeaceus*, *Vulpia bromoides*,

*Aira* spp., *Stellaria media*, *Hypochoeris glabra* and the biennial exotic *Cirsium vulgare*. The only native species with cover of any consequence were *L. hyssopifolium*, *Stipa* spp. and *Einadia nutans*. The cover of exotic species increased following autumn germination and was maximal in September. The total weed cover was considerably higher in 1990 because it was a particularly good year for *Hypochoeris glabra*. The yearly variation in onset of germination observed for *L. hyssopifolium* was also observed for weeds, which had much lower cover in June 1991 than in May 1990 or June 1992 (Fig. 5.6).

### *Bellerive*

Over the three years of the study from 1990-1992, the rainfall at Bellerive was close to or above the long term median in the winter and early spring months of July, August and September. However, the rainfall in autumn was well below the median for at least two months in each year. It was only slightly more than half the median for the autumn months of May and June in both 1990 and 1992 and in 1991, a severe autumn drought was recorded for April and May (Fig. 5.7).

In both 1991 and 1992, germination of most species took place in the autumn and winter months. Germination was strongly influenced by the distribution of rainfall over this period. In 1991, although germination had commenced by mid-April, the autumn germination of many species was checked by the April/May drought. In 1992, very little germination was observed in early April, with the bulk of seedling emergence for the year being recorded in June. Virtually no germination was recorded in the summer months of December to February and there was very little spring germination, with the exception of a few species such as *Arthropodium milleflorum* (Fig. 5.8). The germination of *Velleia paradoxa* was also coincident with autumn rainfall; in 1991 germination had started by the April observation, but none was observed in April 1992 (Fig. 5.8b). In 1993, germination of *V. paradoxa* had commenced by mid-March.

Over the whole of 1991 and 1992, the densities of newly emerged seedlings were significantly greater on digging mounds when compared with undisturbed controls for *Crassula sieberana*, *Helichrysum apiculatum*, *Scleranthus*

*biflorus*, *Senecio* spp., *Wahlenbergia stricta* and combined native Asteraceae spp. The opposite trend was recorded for only one species, *Arthropodium milleflorum*. A number of non-significant results were probably a consequence of very low densities. However, *Stackhousia monogyna* was one species where numbers were sufficiently high to place reasonable confidence on the finding of equal densities on both mounds and controls. The densities of seedlings on holes were significantly lower compared with mounds for *Schoenus apogon*, *Scleranthus biflorus* and for combined native Asteraceae spp. The only significant difference between holes and controls for seedlings was for *Thysanotus patersonii*, which was more abundant on the controls (Table 5.2).

New rosettes (*Pterostylis* spp.) and leaves (*Caladenia* spp., *Diuris* spp. and *Thelymitra pauciflora*) of orchids appeared more frequently on mounds and controls compared with holes. However, significant differences were only recorded for *Caladenia* spp. in the mound/hole comparison and for *Caladenia* spp. and *Diuris* spp. in the control/hole comparison. No significant differences were recorded for the mound/control comparisons (Table 5.2).

Taking the control quadrats on their own, there was a significant correlation for a number of species between the densities of newly emerged seedlings and the percentage cover of exposed mineral soil. Three of these species were amongst those which had significantly higher densities of seedlings on mounds compared with controls (Table 5.2). The percentage bare soil was very closely related to the cover of litter on mounds, holes and controls, because the total cover of living biomass in the understorey was quite low (Fig. 5.9).

The GNMDS ordination in 3 dimensions identified a trend in the species composition of seedling emergence which was correlated with the cover of litter and bare soil. The angle between the vectors for litter and bare soil was negligible, although the correlations had opposite signs. This floristic trend was quite distinct from that which was related to the spatial location of the quadrat pairs, based on a rank-ordering of quadrats according to their spatial proximity (Table 5.3). The mound and control quadrats were largely segregated along the bare soil/litter gradient, as identified by a paired comparison of ordination scores for this vector (Wilcoxon signed-rank test  $P=0.006$ ,  $n=19$ ).

Several species, which were not sufficiently abundant to produce significant differences in the univariate paired comparisons mentioned above, were nonetheless unambiguously located along the bare soil/litter gradient (Table 5.4). In summary, the species composition of seedling emergence on mounds is quite different from that found in undisturbed areas. For at least some species, this difference appears to be simply related to the presence or absence of litter.

The mortality of seedlings which emerged in 1991 was extremely high, particularly amongst native dicotyledons (Appendix 3). For example, all seedlings of *Helichrysum apiculatum* and all but one seedling of *Wahlenbergia stricta* died and very few grew beyond the two-leaf cotyledon stage. The growth of seedlings in 1992 was better, with some seedlings of these two species having grown beyond the two-leaf stage by December 1992. Only a few paired comparisons could be made on the densities of individual taxa that were still alive at the conclusion of the field study in December 1992. All of these comparisons for seedlings were not significant and low numbers almost certainly obscured some real differences. The density of ramets of *Caladenia* spp. and *Diuris* spp. which appeared for the first time in 1991 and then reappeared in 1992, was significantly greater on controls compared with holes. The density of reappeared ramets of *Pterostylis* spp. was significantly higher on controls compared with mounds (Table 5.5).

There were sufficient survivors of *Stackhousia monogyna* in December 1992 to place reasonable confidence in accepting the null hypothesis that the densities of survivors on mounds and controls were equal. Survivorship curves for *S. monogyna* indicate a steady mortality rate in the first 18 months, but with an increase over summer. The curves for mounds and undisturbed areas appear to be similar, although insufficient seedlings were recorded on mounds to make a formal comparison (Fig. 5.10a). Some individuals of *S. monogyna* which germinated in 1991 had flowered and were setting seed by December 1992.

For survivorship curves, it was not meaningful to pool seedlings from different recording times (and therefore germination times), because of the effect of summer mortality. The number of seedlings from individual recording

times was very limited and no other survivorship curves are presented for the paired quadrats. *Luzula meridionalis* was the only individual species for which a significant difference in survivorship was recorded for all seedlings mapped over 1991 and 1992, with a higher proportion of seedlings surviving on mounds compared with controls at the conclusion of the study (Fisher's exact  $2 \times 2$ ,  $P=0.042$ , excluding December 1992 germinants). Comparisons were only made between mounds and controls and only for species which had at least 10 germinants on each area. A complete summary of the survivorship of mapped species is given in Appendix 3.

With the exclusion of *S. monogyna*, the density of surviving native dicotyledons (at December 1992) when pooled together was higher on mounds compared with controls for 1992 germinants and for combined 1991/1992 germinants. Surviving dicotyledons (excluding *S. monogyna*) were significantly denser on mounds compared with holes for 1991 germinants and combined 1991/1992 germinants (Table 5.5). The survivorship of all identified native dicotyledons (excluding the annual *Crassula sieberana*), from both 1991 and 1992 combined, was significantly higher on controls compared with mounds, with proportions of 25.7% ( $n=284$ ) and 18.1% ( $n=359$ ) respectively (Fisher's exact  $2 \times 2$ ,  $P=0.021$ , excluding December 1992 emergents). With the exclusion of *Luzula meridionalis* and all *Orchidaceae* spp., there was no significant difference in the same comparison for identified native monocotyledons, with survivorship of 39.7% ( $n=121$ ) on controls and 51.7% ( $n=58$ ) on mounds (Fisher's exact  $2 \times 2$ ,  $P=0.15$ ).

At the conclusion of the study when the diggings were at least 30 months old, the cover of live plants was still considerably less on the mounds and holes compared with controls (both comparisons:  $n=19$ ,  $P<0.01$ ). This live cover on diggings was almost entirely vegetative recovery from underneath mounds and from the edges of holes. The cover of live plants was correlated between paired controls, mounds and holes, indicating that revival was a function of the original cover present before the diggings were created (all three comparisons: Spearman  $R=0.63-0.76$ ,  $n=19$ ,  $P<0.005$ ). There was no difference between mounds and holes in the cover of live plants after 30 months ( $n=19$ ,  $P>0.3$ ). Also at the conclusion of the study, the cover of litter

was significantly different between mounds, holes and controls, with the median values increasing in that order; bare soil showed the opposite trend (all comparisons:  $n=19$ ,  $P<0.005$ ; Fig. 5.9).

In the  $7.2 \times 4.8$  m and  $2.4 \times 4.8$  m areas in 1991, the density of newly emerged seedlings of *Velleia paradoxa* was significantly higher than expected on newer diggings. Fifty of these seedlings were mapped in April and another 38 in July. The expected value was less than 5 for the density of seedlings on all diggings in the  $6 \times 12$  m area in 1992, preventing comparison for these data on their own. The densities of seedlings on both old and new diggings were significantly higher than expected for the combined 1991 and 1992 observations (Table 5.6). A total of 12.3% of the total area was disturbed by diggings in the combined three areas.

The test which compared the distances of seedlings and adults from 50 random points showed strong evidence of attraction (Spearman  $R=0.79$ ,  $n=34$ ,  $P<0.0001$ ). Sixteen random points were rejected in this test because they were closer to the boundary of the area than the nearest adult, seedling or both. The mean distances from the random points to the nearest adult and seedling were 22.1 cm and 49.6 cm respectively (range: adults 2-95 cm, seedlings 7-117 cm). Only 6.1% of the seedlings were more than 20 cm from an adult plant.

The survivorship curves for seedlings of *V. paradoxa* on diggings and undisturbed areas are similar, with no evidence of differential mortality rates (April seedlings: Wilcoxon test  $\chi^2_2=0.64$ ,  $P=0.7$ ; Log-rank test  $\chi^2_2=0.39$ ,  $P=0.8$ ). There was an increase in the mortality rate in the summer following germination for both cohorts of seedlings. By March 1992, 16% of the April 1991 cohort were still alive compared with 2.6% of the July 1991 cohort (Fisher's exact  $2 \times 2$ ,  $n=88$ , 2-tailed  $P=0.072$ ; Fig. 5.10), with five individuals on undisturbed ground and four on diggings. Seedlings which were still alive in March 1992 were still quite small, with one to five rosette leaves.

#### *Chimney Pot Hill*

No germination was observed of either *Gahnia rodwayi* or *Olearia ericoides*, either on or off diggings.

*Dukes Marshes*

The annual herb *Euphrasia scabra* was found to germinate readily in the absence of animal digging. A total of 276 germinants was recorded in the quadrats in February 1991, but none of these was associated with the very sparse diggings created by rabbits. No diggings by other animal species were observed.

*East Risdon*

No seedlings of the shrub *Olearia hookeri* were observed, either on or off diggings. Seedling germination of other species was extremely sparse. In five visits from September 1990 to March 1992, only 43 new seedlings of vascular plant species were recorded, at a density of 9.6 seedlings m<sup>-2</sup> over the 28 quadrats (cf. 152.2 seedlings m<sup>-2</sup> at Bellerive in 1991, excluding all Poaceae spp. and Orchidaceae spp.). The taxa with the most seedling emergence, out of those seedlings that were identified, were *Stipa* spp. and *Helichrysum obcordatum*. There were no significant differences in pairwise comparisons of total seedling densities, although the overall densities were much higher on mounds and holes compared with undisturbed areas (all comparisons: effective n=14, P>0.1; Table 5.7).

*Hospital Creek*

In May 1991, there was no significant difference in the density of seedlings recorded on the three microsite categories, for either *Dodonaea filiformis* or *Acacia genistifolia* (all comparisons: n=51, P>0.14). For *Odixia achlaena* at the same time, there was no significant difference in the densities of seedlings between mounds and controls, or mounds and holes (n=51, P>0.4), but the density on controls was greater compared with holes (n=51, P=0.04; Fig. 5.11). The emergence rate of seedlings of *D. filiformis* and *O. achlaena* declined with successive sample times and was near zero by the time of the final sample in May 1992, some 20 months after the fire (Fig. 5.12).

For the seedlings of *O. achlaena* which were first mapped in May 1991, survivorship was not homogeneous across the three microsite categories



according to the Log-rank test (Wilcoxon test  $\chi^2_2=5.5$ ,  $P=0.065$ ; Log-rank test  $\chi^2_2=7.1$ ,  $P=0.029$ ). The survivorship curves indicate that seedlings of *O. achlaena* died much faster on holes compared with both mounds and control areas, but the curves are similar for mounds and controls (Fig. 5.13a). Most of the seedlings which were mapped after May 1991 emerged on control areas and no more were recorded on holes (Fig. 5.13b).

Testing all microsites together, the survivorship was homogeneous across the microsite categories for those seedlings of *D. filiformis* that were first mapped in May 1991 (Wilcoxon test  $\chi^2_2=3.72$ ,  $P=0.2$ ; Log-rank test  $\chi^2_2=1.92$ ,  $P=0.4$ ; Fig. 5.13c). In a pairwise comparison, the curves for holes and mounds were significantly different, with greater mortality on mounds in the first two months after 7 May (Wilcoxon test  $\chi^2_1=4.23$ ,  $P=0.04$ ; Log-rank test  $\chi^2_1=2.89$ ,  $P=0.089$ ). The proportions of seedlings surviving were not significantly different at the conclusion of the study (Fisher's exact  $2 \times 3$ ,  $n=156$ ,  $P=0.49$ ).

The survivorship curves for seedlings of *D. filiformis* that emerged after May 1991 were not significantly different (Wilcoxon test  $\chi^2_1=1.47$ ,  $P=0.23$ ; Log-rank test  $\chi^2_1=2.63$ ,  $P=0.11$ ; Fig. 5.13d; holes excluded from these tests because  $n=2$ ). The proportion of seedlings surviving at the conclusion of the study, out of those that emerged after May 1991, was significantly higher on mounds and holes compared with undisturbed areas (Fisher's exact  $2 \times 3$ ,  $n=57$ ,  $P=0.026$ ).

There was no difference in height growth rates that could be attributed to microsites, for seedlings of either *O. achlaena* or *D. filiformis* that were still alive at the conclusion of the field study in May 1992 (*O. achlaena*:  $F_{1,31}=1.22$ ,  $P=0.3$ ; *D. filiformis*:  $F_{2,82}=1.17$ ,  $P=0.3$ ; Table 5.8). The tallest seedlings of these two species in May 1992 were 19 and 20 cm respectively.

#### Kellevie Road

Only one new seedling of *Odixia achlaena* was observed and positively identified in September 1990 and this one was located on a digging mound. In the same visit, a group of 29 seedlings was observed on one digging. These seedlings all died before they could be positively identified, but all were definitely Asteraceae and could have been either *O. achlaena* or

*Helichrysum dendroideum*, both of which were overhanging the quadrat. In April 1991, only one *O. achlaena* seedlings was observed after several hours of searching in an area 50 x 2 m. This seedling was located on a recently created digging mound. Bettong diggings were quite common amongst adult *O. achlaena* at this site.

### *Old Coach Road*

Only two seedlings of *Lasiopetalum micranthum* were observed growing on animal diggings over the period of the study, either in the permanent quadrats or on any other diggings. One of the seedlings was still alive at the conclusion of field work.

The size distributions of maximum diameters of *L. micranthum* individuals on the bulldozed transect were much smaller in comparison to the undisturbed transect in March 1990, indicating the recent colonisation of this grossly disturbed area. The size distributions two years later in March 1992 were relatively unchanged, but with an indication of subsequent regeneration having occurred on both areas (Figs 5.14).

The impact of grazing on the growth of *L. micranthum* was dramatic. The ends of branches were visibly eaten and many plants were uprooted on the bulldozed transect and found lying on the surface. Uprooting was a major cause of mortality, with even larger individuals completely removed from their mapped locations, although mortality was higher amongst smaller plants (Fig. 5.15). In all, 26.4% of the 106 plants that were mapped in March 1990 on the bulldozed transect were dead by March 1992, compared with 0.9% of the 107 plants on the undisturbed transect. On the basis of scats and footprints, the grazers include wallabies and sheep. The latter were free ranging over a large area, were not observed closer than 0.5 km from the study site on any of the visits, and probably make sporadic forays into the area.

Although mortality was higher amongst smaller plants, the reduction in plant radii with non-lethal grazing was greater amongst larger plants than smaller plants (Fig. 5.16a). The same effect meant that in the final sample of May 1992, smaller plants had positive growth compared with their original

radii, while larger plants had decreased in size (bulldozed transect: Figs 5.16a,b).

The impact of grazing on the radii of *L. micranthum* plants was greatest in the winter months. The grazing intensity was greater on the bulldozed transect compared with the undisturbed transect, with plant radii reduced by greater amounts. On the undisturbed transect, plant radii were less severely reduced by grazing in the areas with dense *Lepidosperma laterale* in comparison to the areas where *L. laterale* was absent. The only example of net positive growth relative to March 1990 was in the undisturbed area with dense *L. laterale* in the final visit of March 1992. Analysis of variance tables are presented only for September 1990 and March 1992 (Table 5.9; Fig. 5.17).

The highest seedling emergence of *L. micranthum* was observed in September 1991, but emergence was also observed in September 1990, January 1991 and May 1991 (Fig. 5.18). The densities of seedlings of *L. micranthum* which emerged over the total two year period of the study were not significantly different between the three transect categories. The densities of seedlings that were still alive at the conclusion of the field work in March 1992, out of the total that emerged over two years, were greater on the bulldozed transect compared with the parts of the undisturbed transect without *L. laterale*. The density of those seedlings still alive in the area with dense *L. laterale* were close to what would be expected under the null hypothesis of equal densities (Table 5.10). The proportions of the total germinants that survived to March 1992 were not significantly different with all three transect categories included (Fisher's exact  $2 \times 3$ ,  $P=0.092$ ), but survival was higher on undisturbed areas that lacked *L. laterale* in comparison with bulldozed areas alone (Fisher's exact  $2 \times 2$ ,  $P=0.042$ ; bulldozed: 61.5%,  $n=26$ ; undisturbed + *L. laterale*: 55.6%,  $n=9$ ; undisturbed - *L. laterale*: 30.0%,  $n=20$ ).

The diameter growth rates of new seedlings of *L. micranthum* that were still alive at the conclusion of the study were faster on the bulldozed transect compared with the undisturbed transect ( $P=0.015$ , Table 5.11). The largest diameter amongst these seedlings in March 1992 was 7 cm.

*Powranua*

No seedlings of *Glycine latrobeana* were observed, either on or off diggings.

*Westwood*

There was no difference in the densities of newly emerged seedlings of *Brunonia australis* in the paired comparisons between the bettong diggings and control areas, neither for 'very old' diggings nor for 'old' diggings (very old diggings:  $n=29$ ,  $P>0.9$ ; old diggings:  $n=24$ ,  $P>0.7$ ). The densities of seedlings were greater on the control areas compared with 'new' diggings ( $n=23$ ,  $P<0.01$ ; Fig. 5.19). There was no difference in the densities of seedlings on the control quadrats alone, when categorised according to the three age classes of bettong diggings to which they were paired (Kruskal-Wallis d.f.=2,  $P>0.5$ ).

A total of 157 seedlings of *B. australis* was counted in the stratified random quadrats on transects, at a density of  $3.3 \text{ m}^{-2}$ . Only two of these seedlings were found on bettong diggings, which covered 4.9% of the total sampled area. It was necessary to combine the areas of the three age categories of diggings to meet the requirements of the  $\chi^2$  test, which then showed that slightly fewer seedlings were located on diggings compared with undisturbed ground than would be expected if the densities were equal. This result was the same, either with or without the inclusion of the areas of 'new' diggings (Table 5.12).

Only 3.2% of the 157 seedlings were more than 0.5 m from an adult plant that had flowered in the previous year and 70% were within 0.3 m. However, seedlings were less likely to be found at very short distances from flowering adults, with a modal distance of around 0.2 m (Fig. 5.20). A total of 496 adult plants of *B. australis* were counted, at a density of  $10.3 \text{ m}^{-2}$ . At least 56.3% of the adult plants were 0.5 m or more away from bettong diggings (Fig. 5.21).

The index of dispersion test on counts of *B. australis* in quadrats showed that both adult and seedlings were highly clumped, with variance to mean ratios of 6.6 and 8.7 respectively (adults:  $\chi^2_{149}=979.2$ ,  $P<0.0001$ ; seedlings:

$\chi^2_{149}=1294.3$ ,  $P<0.0001$ ). The  $2 \times 2$  contingency test for presence/absence of bettong diggings and adults in quadrats provided no evidence to reject the null hypothesis that their spatial distributions are independent ( $\chi^2_1=0.04$ ,  $P=0.8$ ). The spatial pattern of seedlings and diggings were similarly independent ( $\chi^2_1=0.45$ ,  $P=0.5$ ). The same test provided strong evidence of association between seedlings and adults ( $\chi^2_1=9.25$ ,  $P=0.002$ ).

**Table 5.1** Tests for the homogeneity of survivorship curves of seedlings of *Lepidium hyssopifolium* on different microsites at Annandale.

Test	$\chi^2$	d.f.	Prob.
<i>Original sample intervals:</i>			
Wilcoxon	13.68	2	0.001
Log-rank	17.54	2	0.0002
<i>Randomised death within sample intervals:</i>			
Wilcoxon	17.70 (max.)	2	0.0001
Wilcoxon	6.40 (min.)	2	0.04
Log-rank	21.26 (max.)	2	<0.0001
Log-rank	10.70 (min.)	2	0.005

Maximum and minimum  $\chi^2$  values are from 20 replications.

**Table 5.2** Summary of the average densities and total counts of newly emerged seedlings and ramets at Bellerive, also indicating Spearman rank-order correlations with bare soil cover (%) in control quadrats. Data are for the full 2 year period (1991/92).

Species	Mean density (total count)			Significance for paired tests			Control & bare soil
	M	H	C	MH	MC	HC	Rho
Seedlings:							
<i>Arthropodium milleflorum</i>	0.66 (13)	1.82 (5)	1.56 (44)	ns	*	ns	0.05
<i>Bulbine glauca</i>	0.14 (2)	0.80 (4)	0.64 (18)	-	ns	ns	0.28
<i>Carex breviculmis</i>	0.21 (3)	1.05 (2)	0.31 (9)	-	ns	-	-0.20
<i>Crassula sieberana</i>	10.40 (179)	5.31 (25)	1.87 (48)	ns	*	ns	0.59 **
<i>Dodonaea viscosa</i>	0.51 (11)	0.70 (3)	0.51 (15)	ns	ns	ns	0.26
<i>Eucalyptus</i> spp.	0.87 (15)	1.11 (7)	0.73 (19)	ns	ns	ns	0.66 **
<i>Helichrysum apiculatum</i>	3.03 (55)	2.02 (11)	0.98 (26)	ns	**	ns	0.76 ***
# <i>Hypochoeris radicata</i>	0.07 (1)	0	0.26 (7)	-	ns	-	0.34
<i>Leptorhynchos squamatus</i>	0.64 (12)	0.35 (1)	0.35 (10)	-	ns	ns	0.09
<i>Luzula meridionalis</i>	0.63 (13)	0.36 (2)	0.91 (25)	ns	ns	ns	0.48 *
<i>Oxalis perennans</i>	0.47 (8)	0.40 (2)	0.35 (9)	ns	ns	ns	0.43
<i>Schoenus apogon</i>	0.63 (11)	0	0.15 (4)	*	ns	-	0.53 *
<i>Scleranthus biflorus</i>	1.87 (41)	0.19 (1)	0.10 (3)	*	*	-	0.08
<i>Senecio</i> spp.	1.37 (21)	0.56 (3)	0.39 (11)	ns	*	ns	0.24
# <i>Silene gallica</i>	0.21 (4)	0.19 (1)	0.17 (5)	-	ns	-	0.02
<i>Stackhousia monogyna</i>	2.24 (31)	1.38 (5)	2.45 (70)	ns	ns	ns	0.20
<i>Thysanotus patersonii</i>	0.59 (11)	0.38 (2)	0.87 (25)	-	ns	*	0.02
<i>Velleia paradoxa</i>	0.73 (9)	0.84 (5)	1.17 (31)	-	-	ns	0.42
<i>Wahlenbergia stricta</i>	7.04 (109)	6.20 (31)	2.32 (59)	ns	***	ns	0.53 *
native Asteraceae spp.	6.07 (112)	3.66 (17)	2.23 (62)	*	**	ns	0.57 *
native Liliaceae spp.	1.96 (36)	4.30 (14)	3.80 (107)	ns	ns	ns	0.33
Ramets and seedlings:							
<i>Caladenia</i> spp.	0.58 (9)	0	0.36 (10)	*	ns	*	0.32
<i>Diuris</i> spp.	1.02 (17)	0.25 (2)	1.23 (35)	ns	ns	**	0.27
<i>Pterostylis</i> spp.	0.49 (7)	0.42 (2)	2.33 (69)	-	ns	ns	-0.16
<i>Thelymitra pauciflora</i>	0.31 (5)	0	0.21 (6)	-	ns	-	0.10

Mean densities are per  $\text{cm}^2 \times 10^3$ .  $n=19$  for all means and correlations. Significance levels for density comparisons are from the Wilcoxon signed-rank test. Tests were only performed when there were at least 6 pairs of differing densities.

M=mound; H=hole; C=control. Native Liliaceae = *Arthropodium milleflorum*, *Bulbine glauca* and *Thysanotus patersonii*.

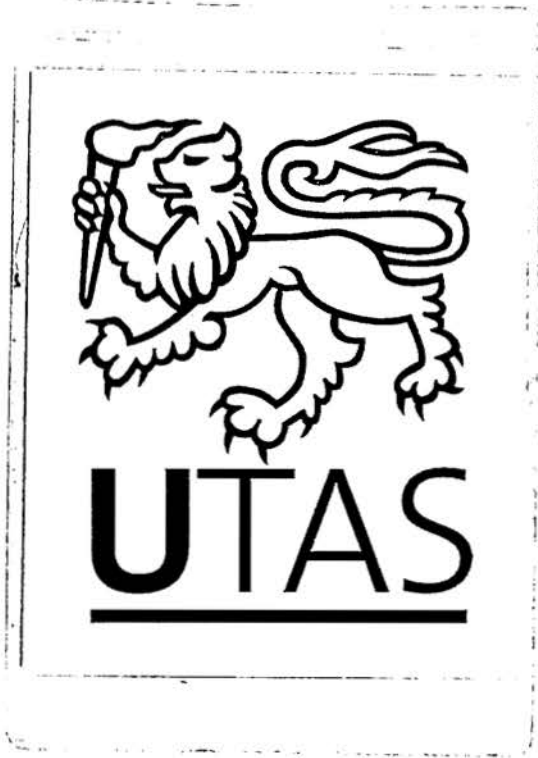
# denotes exotic species.

\*  $0.01 < P < 0.05$ ; \*\*  $0.001 < P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns=not significant.

**Table 5.3** Maximum correlation coefficients ( $R_{\max}$ ), angles between fitted vectors and configuration axes, and angles between fitted vectors in the 3 dimensional GNMDS ordination of the seedling emergence data at Bellerive.

Variable	$R_{\max}$	Angles to axes			Angle to variable	
		1	2	3	Q	B
Quadrat no. (Q)	0.61 ***	156	114	96		
Bare mineral soil (B)	0.57 **	101	150	62	62	
Litter (L)	0.59 **	79	28	116	119	178

\*\*0.001<P<0.01; 
 \*\*\*P<0.001.





**Table 5.3** Maximum correlation coefficients ( $R_{\max}$ ), angles between fitted vectors and configuration axes, and angles between fitted vectors in the 3 dimensional GNMDS ordination of the seedling emergence data at Bellerive.

Variable	$R_{\max}$	Angles to axes			Angle to variable	
		1	2	3	Q	B
Quadrat no. (Q)	0.61 ***	156	114	96		
Bare mineral soil (B)	0.57 **	101	150	62	62	
Litter (L)	0.59 **	79	28	116	119	178

\*\*0.001<P<0.01; \*\*\*P<0.001.

**Table 5.4** Two-way table of quadrats and species sorted by a vector fitted for bare soil cover (increasing left to right), in a 3 dimensional GNMDS ordination of seedling emergence data for 1991/92 at Bellerive.

Species	Seedling density (cm <sup>-2</sup> × 10 <sup>3</sup> )																			
Quadrat pair no.	11 11    11 11 2        111111 1112 1 18957419592876236160543463829572478013																			
Mound/control	cmcccccmcccccmcccmcmmmmmcmcmmmmmmmcccm																			
Bare soil (%)	1        1        74 1224        1611681        78 26002341002072223206030432767832668458																			
<i>Carex breviculmis</i>	31	3		2	1		2	2												
<i>Brachyscome spathulata</i>		7			9	1														
<i>Stackhousia monogyna</i>	291549821	7	7	37			9241								2		2			
* <i>Hypochoeris radicata</i>	1		13	1	1										2					
<i>Arthropodium milleflorum</i>		117172			2575214									2						
<i>Thysanotus patersonii</i>	2	21	71	11		1	13	6	2	1	1	2					1			
<i>Bulbine glauca</i>			1	3	1	1	62		3	1								1		
<i>Linum marginale</i>				21										1						
* <i>Cerastium glomeratum</i>	1	1			1			5												
<i>Dodonaea viscosa</i>		5	4		33	4		1						1			12			
<i>Hypericum gramineum</i>	1							22	1											
<i>Velleia paradoxa</i>			15	1		9								9	1		2			
<i>Wahlenbergia stricta</i>	7222	95		2	9	6149		9634518534242271												
<i>Leptorhynchos squamatus</i>		2			121	1	1	2	9						11	3				
<i>Oxalis perennans</i>	1		4		1	11		2	1		4	2	11		1					
<i>Luzula meridionalis</i>		11	3		1	331	3	3	13					22	216					
<i>Crassula sieberana</i>			9			1	349	49972	2	38	5215	9								
<i>Senecio</i> spp.			1	22		21117			2	444112	11	2								
<i>Scleranthus biflorus</i>	1				1	1		2	21			1	92							
<i>Helichrysum apiculatum</i>		11			2	114		14768	55	19593522										
<i>Eucalyptus</i> spp.		1		1	1	11		2232	222	21344121										
<i>Plantago varia</i>					1	2				1	4	31								
<i>Schoenus apogon</i>		1			1		1			1	7	11	11	2						
<i>Gonocarpus tetragynus</i>		1													11	1				
* <i>Silene gallica</i>						1	1					2	221							
<i>Podolepis jaceoides</i>												2		21						

Densities rounded up to integers, with the exception of 9 which indicates greater than 8 seedlings. Only species which occur in at least 3 quadrats are included.

\* denotes exotic species.

**Table 5.4** Two-way table of quadrats and species sorted by a vector fitted for bare soil cover (increasing left to right), in a 3 dimensional GNMDS ordination of seedling emergence data for 1991/92 at Bellerive.

Species	Seedling density (cm <sup>2</sup> x 10 <sup>3</sup> )																			
Quadrat pair no.	11 11 11 11 2 111111 1112 1 18957419592876236160543463829572478013																			
Mound/control	cmcccccmccccmcccmcmcmcmcmcmcmcmcmcmcmcmcmcm																			
Bare soil (%)	1 1 74 1224 1611681 78 26002341002072223206030432767832668458																			
<i>Carex breviculmis</i>	31	3		2	1		2	2												
<i>Brachyscome spathulata</i>		7			9	1														
<i>Stackhousia morogyna</i>	29	15	49	82	1	7	7	37		9	2	41					2		2	
* <i>Hypochoeris radicata</i>	1		13		1		1										2			
<i>Arthropodium milleflorum</i>		11	7	17	2		25	7	5	2	14						2			
<i>Thysanotus patersonii</i>	2	21	71	11		1	13		6	2	1	1	2							
<i>Bulbine glauca</i>		1	3	1		1	6	2		3	1								1	
<i>Linum marginale</i>				2	1												1			
* <i>Cerastium glomeratum</i>	1	1			1		1				5									
<i>Dodonaea viscosa</i>		5	4		3	3	4			1							1		12	
<i>Hypericum gramineum</i>	1									2	2	1								
<i>Velleia paradoxa</i>			15	1			9										9	1		2
<i>Wahlenbergia stricta</i>	7	22	2	95		2	9	6	1	49		9	6	3	4	5	1	8	5	3
<i>Leptorhynchus squamatus</i>		2				1	2	1		1	2	9						1	1	3
<i>Oxalis perennans</i>	1		4		1	11				2	1		4	2	11				1	
<i>Luzula meridionalis</i>		11	3		1		3	3	1	3	3	13			22		2	1	6	
<i>Crassula sieberana</i>			9			1	3	4	9		4	9	9	7	2	2	3	8	5	9
<i>Senecio</i> spp.			1	22			2	1	1	7			2		4	4	1	1	2	2
<i>Scleranthus biflorus</i>	1				1	1				2	2	1				1		9	2	
<i>Helichrysum apiculatum</i>		11				2	1	1	4		1	4	7	6		5	5	1	9	3
<i>Eucalyptus</i> spp.		1		1	1	1				2	2	3	2	2	2	2	2	1	3	4
<i>Plantago varia</i>						1		2							1	4			3	1
<i>Schoenus apogon</i>		1				1			1						1	7	1	1	1	2
<i>Gonocarpus tetragynus</i>			1																1	1
* <i>Silene gallica</i>							1	1									2		2	2
<i>Podolepis jaceoides</i>																	2			1

Densities rounded up to integers, with the exception of 9 which indicates greater than 8 seedlings. Only species which occur in at least 3 quadrats are included.

\* denotes exotic species.

**Table 5.5** Summary of the average densities and total counts of seedlings and ramets which survived until at least December 1992 at Bellerive. The data are shown for emergence from two separate years and then the two years combined.

Species	Mean density (total count)			Significance for paired tests		
	M	H	C	MH	MC	HC
1991 seedlings:						
<i>Bulbine glauca</i>	0.07 (1)	0.21 (1)	0.41 (11)	-	ns	ns
<i>Thysanotus patersonii</i>	0.19 (4)	0.19 (1)	0.27 (8)	-	ns	ns
native Liliaceae spp.	0.30 (6)	0.93 (3)	0.93 (26)	ns	ns	ns
native Dicotyledonae spp. (excl. <i>S. monogyna</i> )	0.44 (11)	0	0.39 (18)	*	ns	*
1991 ramets & seedlings:						
<i>Caladenia</i> spp.	0.30 (6)	0	0.20 (6)	-	ns	*
<i>Diuris</i> spp.	0.73 (13)	0.25 (2)	0.83 (23)	ns	ns	*
<i>Pterostylis</i> spp.	0.31 (4)	0.21 (1)	1.28 (36)	-	*	ns
<i>Thelymitra pauciflora</i>	0.17 (3)	0	0.14 (4)	-	ns	-
1992 seedlings:						
<i>Arthropodium milleflorum</i>	0.38 (7)	0.56 (2)	0.34 (10)	-	ns	-
<i>Helichrysum apiculatum</i>	0.41 (7)	0.19 (1)	0.14 (3)	ns	ns	-
<i>Luzula meridionalis</i>	0.44 (9)	0.12 (1)	0.16 (4)	-	ns	-
<i>Stackhousia monogyna</i>	1.29 (17)	0.65 (3)	0.85 (24)	ns	ns	ns
native Asteraceae spp.	0.90 (19)	0.19 (1)	0.38 (10)	ns	ns	-
native Liliaceae spp.	0.47 (9)	0.56 (2)	0.56 (16)	ns	ns	ns
native Dicotyledonae spp. (excl. <i>S. monogyna</i> )	2.34 (56)	0.76 (8)	1.29 (58)	ns	**	ns
1991/92 seedlings:						
<i>Arthropodium milleflorum</i>	0.42 (8)	1.09 (3)	0.58 (17)	-	ns	ns
<i>Bulbine glauca</i>	0.07 (1)	0.21 (1)	0.41 (11)	-	ns	ns
<i>Helichrysum apiculatum</i>	0.41 (7)	0.19 (1)	0.14 (3)	ns	ns	-
<i>Luzula meridionalis</i>	0.44 (9)	0.33 (2)	0.30 (8)	-	ns	ns
<i>Schoenus apogon</i>	0.40 (7)	0	0.12 (3)	-	ns	-
<i>Stackhousia monogyna</i>	1.48 (20)	0.65 (3)	1.09 (31)	ns	ns	ns
<i>Thysanotus patersonii</i>	0.29 (6)	0.19 (1)	0.46 (13)	-	ns	ns
native Asteraceae spp.	0.95 (20)	0.19 (1)	0.55 (15)	ns	ns	ns
native Liliaceae spp.	0.78 (15)	1.49 (5)	1.49 (42)	ns	ns	ns
native Dicotyledonae spp. (excl. <i>S. monogyna</i> )	2.78 (67)	0.76 (8)	1.68 (76)	*	*	ns

Mean densities are per  $\text{cm}^2 \times 10^3$ ;  $n=19$  for all means. Survivors for 1992 exclude new germinants recorded in December 1992. Significance levels for density comparisons are from the Wilcoxon signed-rank test. Tests were only performed where there were at least 6 pairs of differing densities.

M=mound; H=hole; C=control. Native Liliaceae = *Arthropodium milleflorum*, *Bulbine glauca* and *Thysanotus patersonii*.

\*  $0.01 < P < 0.05$ ; \*\*  $0.001 < P < 0.01$ ; ns=not significant.

**Table 5.6** Results of chi-squared tests on the densities of newly emerged seedlings of *Velleia paradoxa* at Bellerive.

Treatment	Area (m <sup>2</sup> )	Obs.	Exp.	$\chi^2$	Density (seedlings m <sup>-2</sup> )
1991 (7.2 x 4.8 m & 2.4 x 4.8 m areas):					
undisturbed	37.89	59	72.3	2.46	1.6
new diggings	3.23	16	6.2	15.73	5.0
old diggings	4.97	13	9.5	1.30	2.6
total	46.08	88	88.0	19.49***	1.9
1992 (6 x 12 m area):					
undisturbed	66.48	44	52.6	-	0.7
new diggings	3.02	5	2.4	-	1.7
old diggings	2.50	8	2.0	-	3.2
total	72.00	57	57.0	-	0.8
1991+1992:					
undisturbed	104.37	103	128.2	4.94	1.0
new diggings	6.25	21	7.7	23.17	3.4
old diggings	7.47	21	9.2	15.26	2.8
total	111.08	145	145.0	43.37***	1.3

\* \*\*P&lt;0.001.

**Table 5.7** Densities of newly emerged seedlings observed at East Risdon.

Species	Seedling density (Total count)		
	Mound	Hole	Undisturbed
<i>Acacia</i> spp.	1.8 (2)	0	0.4 (1)
<i>Dichelachne inaequiglumis</i>	0	0	0.4 (1)
Dicotyledon spp. <sup>1</sup>	4.5 (5)	7.0 (4)	1.8 (6)
<i>Dodonaea viscosa</i>	0.9 (1)	0	0
<i>Helichrysum obcordatum</i>	0.9 (1)	7.0 (4)	0.7 (2)
Monocotyledon spp. <sup>1</sup>	0	1.8 (1)	0
Poaceae spp.	1.8 (2)	1.8 (1)	1.1 (3)
<i>Stipa</i> spp.	3.6 (4)	1.8 (1)	1.4 (4)
Total	13.4 (15)	19.3 (11)	6.1 (17)

Seedling densities per m<sup>2</sup>.<sup>1</sup> Unidentified seedlings.

**Table 5.8** Mean height growth rates and 95% confidence limits for seedlings of *Odixia achlaena* and *Dodonaea filiformis* at Hospital Creek.

Treatment	n	LCL	Mean	UCL
<i>Odixia achlaena</i> :				
mounds	9	3.23	4.66	6.72
control areas	24	2.95	3.69	4.62
<i>Dodonaea filiformis</i> :				
mounds	11	3.08	4.78	7.44
holes	11	3.50	5.45	8.47
control areas	63	3.25	3.90	4.69

Note: means and 95% confidence limits are back-transformed ( $\text{cm year}^{-1}$ ). Within each species, no means are significantly different ( $P < 0.05$ ).

**Table 5.9** Results of analysis of variance on the change in radii of *Lasiopetalum micranthum* plants at the Old Coach Road.

Source of variation	d.f.	M.S.	F	P
<i>Change from March 1990 - September 1990:</i>				
Model	23	20.6	6.24	0.0001
Error	139	3.3		
Plant size	7	19.1	5.79	0.0001
Microsite	2	84.1	25.47	0.0001
Plant size x microsite	14	4.4	1.33	0.1991
Tests using the Type III M.S. for Plant size x microsite as an error term:				
Plant size	7	19.1	4.37	0.0092
Microsite	2	84.1	19.20	0.0001
<i>Change from March 1990 - March 1992:</i>				
Model	23	26.6	4.03	0.0001
Error	131	6.6		
Plant size	7	34.3	5.21	0.0001
Microsite	2	148.3	22.53	0.0001
Plant size x microsite	14	9.1	1.39	0.1681
Tests using the Type III M.S. for Plant size x microsite as an error term:				
Plant size	7	34.3	3.76	0.0168
Microsite	2	148.3	16.24	0.0002

**Table 5.10** Results of chi-squared tests on the densities of newly emerged seedlings of *Lasiopetalum micranthum* at the Old Coach Road, comparing transect categories.

Treatment	Area (m <sup>2</sup> )	Obs.	Exp.	$\chi^2$	Density (m <sup>-2</sup> × 10)
<i>Total seedlings March 1990 - March 1992:</i>					
undisturbed + <i>L. laterale</i>	33	9	11.79	0.66	2.7
undisturbed - <i>L. laterale</i>	65	20	23.21	0.45	3.1
bulldozed	56	26	20.00	1.80	4.6
total	154	55	55	2.90 ns	3.6
<i>Still alive in March 1992:</i>					
undisturbed + <i>L. laterale</i>	33	5	5.79	0.11	1.5
undisturbed - <i>L. laterale</i>	65	6	11.40	2.56	0.9
bulldozed	56	16	9.82	3.89	2.9
total	154	27	27	6.55*	1.8

\* 0.01 < P < 0.05; ns = not significant.

**Table 5.11** Means and 95% confidence limits for the diameter growth rates (horizontal spread of branches) of seedlings of *Lasiopetalum micranthum* on the two transects at the Old Coach Road.

Treatment	n	LCL	Mean	UCL
Bulldozed	15	1.35	1.76	2.30
Undisturbed	11	0.77	1.05	1.43

Note: means and 95% confidence limits are back-transformed (cm year<sup>-1</sup>). The means are significantly different (P < 0.05).



Table 5.12 Results of chi-squared tests on the densities of newly emerged seedlings of *Brunonia australis* at Westwood.

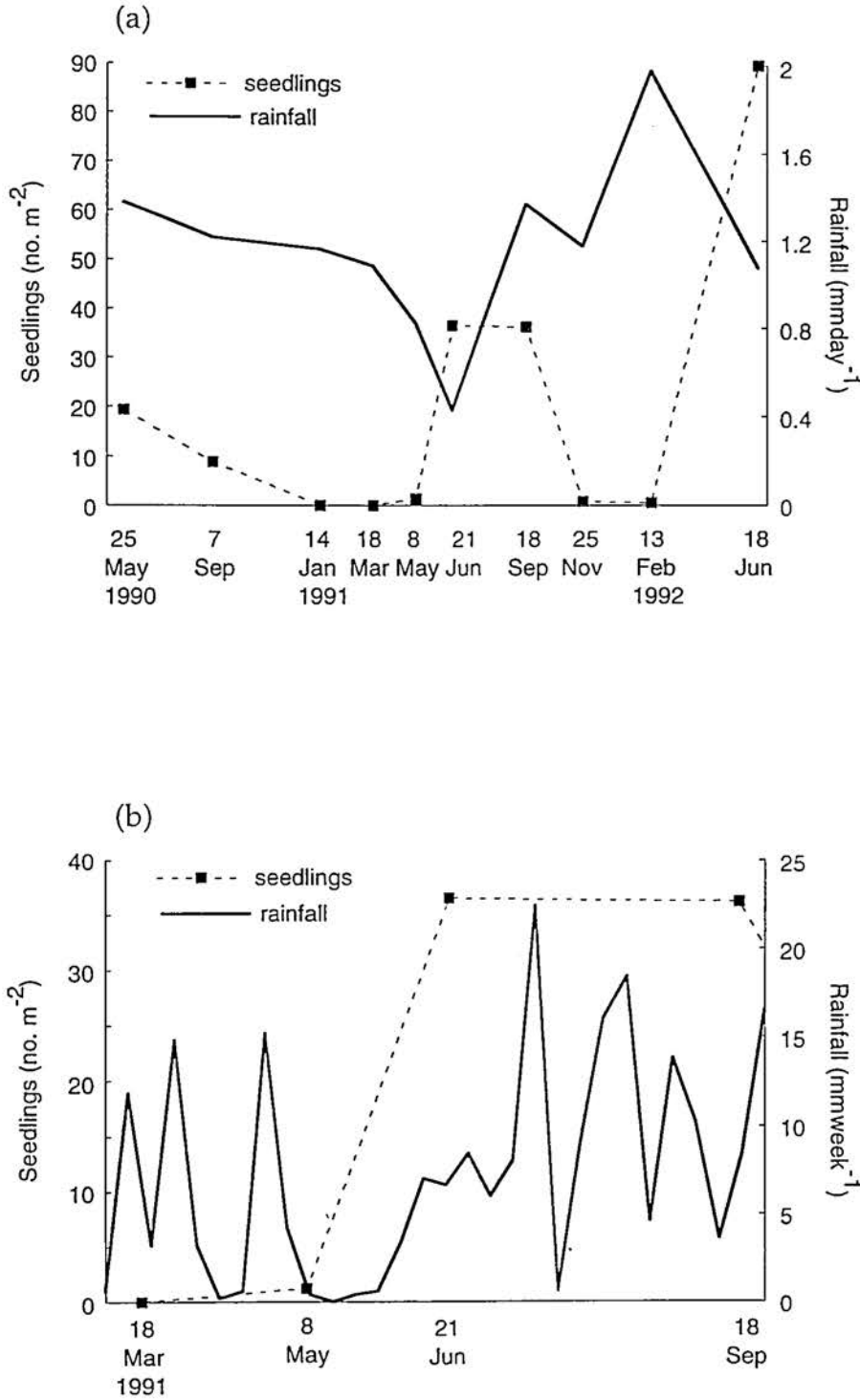
Treatment	Area (m <sup>2</sup> )	Obs.	Exp.	$\chi^2$	Density (m <sup>-2</sup> )
Including 'new' diggings:					
undisturbed	45.65	155	149.3	0.22	3.4
diggings	2.35	2	7.7	4.21	0.9
total	48.00	157	157.0	4.43*	3.3
Excluding 'new' diggings:					
undisturbed	45.65	155	149.8	0.18	3.4
diggings	2.19	2	7.2	3.74	0.9
total	45.65	157	157.0	3.92*	3.4

\* 0.01 < P < 0.05.

Table 5.13 Mean seed (including indehiscent fruits) weights of selected species.

Species	No. seeds	Mean seed wt (mg)
<i>Crassula sieberana</i>	100	0.0081
<i>Wahlenbergia stricta</i>	100	0.0299
<i>Helichrysum apiculatum</i>	60	0.08
<i>Odixia achlaena</i>	100	0.13
<i>Senecio quadridentatus</i>	100	0.17
<i>Vittadinia muelleri</i> #	200	0.17
<i>Leptorhynchus squamatus</i> #	200	0.20
<i>Helichrysum scorpioides</i>	60	0.22
<i>Lepidium pseudotasmanicum</i>	60	0.34
<i>Brachyscome spathulata</i>	30	0.38
<i>Lepidium hyssopifolium</i>	60	0.38
<i>Schoenus apogon</i> #	200	0.54
<i>Scleranthus biflorus</i>	50	0.85
<i>Linum marginale</i>	50	1.07
<i>Stackhousia monogyna</i>	30	1.17
<i>Podolepis jaceoides</i>	30	1.19
<i>Arthropodium milleflorum</i>	50	1.27
<i>Lasiopetalum micranthum</i>	60	1.60
<i>Bulbine glauca</i>	40	2.24
<i>Brunonia australis</i> #	200	2.89
<i>Velleia paradoxa</i>	50	3.53

# Ian Lunt & John Morgan, pers. comm.



Figs 5.1 The number of new seedlings of *Lepidium hyssopifolium* recorded on the sample dates indicated for (a) all sample dates, showing rainfall totals, and (b) with weekly rainfall for part of 1991.

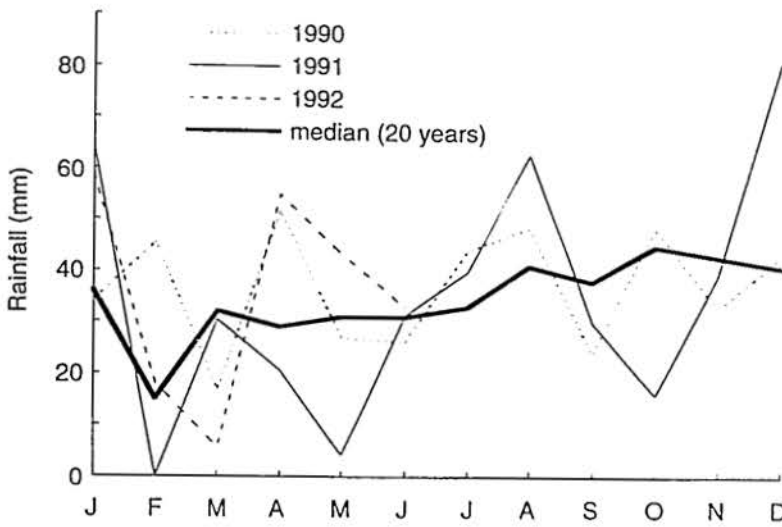


Fig. 5.2 Total monthly rainfall at Annandale for the period of the study, indicating the long term medians for 1972-1991.

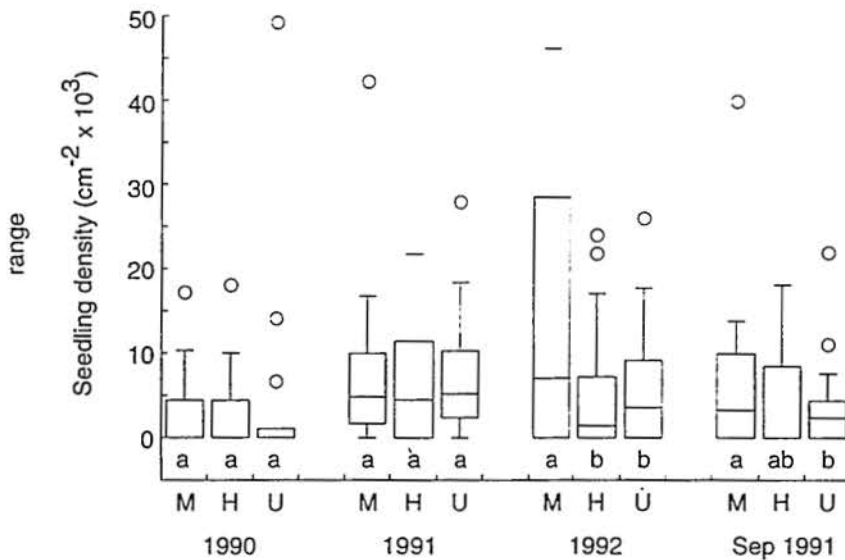


Fig. 5.3 The densities of newly emerged seedlings of *Lepidium hyssopifolium* recorded in the quadrats at Annandale (September 1991 data include all seedlings alive at that time) (4 outlying points not shown). Within each year, microsites with the same letter are not significantly different ( $P < 0.05$ ) M=mounds; H=holes; U=undisturbed.

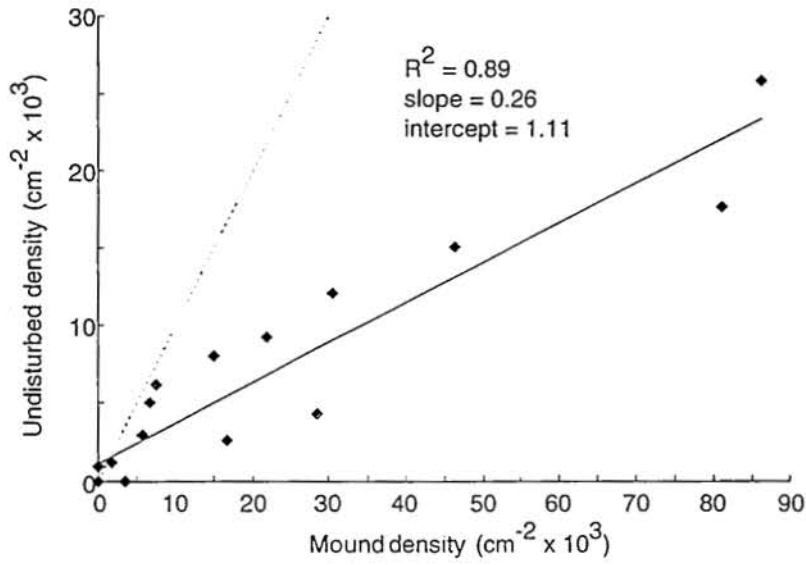
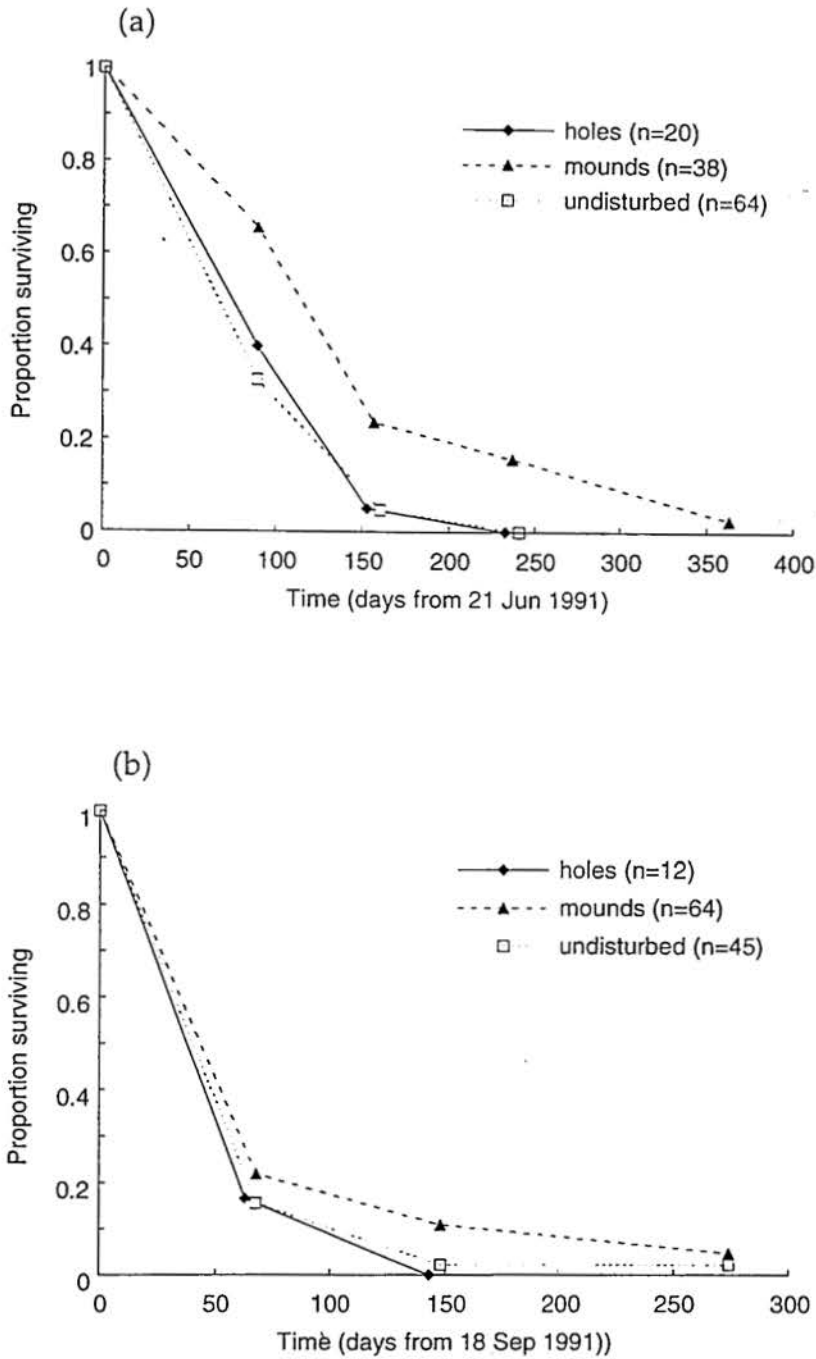


Fig. 5.4 Comparison of densities of seedlings of *Lepidium hyssopifolium* on mounds and undisturbed ground in June 1991 at Annandale. The broken line indicates the line of equal density.



**Figs 5.5** Survivorship curves showing the proportion of seedlings surviving plotted against time for seedlings of *Lepidium hyssopifolium* which were first recorded on (a) 21 June 1991 and (b) 18 September 1991.

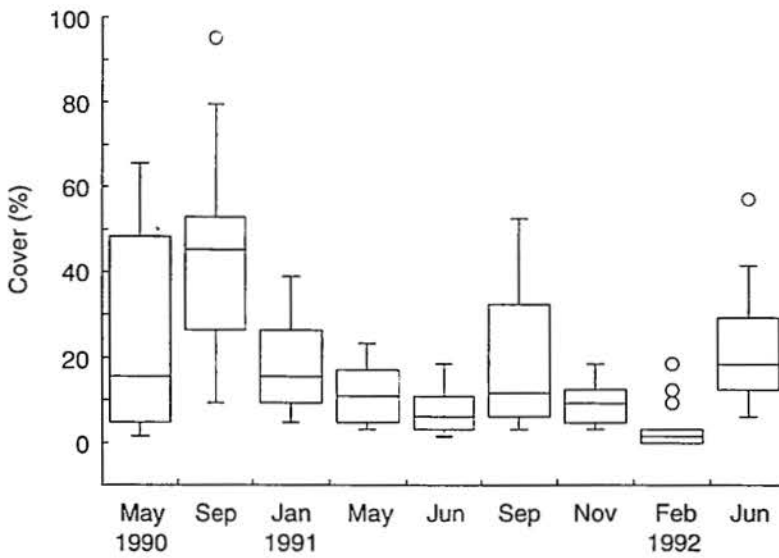


Fig. 5.6 The projected live foliage cover of exotic forbs and grasses (mostly annuals) in the quadrats at Annandale.

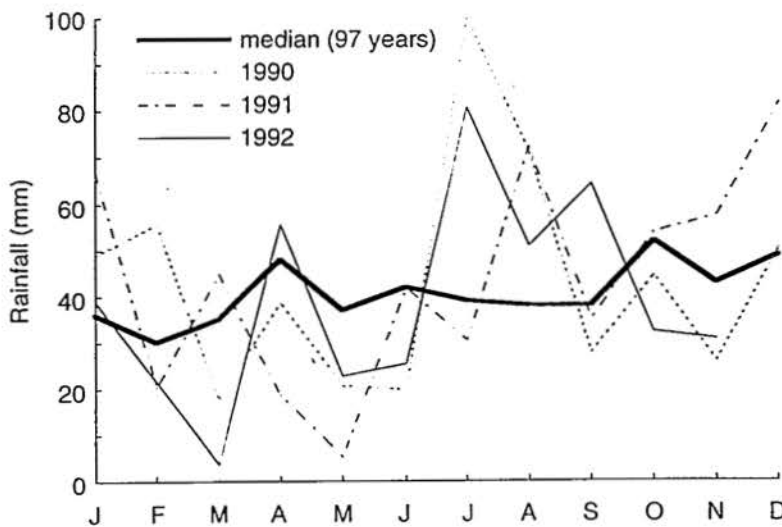
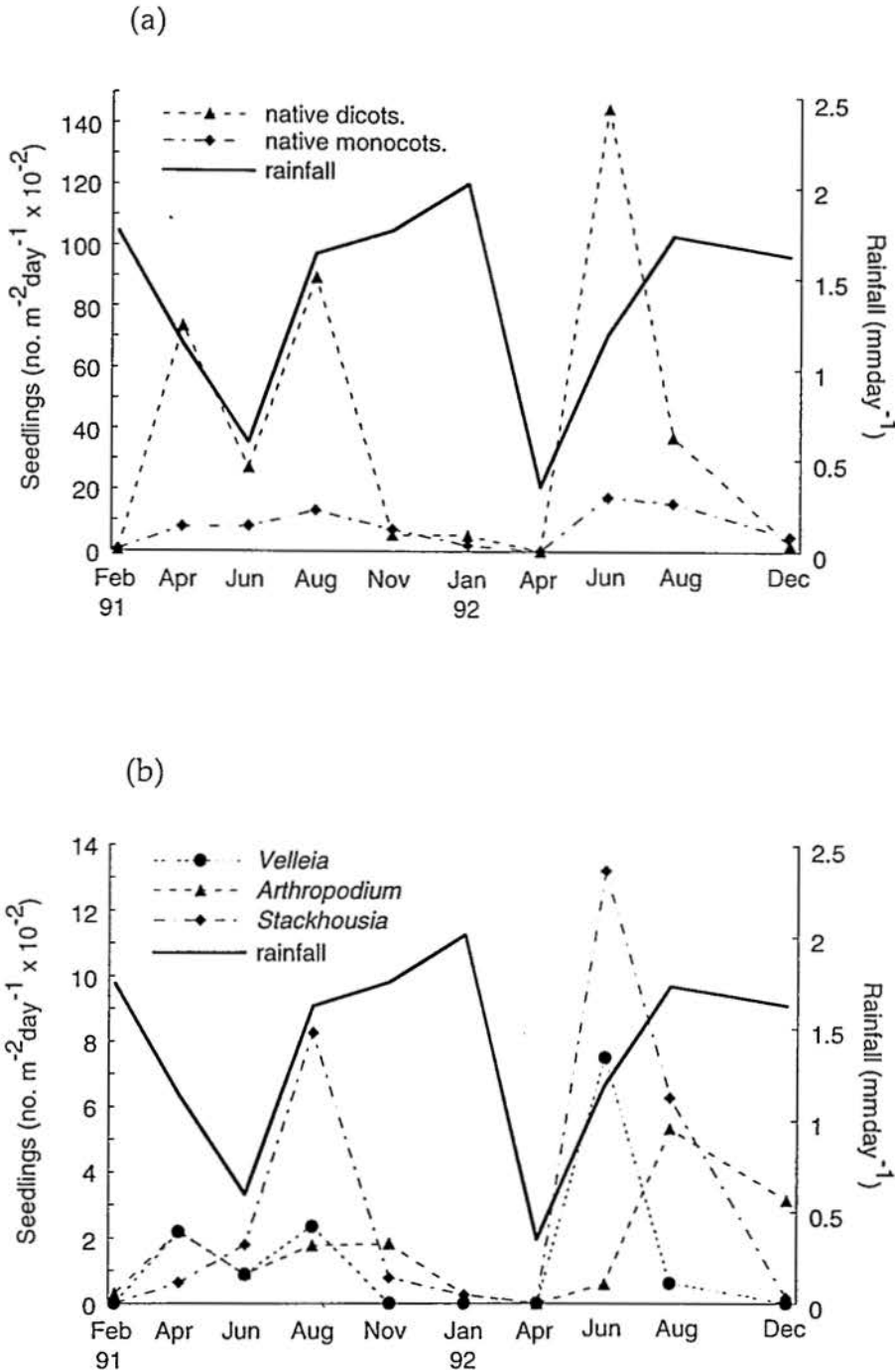
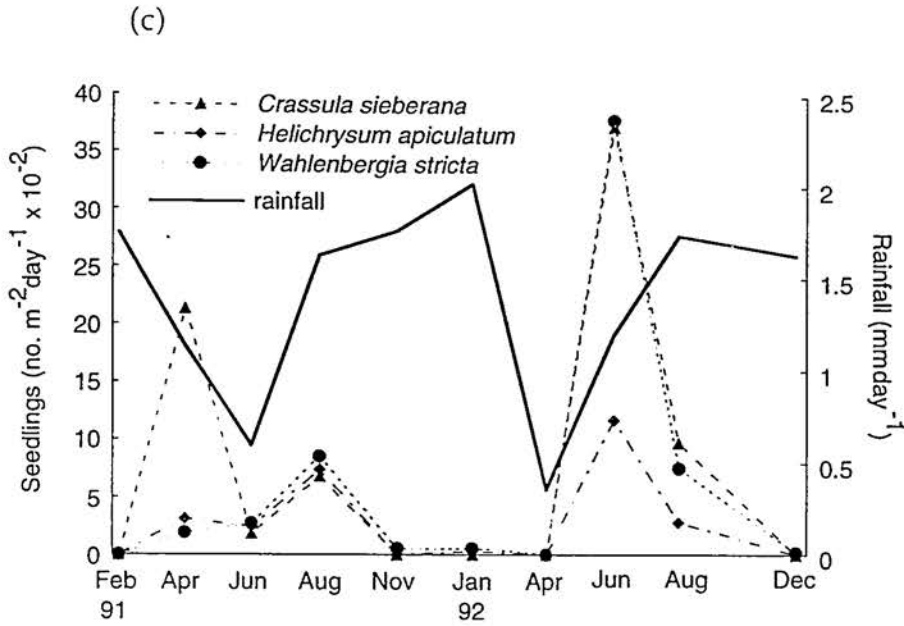


Fig. 5.7 Monthly rainfall at Bellerive for 1990-1992, also indicating the long term median.



Figs 5.8 The rate of emergence of new seedlings and the rainfall for sample intervals at Bellerive, showing (a) total native monocotyledons and dicotyledons; (b) and (c) individual species as indicated.





Figs 5.8 (cont.)

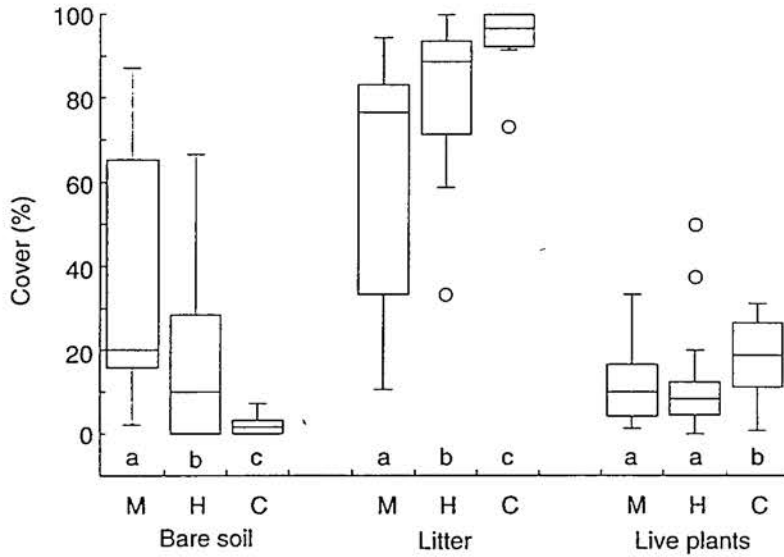
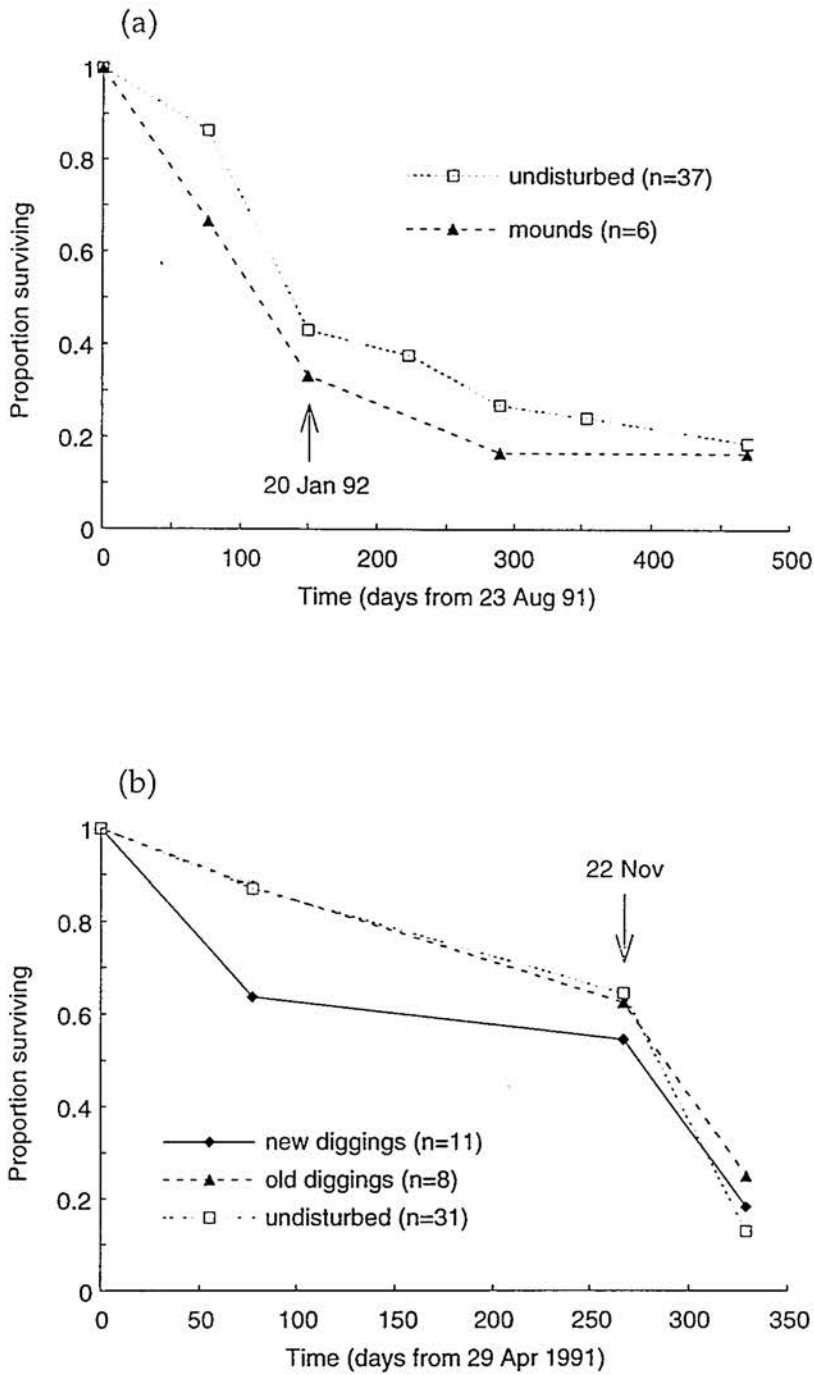
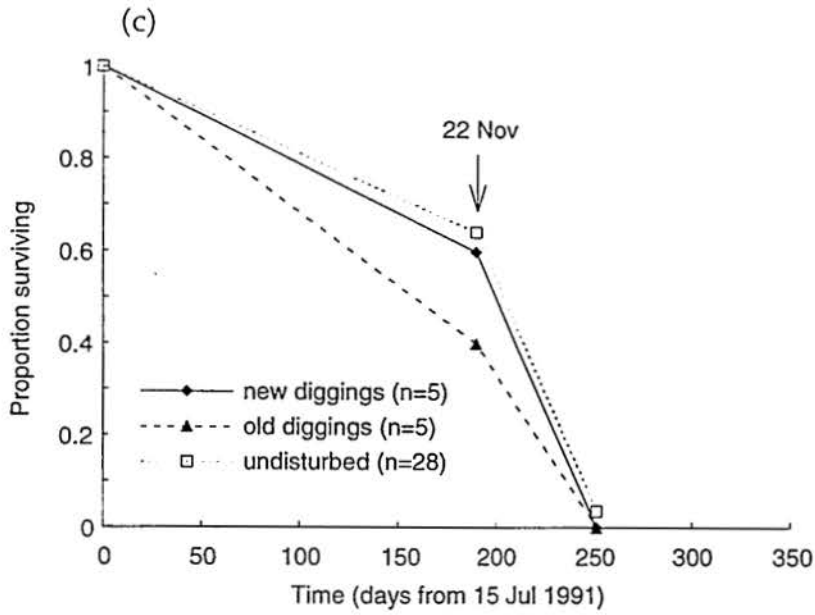


Fig. 5.9 The cover of bare soil, litter and live plants in the permanent quadrats at Bellerive at the end of the field study. Within each variable, microsites with the same letter are not significantly different ( $P < 0.05$ ). M=mounds; H=holes; C=controls.



**Figs 5.10** Survivorship curves showing the proportion of seedlings surviving plotted against time for seedlings of (a) *Stackhousia monogyna*; (b) *Velleia paradoxa* (April 1991 cohort); and (c) *V. paradoxa* (July 1991 cohort).



Figs 5.10 (cont.)

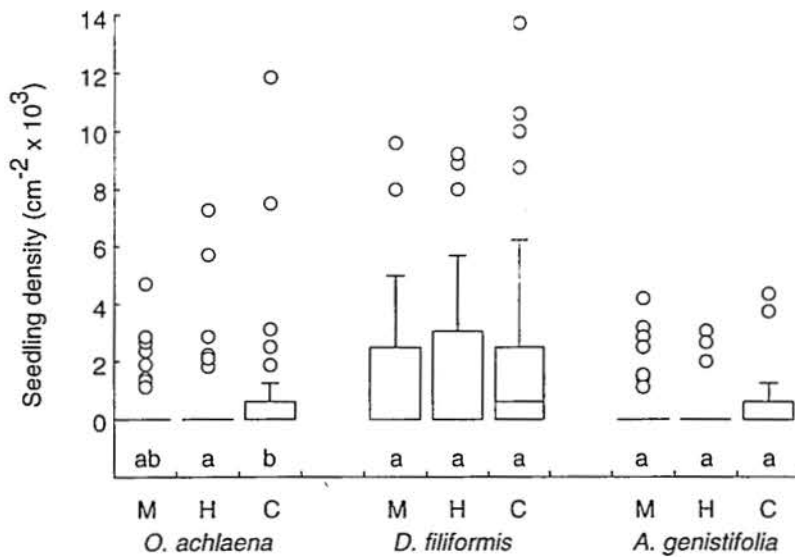


Fig. 5.11 The densities of newly emerged seedlings of three species at Hospital Creek in May 1991 (1 outlier not shown for *D. filiformis* on holes). For each species, microsites with the same letter are not significantly different ( $P < 0.05$ ). M=mounds; H=holes; C=controls.

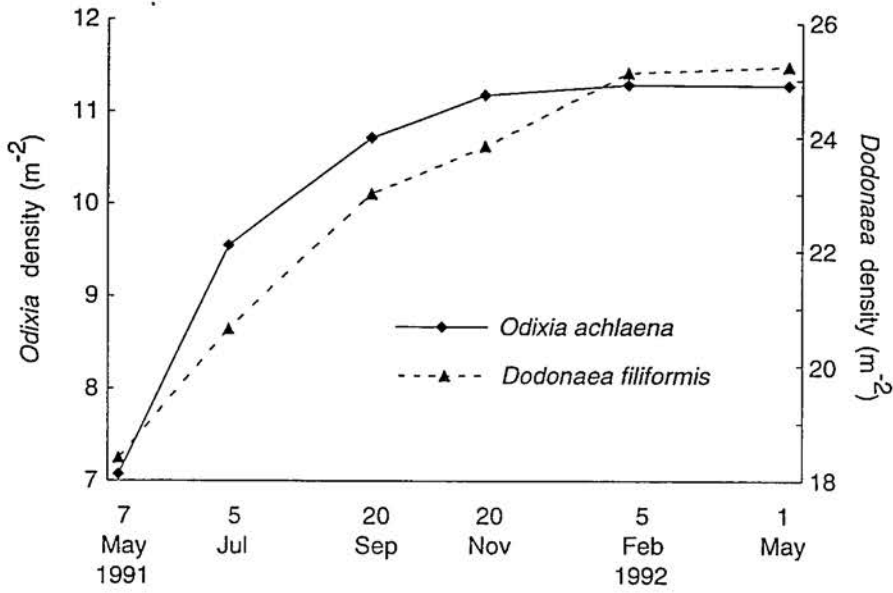
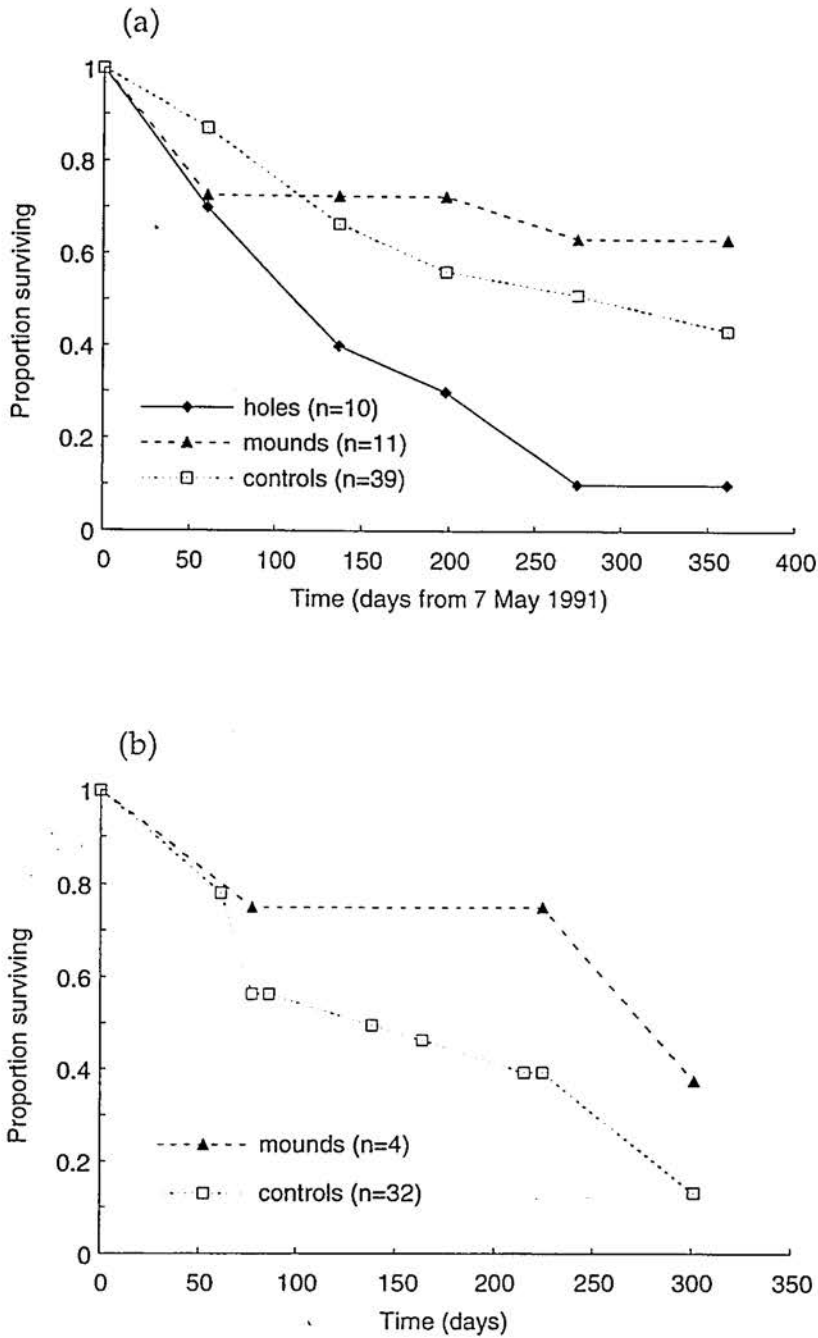
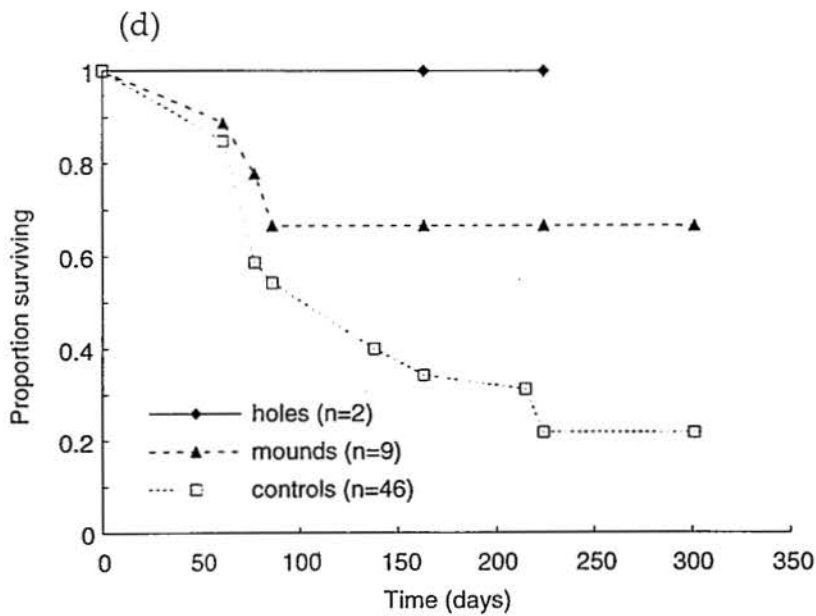
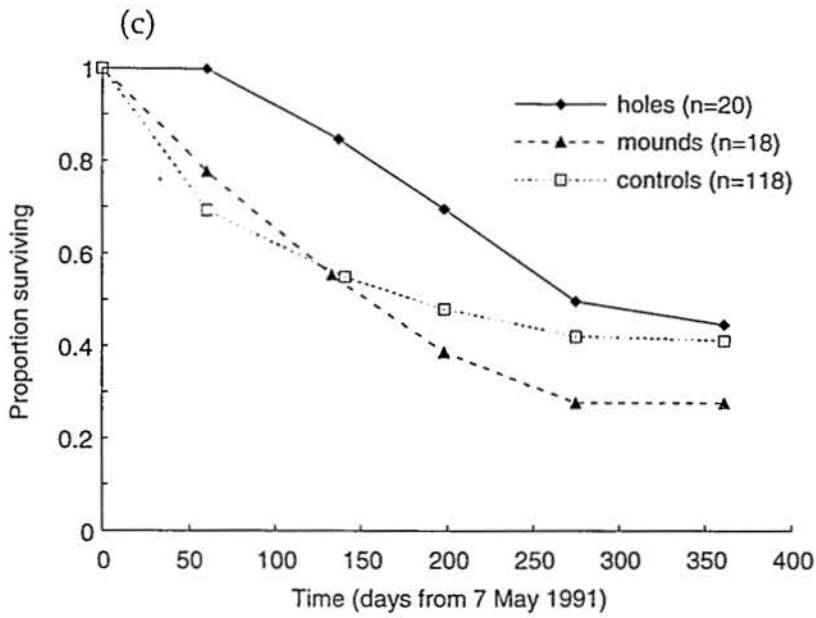


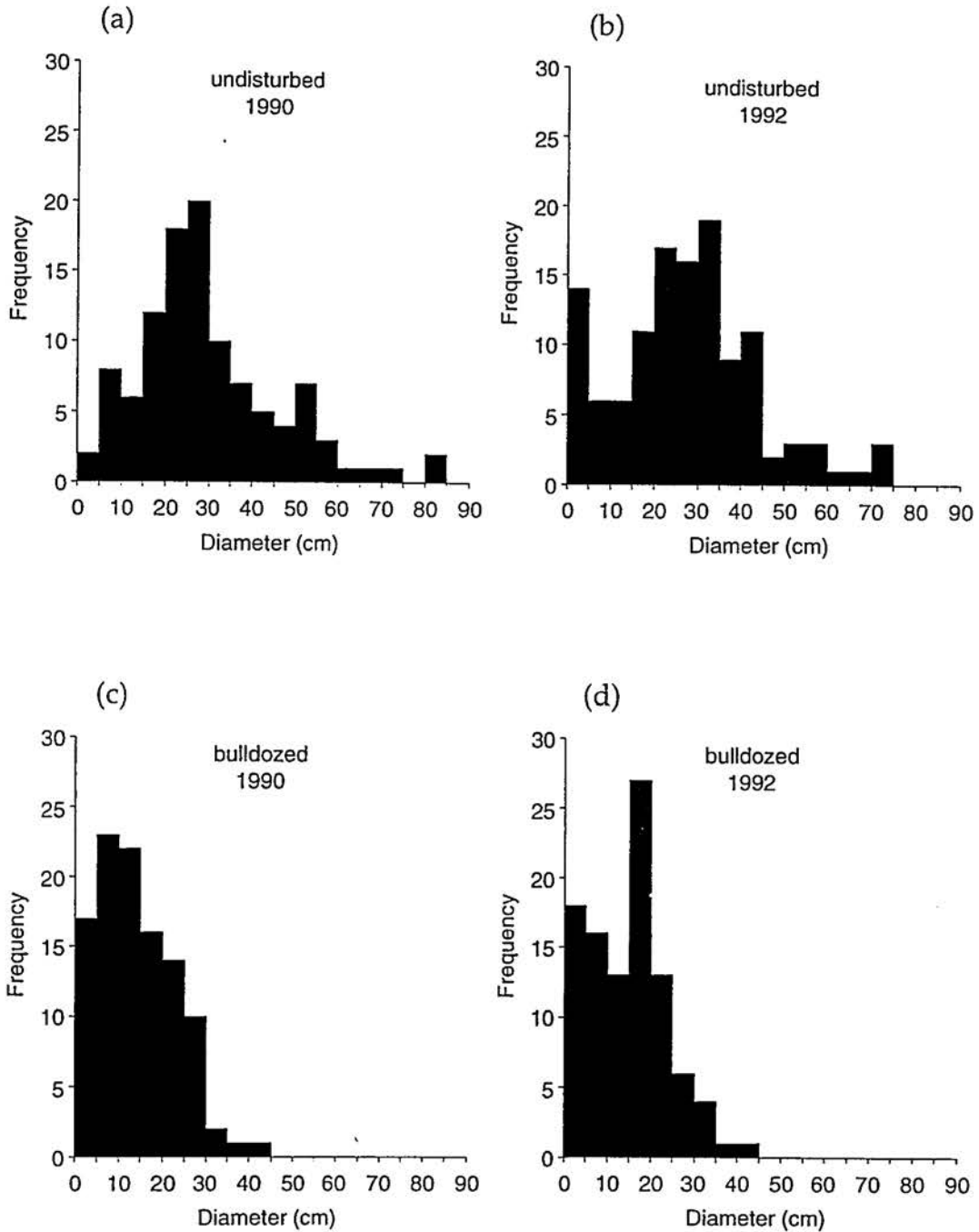
Fig. 5.12 The cumulative emergence of seedlings, expressed as a density, for two species at Hospital Creek. The densities for May 1991 include all seedlings alive at that time.



**Figs 5.13** Survivorship curves showing the proportion of seedlings surviving plotted against time, for seedlings at Hospital Creek, showing seedlings first mapped on 7 May 1991 (a) and (c) or after that date (b) and (d). (a) and (b) *Odixia achlaena*; (c) and (d) *Dodonaea filiformis*.



Figs 5.13 (cont.)



Figs 5.14 Size distribution of *Lasiopetalum micranthum* plants, on the basis of the maximum diameter covered by the lateral spread of branches. Class intervals include lowest values. (a) undisturbed transect, March 1990; (b) March 1992; (c) bulldozed transect, March 1990; (d) March 1992.



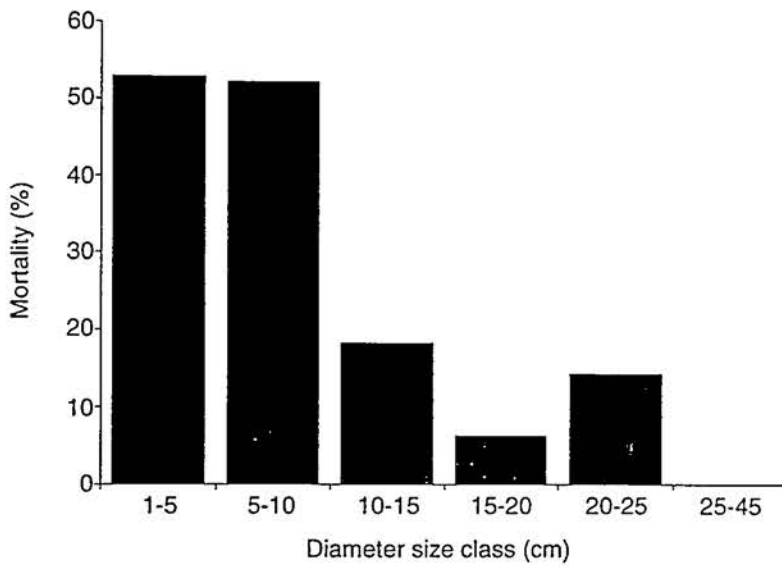
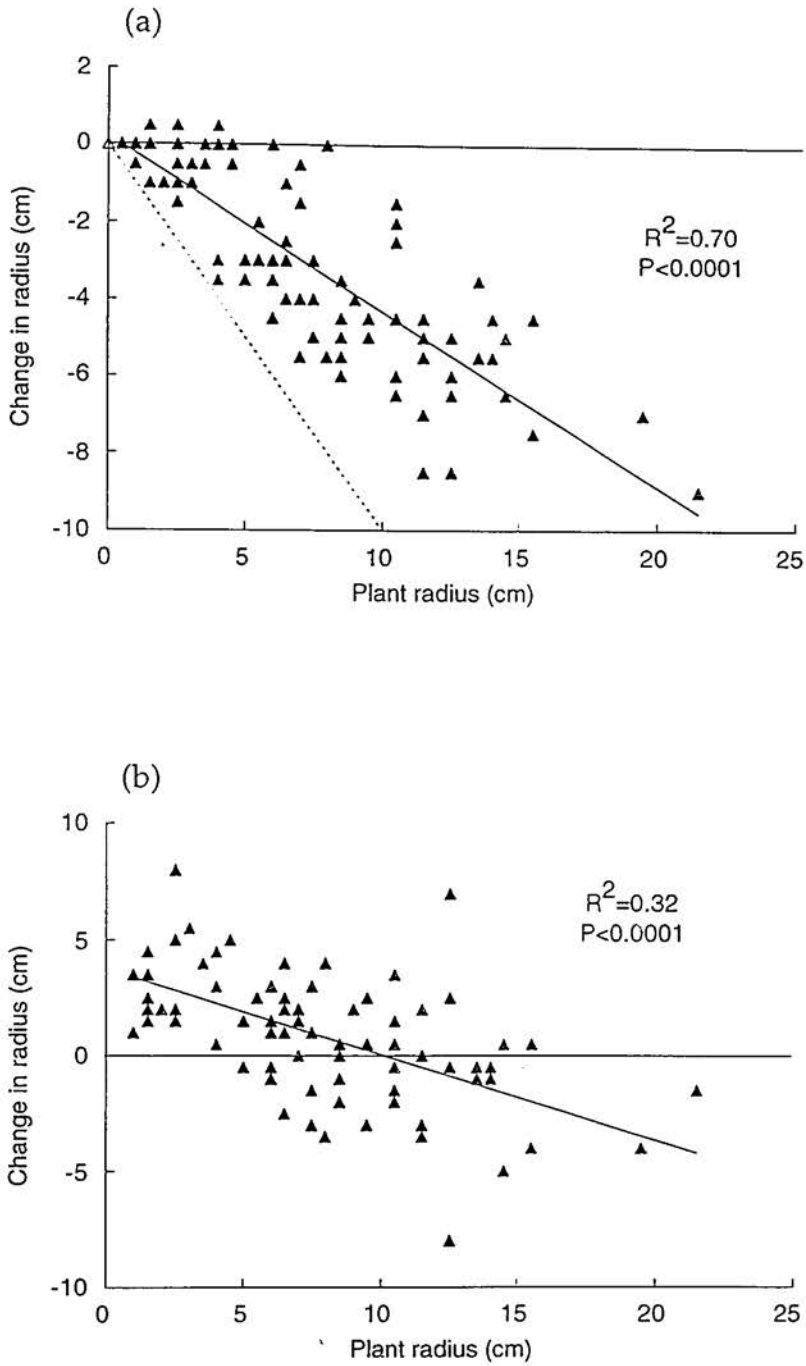


Fig. 5.15 The mortality of established plants of *Lasiopetalum micranthum* in relation to plant size, on the basis of the maximum diameter covered by the lateral spread of branches. Class intervals include lowest values.



**Figs 5.16** The change in radii of plants of *Lasiopetalum micranthum* in relation to the original radii measured in March 1990, as recorded in (a) September 1990 (broken line indicates line of equal change in relation to original radii) and (b) March 1992. Radii are half of the maximum lateral spread of branches. Data are from the bulldozed transect only.

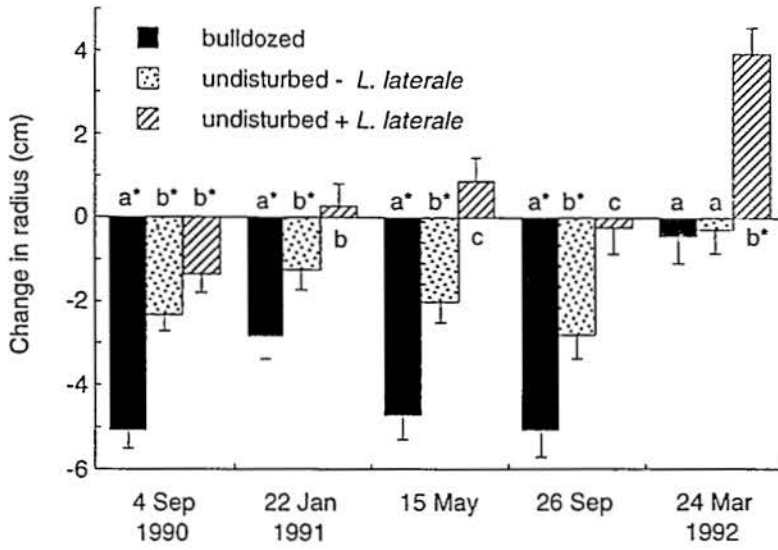


Fig. 5.17 Mean radii changes (least squares means  $\pm$  s.e.m.) of plants of *Lasiopetalum micranthum* in comparison to the original measurements made in March 1990. Radii are half of the maximum lateral spread of branches. Within in each date, means with the same letter are not significantly different ( $P < 0.05$ ). \* denotes mean not equal to zero ( $P < 0.05$ ).

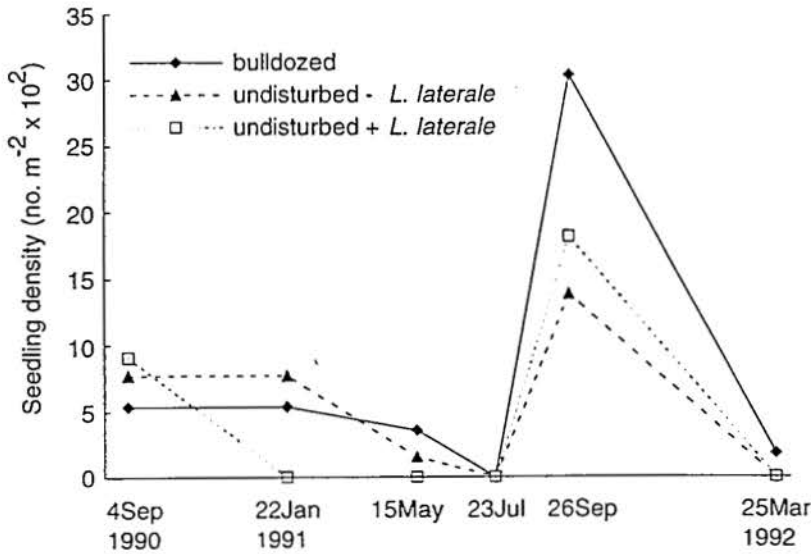


Fig. 5.18 The density of newly emerged seedlings of *Lasiopetalum micranthum* on the transects at the Old Coach Road.

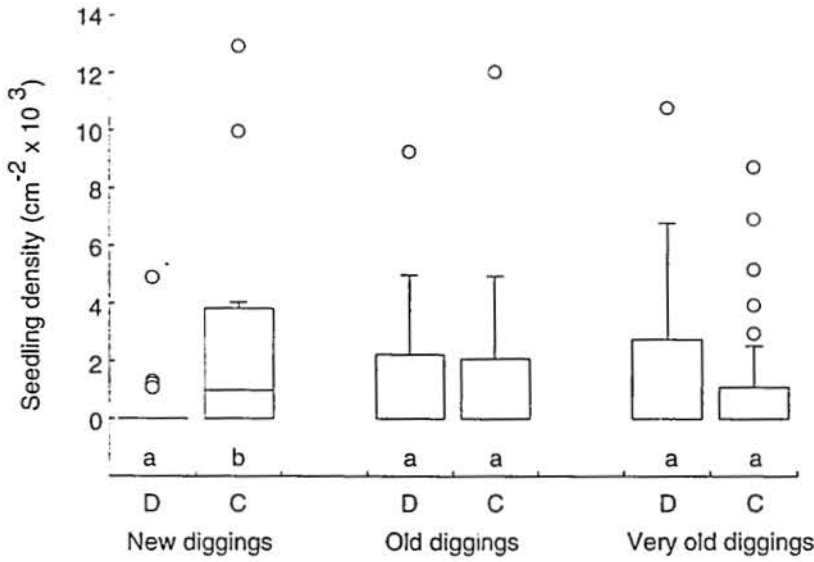


Fig. 5.19 The density of newly emerged seedlings of *Brunonia australis* in the paired quadrats at Westwood. Within each digging age, microsites with the same letter are not significantly different ( $P < 0.05$ ). D=diggings; C=controls.

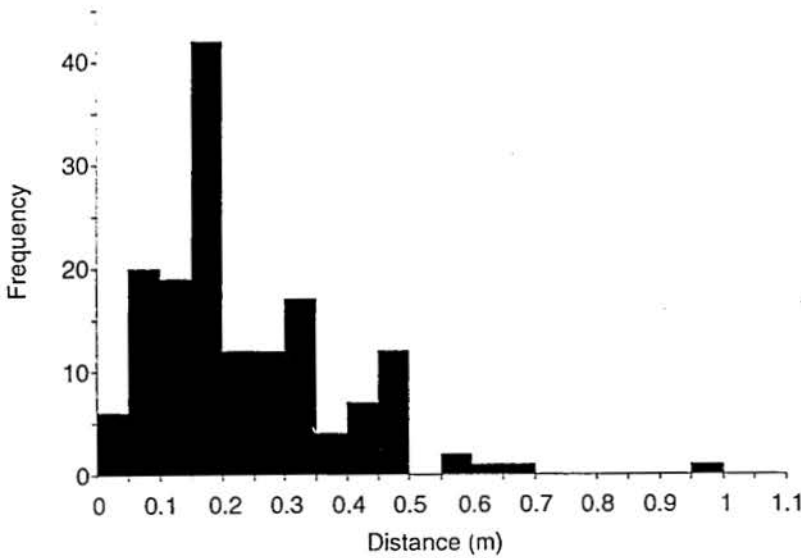


Fig. 5.20 Frequency of distances between seedlings and the nearest flowering adult of *Brunonia australis* at Westwood.

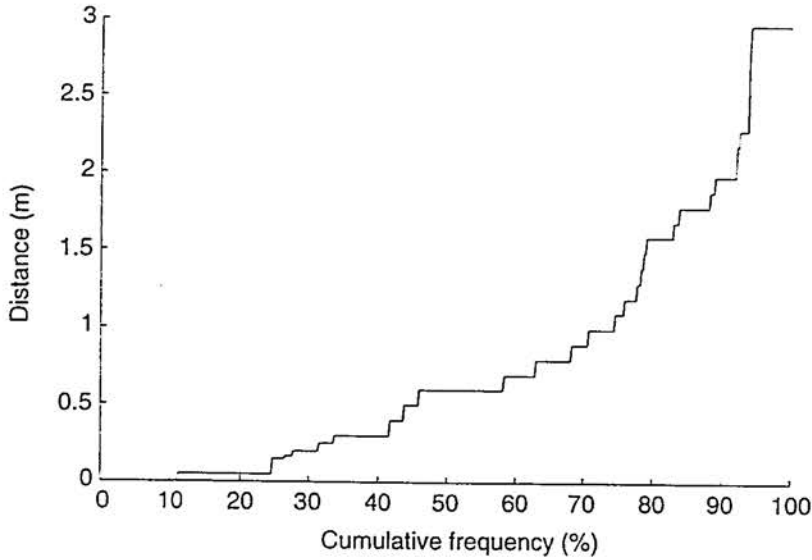


Fig. 5.21 The cumulative frequency of distances between adult *Brunonia australis* and the nearest bettong digging in the transect quadrats at Westwood.

## Discussion

These data provide many examples of seedling germination and survival being enhanced on animal diggings. Because the methods differ from one study site to the next, the results are difficult to compare and will therefore be discussed separately for each study site and set of data.

### *Lepidium hyssopifolium* at Annandale

The onset of germination of *Lepidium hyssopifolium* in autumn appears to be strongly related to available soil moisture. Early autumn rainfall is perhaps inadequate to stimulate germination because of higher evapotranspiration and/or more rapid infiltration. A seed dormancy mechanism involving temperature or day length may also be involved.

These data indicate that seedlings of *Lepidium hyssopifolium* emerge in similar densities on mounds and undisturbed areas. The large difference in density observed in June 1992 was probably a result of differential mortality, as was observed in the survivorship of the June 1991 cohort of seedlings and the total densities of living seedlings in September 1991 (Figs 5.3, 5.5a).

The cause of this differential mortality cannot be determined from the observations that were recorded. There is some evidence that competition from exotic species was responsible, but this cannot be tested directly because the cover of exotics in the quadrats was not determined for different microsite areas. However, it was clearly evident in the field that *Hypochoeris glabra* and *Stellaria media* were completely covering and killing seedlings of *L. hyssopifolium* in some places and that the cover of weeds on mounds was lower. The lack of differential mortality in the September 1991 cohort could reflect the fact that the cover of exotics had become maximal by that time and weeds were no longer growing over seedlings of *L. hyssopifolium* (Figs 5.5b, 5.6). It is also possible that in the undisturbed areas in June 1991, the dense humus layer arising from litter of *Acacia dealbata* prevented the roots of seedlings getting to adequate moisture. This humus may have become quite moist by September 1991 and similar in moisture status to the mound areas which lacked the humus layer.

There is some evidence provided by these data to suggest that diggings are important for the regeneration of *L. hyssopifolium*. However, no recruitment of any consequence was observed in 1990 or 1991. If the short-term survivorship of seedlings germinating early in the year on mounds is consistently better from year to year, and carries through to more substantial recruitment in the years with more favourable climatic conditions, then diggings may well be significant. It is also possible that seedlings that germinate early in the year are better survivors than those which germinate later, independent of microsite effects (see Discussion for Bellerive), which would further enhance the importance of diggings. *Lepidium hyssopifolium* and *L. pseudotasmanicum* are very similar in morphology and phenology, with the exception of the differences outlined in Chapter 2. It would therefore not be surprising if

*L. hyssopifolium* has pulses of recruitment in favourable years, as observed for *L. pseudotasmanicum* at Rosny Point (see Chapter 6).

The occurrence of *L. hyssopifolium* and diggings together underneath trees suggests that there is a causal relationship, but this may be coincidental. *Lepidium hyssopifolium* nearly always grows underneath trees, but the Annandale population is the only one in Tasmania which is known to co-occur with animal diggings. The apparent preference that *L. hyssopifolium* has for the bare areas underneath trees suggests that this species is a poor competitor in dense herbaceous vegetation, but is tolerant of any competition exerted by trees.

#### *Velleia paradoxa and other species at Bellerive*

##### *Germination strategies*

The floristic composition of newly emerged seedlings and the densities after a short period of time are quite different between bandicoot digging mounds and undisturbed areas. Several of the species examined in the field at Bellerive have been subjected to laboratory germination trials by other workers. For example, germination of *Wahlenbergia stricta* (Hitchmough *et al.*, 1989; McIntyre, 1990) and *Crassula sieberana* (McIntyre, 1990) was found to be inhibited by darkness. In contrast, Willis & Groves (1991) found that germination of *W. stricta* was inhibited by light, but that germination of *Helichrysum apiculatum* was promoted by light and fluctuating temperatures. In my study, all three of these species germinated in the field in greater densities where litter cover was lower (and where bare soil was higher), a finding consistent with the positive light responses of the *ex situ* germination studies (see also Goldberg & Werner, 1983; Gross, 1984; Wilson & Zammit, 1992). McIntyre (1990) predicted that these same light responsive species would be dependent on gaps and open spaces for their regeneration. The lower litter cover and greater bare soil provided by digging mounds enables the germination of these species.

McIntyre (1990) also suggested that small-seededness could be part of the gap dependent syndrome. There is evidence of this in my data; most of the species which germinated under higher light conditions (i.e. greater bare

soil and less litter) have very small seeds (Fig. 5.13). The germination of some larger-seeded species, such as *Stackhousia monogyna*, *Arthropodium milleflorum* and *Bulbine glauca*, is not enhanced on digging mounds. The germination of *Bulbine bulbosa*, a close relative of *B. glauca*, did not respond to light in trials by Willis & Groves (1991) and seeds germinate when buried at 20 mm depth (Hitchmough *et al.*, 1989).

However, the species with the largest seeds in my study, *Velleia paradoxa* (Fig. 5.13), was found by John Morgan (pers. comm.) to have a higher germination response in light compared with dark in growth cabinet trials (under temperature conditions typical of daily maxima and minima at Bellerive in autumn). *Velleia paradoxa* germinated in higher densities on diggings in my study, which also suggests a light response, but it is anomalous if there is a general trend relating to seed size. One would expect to find few species with very small seeds that were not dependent on light for germination. This is because the seeds of such species have very small energy reserves and would presumably have evolved a strategy which ensured that photosynthesis could occur soon after germination. Amongst larger seeded species, a variety of strategies may have evolved in response to different pressures, only some of which involved selection for light dependency.

#### *Seedling mortality*

This study presents only a brief view of processes that are likely to vary considerably with annual differences in rainfall and temperature. The three years at Bellerive were each characterised by several months of atypically low rainfall in autumn (Fig. 5.7). Given the propensity of many species to germinate in autumn, it is possible that these years have had lower germination rates and poorer survivorship than more typical years. Seedlings which germinate early in the year are known to survive in greater proportions than those which germinate later (e.g. Harper, 1977; Miller, 1987; Fowler, 1988; Espigares & Peco, 1993), as was observed (although not quite significantly) with *Velleia paradoxa* (Figs 5.10b,c). It stands to reason that seedlings will survive better if they have had longer to develop a root system before the high evapotranspiration stress encountered in summer.



It is not known whether the nearly 100% mortality rates observed in 1991, particularly amongst the species with smaller seeds, are typical of most years. It is possible that these species have pulses of seedling establishment in the occasional years with the right combination of favourable conditions (Daubenmire, 1968; Grubb, 1977; see also Hobbs & Mooney, 1991). These conditions would presumably involve sustained soil moisture and milder temperatures, possibly in combination with good seed production in the previous season.

Mortality was slightly higher overall for native dicotyledons on mounds, although this result no doubt hides a variety of responses which may not all have been in the same direction. Negative effects of litter have been reported to cause higher mortality under some circumstances (Fowler, 1986; Fowler, 1988). In my study, those species which were surviving better on undisturbed areas were probably responding to more favourable moisture conditions (see Chapter 3). This moisture difference may have been more important for smaller-seeded species. Larger-seeded species, such as *Arthropodium milleflorum*, *Stackhousia monogyna* and *V. paradoxa*, had higher survivorship overall compared with smaller-seeded species and seem to be capable of at least some level of recruitment in more years than the smaller-seeded species (Appendix 3). In contrast, seedling survival amongst small-seeded species was found to be greater on bare ground by Gross & Werner (1982), presumably because of relief from competition in that environment.

The amount of plant cover on digging mounds at the end of the study was quite low (Fig. 5.9). Therefore the colonization of mounds will have been largely non-interactive (*sensu* Platt, 1975), even after two years (but see also the response of the exotic *Briza maxima* in Chapter 8). There was unlikely to have been much competition for moisture or light between native species which had germinated on the mounds. However, species resprouting from under the mounds may have exerted some competitive influence.

Ryser (1993) found that in an unproductive environment, competition had little influence on seedling survival compared with the effects of the abiotic environment, with vegetation conferring protection for seedlings. The Bellerive study site is similarly unproductive with a nutrient poor sandy soil,

poor moisture retention and erratic rainfall. While there is evidence of a gap dependent syndrome in some species, similar to that found by Gross & Werner, 1982; Goldberg & Werner (1983) and Gross (1984), the harsh environment of digging mounds may strongly limit the overall importance of these microsites for effective recruitment. Burning periodically produces bare mineral soil on a large scale at this site and may be a more important disturbance factor.

#### *The effect of digging size*

In the paired quadrats, only larger bandicoot diggings were examined, although most of the bandicoot diggings at this site are much smaller. Analysis of seedling emergence and survival on smaller diggings would have been even more troubled by the problems mentioned earlier, with even smaller areas and lower seedling counts per digging. A much larger number of permanent quadrats would also have been required, which increases the logistic problem of finding them all at each visit.

The relationship between disturbance patch size, germination and survivorship cannot be determined from these data. It is possible that there would be little effect on the germination densities of smaller-seeded species, per unit area of digging, given the correlations between bare soil and emergence densities on the control quadrats alone. The effects on survivorship of seedlings on different sized diggings could well be more important. As was illustrated in Chapter 3, the size of diggings has a large bearing on the fertility of the surface soil. The size and therefore depth of the mound increases the distance that roots have to travel to get to the original soil surface underneath. Smaller diggings are also considerably more numerous than larger ones (Chapter 4) and may be more favourable environments for the survival of small-seeded species (Chapter 3), in contrast to the positive gap size/survival relationship reported by McConnaughay & Bazzaz (1987).

#### *Velleia paradoxa*

The strong association and small distances between adults and seedlings of *V. paradoxa* suggest that most seeds disperse only very short distances from parents. Therefore, the proximity of diggings to adult plants is a vital

factor in the ongoing population dynamics. Diggings are certainly widespread in the study area, because 80% of the 140 quadrats from Chapter 4 have at least some digging. Larger diggings are less abundant, are associated with trees and are therefore less widespread (see Chapter 4).

Reasonable confidence can be placed in the finding of higher densities of seedlings of *V. paradoxa* on diggings within the areas sampled. However, at least some patches of established *V. paradoxa* at this study site were located where diggings were much sparser. If freedom from litter is the only factor endowing diggings with higher seedling densities, then other disturbances such as fire also provide similarly litter-free areas. At the time of writing (November 1993), numerous seedlings were observed in a reasonably dense patch of *V. paradoxa* that was burnt in September 1991. No seedlings germinated in this area in 1992, presumably because the fire prevented the production of seed in the summer of 1991/92. Vegetative recovery was quick, but very few plants flowered during that summer. *Velleia paradoxa* appears to have no permanent seed bank in the soil (see Chapter 7). A considerable amount of bare soil resulting from the fire was still present in November 1993.

Survivorship proportions of *V. paradoxa* seedlings were similar on mounds and undisturbed areas, at least in the short-term, and about half of the very few survivors were on disturbed ground. Therefore, it seems unlikely that diggings are crucial to the regeneration of this species, although they may well be important if a long-term absence of fire leads to deep litter accumulation and thus reduces germination.

*Odixia achlaena*, *Dodonaea filiformis*, and *Acacia genistifolia* at Hospital Creek

Fire burnt this study site in September 1990 and germination of *Odixia achlaena*, *Dodonaea filiformis* and *Acacia genistifolia* was well under way when the site was visited in January 1991. The survivorship of *Odixia achlaena* seedlings that were mapped after May 1991 was poorer on mounds and undisturbed areas in comparison to seedlings first mapped in May 1991 (Figs 5.13a,b). Considerable mortality had already taken place by May 1991 and the seedlings mapped on this occasion were already a subset of the total germinants. The total pool of seedlings of *O. achlaena* which emerged on

mounds after May 1991 was too small to make a meaningful comparison of overall survival rates.

Litter which was dropped from fire-scorched trees tended to accumulate in holes and may have been responsible for the higher mortality of *O. achlaena* seedlings, either by complete burial of seedlings and restricting light and/or encouraging attack by pathogens (Fowler, 1988). Holes may have been expected to be a favourable microsite, with presumably more moisture (e.g. Battaglia and Reid, 1993; Gutterman, 1988 cited in Gutterman *et al.*, 1990), but the benefits of higher moisture were clearly unimportant compared with the effect of litter.

Seedlings of *D. filiformis* in holes appeared not to suffer in the same way as those of *O. achlaena*, but seemed to fare worse on undisturbed areas, at least in the first 12 months after emergence (Fig. 5.13d). Unlike the situation with the sandy soils at Bellerive, the availability of moisture in the soil of mounds at Hospital Creek could well be higher than in undisturbed areas, because the clay-rich soil was looser and less compacted. Although there was no difference in densities in May 1991, the initial emergence densities of *D. filiformis* seedlings may have been higher on controls, but counteracted by differential mortality as observed in the seedlings which emerged after May 1991. The net effect was that seedling densities appear to be very similar on mounds, holes and undisturbed areas.

#### *Lasiopetalum micranthum* at the Old Coach Road

The recording of the diameters of *Lasiopetalum micranthum* was originally intended to make possible the comparison of the growth rates of plants between the bulldozed area and the undisturbed area. However, it turned out to be a study of grazing, which nonetheless illustrated some important points for the conservation of this species and may be relevant to the results of other observations and experiments at this site. Whether it was sheep or wallabies which were contributing the bulk of the grazing pressure on *L. micranthum* is not known. The uprooting of entire plants, some of which were quite large, suggests that sheep were responsible.

The selective nature of the grazing suggests that plants were more prone to grazing in places where they were more visible. The bulldozed transect had virtually no plant cover or litter, except for *L. micranthum*, in comparison to the high cover of plants and litter in the undisturbed areas. The patches of dense *Lepidosperma laterale* also seem to protect *L. micranthum* from grazing pressure, relative to the undisturbed areas without it. *Lepidosperma laterale* leaves are quite tough and fibrous and are possibly not very palatable, further discouraging grazing. Plants were probably easier to uproot on the bulldozed transect, with greater root failure in the shallow soil which had been considerably depleted by the bulldozing. Another factor could be that all plants on the bulldozed transect were less than 5 years old, even at the conclusion of the field work. Plants of the same diameters were probably much older on the undisturbed transect, with a more extensive and stronger root system.

Longer lengths of branches were consumed amongst bigger plants, suggesting that grazers were preferentially eating the recent growth at the ends of branches and leaving the previous year's tougher growth. The new growth at the ends of branches tended to be longer on the branches of larger plants compared with smaller ones, and carried most of the flowers. This means that grazing, which was most intense while inflorescences were developing, was systematically removing the bulk of the season's reproductive effort on the bulldozed transect and a substantial proportion on the undisturbed transect.

As a result of differential grazing, seed production by *L. micranthum* was probably highest on the part of the undisturbed transect with *L. laterale* and lowest on the bulldozed transect. The densities of seedlings emerging in these different areas are probably strongly influenced by this effect of grazing. The better survival of seedlings on bulldozed areas compared with undisturbed areas (without *L. laterale*) may be a result of reduced competition with the dominant grasses (*Poa rodwayi* and *Themeda triandra*).



*Brunonia australis* at Westwood

When the field work was performed in August 1991, all seedlings of *Brunonia australis* were recent germinants less than 3 months old and many had cotyledons which had not fully opened. *Brunonia australis* is a large-seeded species with large cotyledons (Fig. 5.13). The ground was sufficiently moist during the time of the study and differential mortality as a result of water stress would be very unlikely to have occurred so soon after germination. Therefore the counts of seedlings made in August 1991 are likely to reflect the emergence pattern closely. The lower density of seedlings on diggings on the transects seems unlikely to be simply a result of differential emergence times, which would possibly favour earlier germination on diggings on the basis of soil temperatures (see Chapter 3). This difference in density was only just significant at the 95% confidence level, with new diggings excluded, and may not be reliable.

For time efficiency, only the minimum distance from adult *B. australis* to the nearest digging was measured in each quadrat, but this still gives an approximate indication of the proximity of adult plants to diggings. Assuming that the propensity to flower and set seed is unrelated to the distance from diggings, diggings are beyond the dispersal range of more than half of the seed rain. The dispersion of bettong diggings could not be assessed with the size of quadrat used in this study, but a visual assessment indicated that they were clumped and associated with trees, which is consistent with other studies of bettong diggings in Tasmania (Taylor, 1992a; Chris Johnson, pers. comm.).

It is possible that diggings actually buried and obscured some adult plants and seedlings, which would have reduced the likelihood of finding a spatial association between diggings and *B. australis*. However, the effect of burial on the spatial analysis is probably very small, with the test using only presence/absence data and nearly all quadrats with digging present having less than half of the total area disturbed. Additionally, some adult plants grow back up through the mound areas and would be visible again on all except the newer diggings. Similarly, seedlings would only be obscured by the very most recent diggings, because most seedlings would have germinated after the appearance of the majority of diggings. The 'new' digging category

covered only 0.34 % of the total sampled area on the transects. The lower densities of seedlings on 'new' diggings in the paired comparisons are probably partly a result of the burial of newly emerged seedlings, but they also suggest that there is very little seed of *B. australis* stored deeper in the soil and that the most recent fall of seed had been buried and rendered unavailable for germination (see Hitchmough *et al.*, 1989).

If either differential germination and/or differential survivorship of seedlings was occurring in favour of diggings, one might expect to find some evidence of attraction between the clustering of adult *B. australis* and the clustering of diggings, as a result of a long-term deterministic process. That this was not the case suggests that bettong diggings are neutral in respect to the germination and establishment of *B. australis* at this site. Further evidence for this comes from the paired quadrats, which showed no difference in the density of seedlings on diggings (more than 3 months old) compared with undisturbed ground, even with the imposition of a highly biased sampling which sought out the juxtaposition of clumps of diggings and adult *B. australis*. These joint clusters were not easy to find in the study area, further suggesting that their occurrence was the result of the coincidence of two processes which were random with respect to each other.

The laboratory germination trials of Hitchmough *et al.* (1989) indicate that *B. australis* germinates readily in the dark. Therefore the germination of this large-seeded species is unlikely to be advantaged by bettong digging creating bare ground.

#### *Other study sites*

Regeneration of *Euphrasia scabra* at Dukes Marshes appeared to have no association with animal disturbance and was not studied after February 1991.

No seedlings of *Olearia ericoides* or *Gahnia rodwayi* were observed at Chimney Pot Hill, of *Olearia hookeri* at East Risdon or of *Glycine latrobeana* at Powranna. The germination requirements of these species may well be disturbance-related, but are clearly not related to mechanical soil disturbance (See Appendix 5 for final comments on these species).

*Methodological and data analysis considerations*

The standardisation to a unit area for pairwise comparisons of seedling densities meant that an error factor was introduced which increased with decreasing size of microsite areas and decreasing seedling densities. This error factor was most prevalent with comparisons involving holes, which were typically smaller than mounds and controls in area and often with lower seedling densities. For example, a hole with one seedling on an area of 150 cm<sup>2</sup> would appear to have a higher density than a mound with four seedlings on 800 cm<sup>2</sup>, but the difference in density would be less reliable than if the counts were 10 and 40. Fortunately, the Wilcoxon signed-rank test gives greater weight to larger differences, which tended to be associated with higher densities (e.g. Fig. 5.4). However, many non-significant comparisons, particularly those involving holes, were probably Type II errors and should be treated with less confidence.

Newly emerged seedlings of several of the species which were mapped at Bellerive were extremely small, with tiny cotyledons and no hypocotyl. These species, which include *Wahlenbergia stricta*, *Crassula sieberana*, *Scleranthus biflorus* and *Helichrysum apiculatum*, were probably overlooked to some extent in places where there was a dense cover of leaf litter. Since leaf litter cover was generally lower on mounds compared with controls, this would have tended to favour the finding of greater densities on mounds. However, I doubt that this error could account for the magnitude of differences which were observed. Besides, the difference in density was still evident in December 1992, when most seedlings that were still alive were somewhat larger and more conspicuous. Finally, the findings are consistent with laboratory germination studies of three of the species mentioned above, which will be discussed later.

Only very early seedling survivorship was examined in this study, with the life of all seedlings being followed for less than 3 years. The spatial scale of microsite differences which was the focus of this work, would be expected to become less important as individuals increased in size and establish roots beyond the immediate neighbourhood of the diggings. For example, in the case of mounds, the physical differences may well be of little relevance



by the time roots have grown through to the original soil surface. Therefore, any differences in survivorship of seedlings that are related to these microsite differences, should be manifest within the first few years and will have been recorded for most species.

The categories such as hole and mound encompass a range of slightly varying conditions, which are possibly also associated with variations in germination and survivorship. Therefore, the scale that was studied here will have tended to average the variation in seedling responses which may be occurring at an even finer scale. The spatial demarcation between mounds and holes was by necessity arbitrary and may not have always reflected real physical differences in microsite (see Fig. 3.1). The microsites classified as holes had a variable amount of area which was similar physically to mounds and a variable amount of area which was filled with deep litter. This variability was another source of error in comparisons involving holes.

In most of the sampling methods used here, the quadrats were subjectively located over diggings so as to be close to target species and increase the efficiency of sampling. This sampling strategy prevents the estimation of an average density of seedlings on and off diggings in the areas overall. It must be recognised, therefore, that the mean densities are presented only for the purpose of relative comparison between diggings and undisturbed areas. Data where the densities *are* indicative for the general area are those for *Brunonia australis* (Table 5.12) and those for the three species at Hospital Creek, but on diggings only (Fig. 5.11).

The sampling interval varied considerably both between and within study sites. The longer sampling intervals may have resulted in very short-lived seedlings being overlooked. This loss of information is offset, however, by the gaining of data from a larger range of sites than would have been possible with more frequent sampling.

### Conclusions

The densities of seedlings emerging on diggings compared with undisturbed areas were the same for a number of species (e.g. *Lepidium hyssopifolium*, *Stackhousia monogyna*), although some non-significant results

were probably affected by very low and 'noisy' densities. Some species had higher densities of seedlings emerging on diggings compared with undisturbed areas (e.g. *Velleia paradoxa*, *Helichrysum apiculatum*, *Wahlenbergia stricta*) while the opposite was true for a very few species (e.g. *Arthropodium milleflorum*).

Differential survivorship in favour of diggings was recorded for some species, which may serve to cause a differential density in some instances (e.g. *L. hyssopifolium*), or simply neutralise a difference in emergence density having an effect in the opposite direction (e.g. *D. filiformis*). Differential survivorship in favour of undisturbed areas compared with mounds was recorded for native dicotyledons as a group at Bellerive, although the density of this group, with the exclusion of *Stackhousia monogyna*, remained higher on mounds. There were no examples of seedlings surviving better on holes, but some examples of them faring worse (e.g. *Odixia achlaena*).

Seed size is an important factor in determining the kinds of responses observed for both emergence and survivorship, with larger-seeded species being generally less affected by the microsite differences at the scale considered here.

## Chapter 6

### Experiments on Disturbance: Simulated Animal Digging, Burning and Germination Trials

#### Introduction

The previous chapter presented observations on the germination and survival of seedlings on disturbances created by small mammals. In this chapter, similar mechanical soil disturbance is examined in designed field experiments. There are several reasons for taking this second approach. First, designed experiments can be imposed specifically in the vicinity of a population of a plant species of interest, thus increasing the probability that seeds may disperse on to diggings, or that soil-stored seed may be stimulated to germinate. Second, the mechanical disturbance can be examined in conjunction with other experimental treatments. Third, the utility of mechanical disturbance as a management tool can be examined. The greater control over variables may produce results that can supplement the knowledge gained in the purely observational approach, although the loss of realism in experiments must be recognised.

Simulated animal digging experiments were set up in the vicinity of populations of *Lasiopetalum micranthum*, *Lepidium hyssopifolium*, *L. pseudotasmanicum*, *Stackhousia gunnii* and *Vittadinia muelleri*. In one of the experiments at the *L. micranthum* study site a burning treatment was also imposed, to compare the effects of burning and mechanical soil disturbance as different disturbance phenomena. The experiment involving *L. hyssopifolium* was set up in an area where the species had been recorded in the past, but had largely disappeared, to see if simple disturbance could resurrect the population. A watering treatment was imposed in the simulated animal digging experiment involving *L. pseudotasmanicum*, to examine how digging and moisture are related in the germination and survivorship of this species.

*Lasiopetalum micranthum* and *Odixia achlaena* are two species which regenerate well after fire, presumably because, for both species, soil heating breaks some kind of seed dormancy mechanism. *Ex situ* experiments were

carried out to further the understanding of the disturbance requirements for the germination of these two species. For *L. micranthum*, oven heating trials of seeds were used to identify the optimum conditions for breaking dormancy. For *O. achlaena* an experiment tested whether dormancy is broken by the direct effect of heat on seeds, or indirectly by changing some property(ies) of the soil which in turn stimulates germination. Both of these experiments have implications for the comparison of mechanical soil disturbance and fire as disturbance mechanisms.

## Methods

### *Lasiopetalum micranthum* field and laboratory experiments

Two field experiments were established at the Old Coach Road study site. The first field experiment, which tested only simulated animal digging, was set up on 15 May 1991 with 15 pairs of permanent 40 x 40 cm quadrats arranged in two columns. Each quadrat was marked by steel rods. Random allocation determined which of the quadrats of each pair was to be disturbed, with the partner remaining undisturbed as a control. All 30 quadrats were contiguous and therefore covered 4.8 m<sup>2</sup>, in an area that was chosen for having a relatively high abundance of established *L. micranthum*. The understorey in this area had a uniform cover of native grasses and forbs, which were less than 10 cm high. There was some surface rock, but very little exposed bare soil. No seedlings of *L. micranthum* were present in any quadrats before treatments were applied.

The disturbed plots had litter, surface rocks and larger plants (including *L. micranthum*) removed and then were intensively dug all over with a small two-pronged garden fork to a depth of approximately 5 cm. All remaining plant material was then removed, but as much soil as possible was returned to the quadrat at all stages. The loose soil was raked to one side to form a mound, leaving a depression which was roughly 15 cm wide (Fig. 6.1). The total cover of live plants, litter, rock and bare soil was estimated after 10 months, using a 5 x 5 cm string grid as a guide. Seedlings of *L. micranthum* were mapped on to graph paper (see Chapter 5 for details of the method) on six occasions over 23 months.

The second field experiment was set up on 1 October 1991 and involved combinations of burning and simulated animal digging in a factorial randomised block design. Within each of fourteen blocks, the following treatments were randomly allocated between four permanent quadrats marked with metal rods: dug/burnt, dug/unburnt, undug/burnt, undug/unburnt. The 40 x 40 cm quadrats were separated by 20 cm between blocks and 25 cm between the outside two quadrats within each block, while the inner two quadrats of each block were separated by 80 cm. Therefore the entire experiment was within an area of 24.36 m<sup>2</sup> and was only a few metres from the first experiment, but with slightly higher cover of exposed rock. Three new seedlings on three quadrats were present before treatments were imposed and two of these were killed by the disturbances.

Simulated animal digging was carried out as described for the first experiment. Burning was carried out with a Companion No. 74 blowtorch, which runs on liquid petroleum gas. The torch produced a large blue flame, some 40 cm long, and was played over the entire quadrat area for 2 min. A metal shield was used to protect neighbouring quadrats from the heat of the torch and to contain the fire. All quadrats which received the burnt/dug treatment were dug first (it is acknowledged that this treatment is somewhat artificial, because in a wildfire, bare soil would have no fuel to burn and heat the soil). Seedlings were mapped on four occasions concluding on 20 April 1993.

An experiment utilising a real wildfire was not practicable at the Old Coach Road study site because of the very limited and patchy distribution of *L. micranthum* and the statistical need to establish plots first and then randomly allocate burning treatments (Hurlbert, 1984). For these reasons, a simulated wildfire was considered preferable. To determine the intensity of heat applied during burning, some trial burns were performed with the blowtorch while soil temperatures were recorded. Nine thermocouples were buried at 1 cm depth, spread out over the 40 x 40 cm quadrat for both the dug and the undug treatments. This was repeated once for each. The temperatures were recorded with a datalogger at 3.6 s intervals for 20 min. These trials were performed on 20 April 1993.

To determine the optimum heating conditions required to stimulate germination of *L. micranthum*, trials were performed with seeds heated in an oven, using a method similar to the one described by Auld & O'Connell (1991). The seeds were collected from the Old Coach Road site on 11 December 1991, at a time when capsules were just starting to dehisce. The seeds and capsules were rubbed between two pieces of wallboard to remove the papery capsules and then the seed was separated with a vacuum extractor.

Small samples of sieved and oven-dried topsoil, which were collected from the study site, were placed in aluminium containers and pre-heated in a convection oven. A thermometer was used to determine when the soil had reached the prescribed temperature, after which thirty seeds of *L. micranthum* were quickly mixed into the soil, lids were placed on the containers and they were returned to the oven. Seeds were heated in combinations of temperatures and time periods as follows: 40, 60, 80, 100, 120°C; and 1, 5, 10 and 30 min. Each temperature/time combination was replicated once. The maximum heating time of 30 min. was intended to mimic the period of soil heating which might occur underneath burning heavy fuels such as fallen trees. When the containers had been removed from the oven and cooled, the seeds were separated from the soil by sieving and placed on filter papers in Petri dishes. A minimum of 27 seeds was recovered for each lot. Two more Petri dishes were prepared, each with 30 unheated seeds. Petri dishes were placed in a dark incubator at 20°C and watered regularly.

Scoring took place at one to two week intervals initially, increasing to four week intervals after ten months. Seeds were considered to have germinated when a radicle appeared. At this stage germinants were removed. An identical experimental design was employed for a second series of heating trials, but with temperatures of 50 and 60°C and times of 1, 2, 4 and 6 h. This second series of oven heating attempted to imitate the situation which occurs in the field on bare ground, that is, soil temperatures near the surface of 50-60°C for several hours on a hot sunny day. The first and second series of trials were set up on 1-3 February 1992 and 18-19 August 1992 respectively.



*Lepidium hyssopifolium simulated digging experiment*

A simulated animal digging experiment was set up at Bagdad on 24 May 1991. A strip of the 0.5 m tall dense sward on the road verge was mowed to 5 cm, to make the finding of seedlings more practicable. After mowing, two transects were marked out with 250 mm nails. There was a gap of 30 m between the two transects, which were both parallel with and the same distance from the road. There were 10 and 11 pairs of 0.5 x 0.5 m quadrats spaced 0.25 m apart along the transects, with alternating digging and control treatments. Digging consisted firstly of removing all plants, with as much soil as possible being returned to the quadrat, followed by hoeing with a mattock to a depth of 5 cm.

Because of the extremely dry conditions of May 1991 and concern that germination might fail completely, each quadrat was watered at a rate of 5 l. Quadrats were watered again on 7 June 1991, when each quadrat received 3 l. No adults or seedlings of *L. hyssopifolium* were observed in any quadrats at the start of the experiment. The nearest adult plant to the southern transect was at least 5 m away, while one solitary adult plant was 0.5 m from a pair of quadrats on the northern transect. Seedlings were counted on 3 July 1991 and mapped on to graph paper on 4 October 1991 (see Chapter 5 for details). The fate of mapped seedlings was checked on 28 January 1992 and finally on 6 May 1992. In the January visit, the projected foliage cover of all live plants and the cover of bare soil was estimated, using a 5 x 5 cm string grid as a guide.

*Lepidium pseudotasmanicum simulated digging experiment*

Two simulated digging experiments were established at the Rosny Point study site, where *Lepidium pseudotasmanicum* was found only along the edges of a recently formed asphalt path. The layout of the replicates for the experiments took account of the linear nature of the distribution of adult plants. In the first experiment, which was set up on 17 August 1990, pairs of quadrats were located along two transects which were perpendicular to the path and 3 m from it at their nearest ends. The transects were located under



the dense canopy of *Allocasuarina verticillata* trees, which had deposited a continuous cover of litter. The understorey was very sparse on one transect, but somewhat denser on the other, where it consisted predominantly of the exotic grass *Dactylis glomerata*. There were no seedlings or adults of *L. pseudotasmanicum* initially in any quadrats.

The 20 x 20 cm quadrats were separated by 30 cm along the transect, with 20 cm between the quadrats of each pair. The transects were marked with 250 mm nails and each had 10 pairs of quadrats. One of the quadrats in each pair was randomly chosen to receive simulated animal digging, which consisted firstly of removing all litter and plants and then digging intensively with a small two-pronged garden fork to a depth of 4 cm. Seedlings in quadrats were counted on five occasions: in October 1990, March 1991, April 1991 and February 1992.

The second experiment was set up on 13 May 1991. The 30 x 30 cm quadrats were spaced 20 cm apart along a transect which was 2 m from the path and parallel with it. All quadrats were within 1.5 m of adult *L. pseudotasmanicum*. The understorey varied from sparse to dense, with a mixture of native and exotic grasses and forbs, on ground that nearly all appeared to have been disturbed during construction of the path. There was no *L. pseudotasmanicum* present in any quadrats initially.

Digging and watering treatments were randomly allocated between blocks of four adjacent quadrats along the transect, with the following combinations: dug/watered, dug/unwatered, undug/watered, undug/unwatered. There were 10 blocks of quadrats, with a 5 m gap between the first and last 5 blocks. Digging was applied as described earlier for *Lasiopetalum micranthum*. Watering was carried out on 20 May 1991 and 5 June 1991, when each watered quadrat received 3 l. Seedlings of *L. pseudotasmanicum* were counted in 1991 on 17 June, 3 July, 1 August, 8 October and finally on 29 January 1992.

#### *Stackhousia gunnii* and *Vittadinia muelleri* simulated digging experiment

A simulated animal digging experiment was set up on 31 July 1991 on the verge of the Tunbridge Tiers Road, using the same design and methods

as described for the first *Lasiopetalum micranthum* experiment. The 15 pairs of quadrats were 30 x 30 cm and were all separated by 10 cm. Mature plants of both *Stackhousia gunnii* and *Vittadinia muelleri* were present in many quadrats before the digging treatments were applied. The vegetation on the transect consisted of a continuous cover of native grasses and forbs up to 20 cm tall, with a projected foliage cover of approximately 60%. The remaining cover consisted mainly of litter, but there were some patches of lichens and mosses. There was very little bare soil or exposed rock (<2%). Seedlings were counted on 23 June 1992. Adults of *S. gunnii* were counted before digging was applied at the start of the experiment and again in June 1992, over a 40 x 40 cm area centred on the quadrats.

#### *Odixia achlaena* pot germination experiment

Seed of *Odixia achlaena* was collected from Hospital Creek on 5 February 1992. Thirty soil cores were collected from the same area on 22 June 1992, all from within an area of 3 x 3 m. The cores, which were 6 cm deep and 4.6 cm in diameter, were carefully removed from the cylindrical metal corer and inverted into pots, attempting as far as possible to keep the cores intact. The pots were slightly larger than the cores and loose soil from the bottom was packed around the sides of the original core to fill the pot. The whole contents were then transferred to another pot of the same size, but inverted yet again so that the original soil surface was on top.

Some of the pots and soil cores were heated in a convection oven with several temperature/time combinations. Thirty seeds were placed on top of the soil in each pot. Some pots had the seed added after soil heating, while in others, the seed was added before soil heating. There were five replicates (pots) per treatment and a total of six treatments as follows:

1. soil heated for 2 h at 100°C, seed added after.
2. soil heated for 2 h at 80°C, seed added after.
3. soil + seed heated for 2 h at 80°C.
4. soil heated for 0.5 h at 80°C, seed added after.
5. soil + seed heated for 0.5 h at 80°C.
6. soil + seed unheated.

The treatments were prepared and the pots randomly arranged in a glasshouse on 26 June 1992. The emergence of seedlings was recorded at two weekly intervals and deaths were noted. The pots were regularly watered and were re-arranged twice to new random positions during the three months until the final scoring.

### *Data Analysis*

For the digging and burning experiments, comparisons of seedling emergence densities by parametric analysis of variance were not possible, because data transformations were unable to make the data meet the assumptions of the test. Comparisons were made using the Friedman two-way analysis of variance by ranks when there were more than two treatment combinations per block, after first removing all blocks with zero seedlings. When there were only two treatments per block and for pairwise comparisons, the Wilcoxon signed-rank test was used. This test needs minimally six pairs with differences before a significant difference can be detected at the  $P=0.05$  level (Sokal & Rohlf, 1969). The comparisons which were not testable are identified, that is, where less than six pairs had seedlings. Data are presented in the form of 'box plots', which indicate the 25th and 75th percentiles (the box), the median (the bar inside the box) and the range of values (lines with bars beyond the box, with circles indicating outliers).

The survivorship of seedlings on differing microsites in the experiments at the Old Coach Road was tested using a  $\chi^2$  test on a contingency table of the proportion of seedlings which lived and died.

The 80°C treatments from the *Odixia achlaena* pot experiment were analysed by parametric two-way analysis of variance, with the two factors being soil heating time and  $\pm$  seed heating (i.e. whether or not the seed as well as the soil was heated). A one-way analysis of variance was performed on the full experiment with the six treatment combinations. Pairwise comparisons were made with the least significant difference test. The seedling counts were log transformed in both analyses. Actual counts were considered preferable to proportions (of the 30 seeds added per pot), because seed that was already present in the soil may also have germinated.

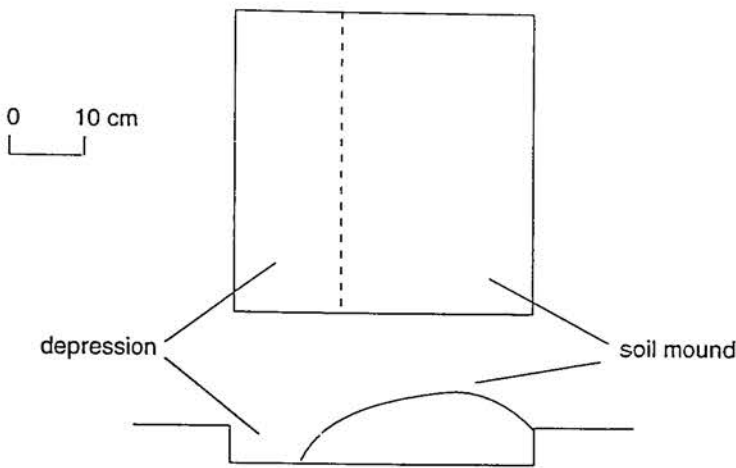


Fig. 6.1 Schematic diagram of simulated digging plots at the Old Coach Road, drawn to scale.

## Results

### *Lasiopetalum micranthum* field and laboratory experiments

In the first simulated digging experiment, the total emergence of seedlings observed over 23 months on diggings was considerably higher than in the controls ( $P=0.003$ ). Only two seedlings were observed on control quadrats out of a total of 81 seedlings (Fig. 6.2). At the conclusion of the study on 20 April 1993, the density of living seedlings was still considerably higher on diggings compared with the undug plots, with counts of 51 and two seedlings respectively ( $P=0.005$ ; Fig. 6.2). A total of 61.4% of the 70 seedlings that were mapped on diggings until 1 September 1992 were still alive in April 1993.

In the second field experiment, the variation between the four treatment combinations was highly significant for the total counts of seedling mapped until 1 September 1992 ( $\chi^2_{3}=17.7$ ,  $P=0.0005$ ). In pairwise comparisons, there was no difference between the dug/burnt and dug/unburnt treatments ( $P=0.52$ ), while both digging treatments had significantly more seedlings than the undug/burnt treatment ( $P<0.05$ ) and the undug/unburnt treatment ( $P<0.005$ ). In the quadrats that were not dug, those that were burnt had

significantly more seedlings than the unburnt quadrats ( $P=0.03$ ; Fig. 6.3). To summarise the results of this experiment, burning stimulated more seedling emergence than no burning, but digging stimulated even higher levels of germination and overrode the effect of burning.

At the final visit in April 1993, only the survivorship of previously mapped seedlings was recorded for all treatment combinations in the second experiment. There was no difference between the treatments in the survivorship of seedlings until April 1993, out of all those mapped until 1 September 1992 (excluding the undug/unburnt treatment which had only two seedlings:  $\chi^2_2=0.57$ ,  $P=0.7$ ). Overall, 44.7% of these 103 seedlings survived.

In the trials with thermocouples, the highest mean soil temperature at 1 cm depth was 48.2°C for the dug quadrats and 35.5°C for the undug quadrats pooling both replicates for each treatment; there were four failed thermocouples on the dug quadrats. The mean temperature peaked after 3.4 minutes on the dug quadrats and after 6.3 minutes on the undug quadrats (Fig. 6.4).

Analyses were performed to compare the densities and survivorship of seedlings on the depressions and mounds of the dug (and unburnt) quadrats from both experiments combined. For these analyses, the quadrats were divided into four rectangular strips which were each 10 x 40 cm. One of these strips covered depressions while the other three covered parts of the mounds. The total densities of seedlings which emerged on the four strips of the dug quadrats were not significantly different ( $\chi^2_3=0.61$ ,  $P=0.89$ ). There was some variation in the survival of seedlings until April 1993, out of those that were mapped up to 1 September 1992, with the best survival near the highest part of the mounds ( $\chi^2_3=9.91$ ,  $P=0.019$ ; Table 6.1).

In both of the field experiments, the majority of seedlings emerged in the interval between the sampling visits of June and September 1993, but with some seedlings emerging at other times. In the first experiment, the count from September 1991 (four months after setting up) was considerably lower than in the following September (Fig. 6.5). In both experiments, there was still a considerable amount of bare soil in the dug quadrats, even after 12 months, with very little vegetative recovery. Most of the cover was from litter and the majority of this was in the depressions (after 10 months in the

first field experiment: Fig. 6.6). In contrast, the vegetative recovery in the burnt/undug quadrats of the second field experiment was quite rapid. By April 1993, some 18 months after burning, the cover of live plants was mostly greater than 60% and the cover of bare ground was mostly less than 10%. The cover of bare ground was still mostly greater than 80% on the mounds in the dug quadrats at this final visit.

After 407 days, the percentage germination of seeds in Petri dishes after oven heating was considerably higher for temperatures of 100 and 120°C compared with the lower temperatures (treating each temperature/time combination as one replicate: Mann-Whitney  $n_1=8$ ,  $n_2=12$ ,  $P=0.0002$ ). Although the maximum amount of heating (i.e. 120°C and 30 min) produced the highest germination at 63.2%, considerable germination was observed as the result of one minute's heating at temperatures of 100 and 120°C. No clear trend in germination response with heating time was evident for temperatures of 80°C or less (Fig. 6.7b). Ten per cent of the unheated seeds germinated, but more than six months passed before the first of these sprouted.

The germination of seeds took place over a protracted period—radicles were still emerging even after 400 days—but the peak rate of germination took place at around 200 days (Fig. 6.8). The profile of the germination response was quite different at 207 days in comparison with 426 days, with the biggest change occurring at 100 and 120°C at shorter times of heating. More seedlings germinated at all temperature/time combinations, however, between 207 and 426 days (cf. Figs 6.7a,b).

Only two out of the 480 seeds germinated after 228 days in the second series of heating trials. After the same period of time in the first series, 12 out of the 526 seeds germinated from all temperature/time combinations of 60°C or less, including the unheated seeds, a significantly higher proportion compared with the second series (Fisher's exact  $2 \times 2$ , 2-tailed  $P=0.024$ ).

#### *Lepidium hyssopifolium simulated digging experiment*

More seedlings of *Lepidium hyssopifolium* were observed on dug plots than undug controls in both the July and October 1991 counts (both tests:  $n=21$ ,  $P<0.001$ ; Fig. 6.9). A total of 180 seedlings was counted in July, with



only one of these on a control. The same counts of seedlings in October were 181 and three, with an overall density of  $33.9 \text{ m}^{-2}$  on the dug quadrats. There had been a considerable amount of turnover of seedlings between the two visits (i.e. germination and mortality), but the densities were not significantly different between the July and October counts (treating each individual quadrat as the stratum unit in a paired comparison between the two sample times,  $n=42$ ,  $P=0.94$ ).

At the final visit in May 1992, 17.4% of the seedlings which were mapped on the dug quadrats in the previous October were still alive, spread over nine quadrats. None of the three seedlings survived on the control quadrats. The proportion of seedlings surviving on dug quadrats, at both the January and the May 1992 visits, was positively correlated with the total live plant cover of other species recorded in January 1992 (January: Spearman  $R=0.67$ ,  $n=15$ ,  $P=0.006$ ; May:  $R=0.58$ ,  $n=15$ ,  $P=0.024$ ). The total live plant cover on these 15 dug quadrats ranged from 55-95%. This was a rapid recovery from the zero cover that was created 8 months earlier and consisted entirely of exotic species, the dominants of which were *Agrostis capillaris*, *Plantago lanceolata*, *Trifolium subterraneum*, *Holcus lanatus* and *Dactylis glomerata*. The areas with lower plant cover were evidently very dry in January, with cracked, bare soil.

Of the 31 mapped seedlings that were still alive in the final visit of May 1992, 58.1% had not grown beyond the rosette stage and only three were taller than 2 cm. The tallest seedling, which was between six and 11 months old, was 7.9 cm. Although each quadrat was not intensively searched, there were only two seedlings observed which had germinated after October 1991. The dug quadrats were only discernible on very close inspection at the final visit, because the whole area was covered with a dense sward of exotic grasses and forbs up to 0.5 m tall. Even the advanced seedlings of *L. hyssopifolium* were very small in comparison.

#### *Lepidium pseudotasmanicum* simulated digging experiment

In the first experiment, no seedlings of *Lepidium pseudotasmanicum* were observed in the visits in October 1990 or January 1991. The distribution of



seedlings along one transect was limited to the four pairs of quadrats closest to the path in March and April 1991, and the five closest in February 1992, with a rapid decline in numbers away from the path (only data from the final visit are presented, Fig. 6.10). The nearest adult plant of *L. pseudotasmanicum* to this transect (at the start of the experiment) was actually overhanging the first pair of quadrats at the path end. The other transect, which had at least 2.5 m separating the nearest adult plant from the first pair of quadrats, had two seedlings only in March and April 1991, both on the first dug quadrat. This transect had no seedlings in February 1992. Although numbers seemed higher in the dug quadrats overall, insufficient pairs of quadrats had seedlings at any one time to make a statistical comparison (Fig. 6.10).

In the second experiment, the abundance of seedlings peaked in October 1991 when the overall density was 106.4 seedlings  $\text{m}^{-2}$ . By the final visit in January 1992, this figure had declined to 51.7  $\text{m}^{-2}$  (Table 6.2). At every sample visit, one particular dug/watered quadrat had more seedlings than all the other 39 quadrats put together. The location of the experiment was particularly conspicuous, being on the edge of a frequently used path. Eleven of the 20 digging quadrats had been 'disturbed' by people when the site was visited in June 1991. The disturbance consisted of pushing the soil that had been formed into a mound back over the whole quadrat. When the site was visited in August, six more digging quadrats had also been tampered with in the same way. These disturbances almost certainly killed seedlings.

There was significant variation overall between treatment combinations for the counts of seedlings in June and July 1991 and January 1992, but not in August and October 1991 (Table 6.2). There were significantly more seedlings on the dug/watered plots than in the dug/unwatered and undug/unwatered quadrats in June, but there were no more than five pairs of quadrats with seedlings in the other pairwise comparisons, which were therefore not testable. By July, sufficient quadrats had seedlings to make all but one pairwise comparison possible. Both the watered and unwatered digging treatments had significantly more seedlings than the undug/unwatered combination, but the undug/watered treatment was not significantly different from either of the digging treatments. The undug/watered versus undug/unwatered comparison was not testable (Fig. 6.11).

In the final visit in January, the density of seedlings on the dug/watered treatments was significantly higher compared with either undug combination, but not the dug/unwatered one (Fig. 6.11). No other pairwise comparisons were testable. Ignoring the watering treatments, the density of seedlings on dug quadrats was much higher than in the undug quadrats at the final visit (Mann-Whitney  $n_1=20$ ,  $n_2=20$ ,  $P=0.008$ ). At this time, some seedlings on a number of digging quadrats had not only flowered and set seed, but were dispersing seed as well. These flowering plants were up to 40 cm tall, although many non-flowering plants had not moved beyond the rosette stage. Only two seedlings remained on undisturbed quadrats from this second experiment and neither had flowered or grown to more than 0.5 cm. A number of plants of *L. pseudotasmanicum* on both undug and dug quadrats in the first experiment had also flowered and were well established.

#### *Stackhousia gunnii* and *Vittadinia muelleri* simulated digging experiment

I believe that no seedlings of *Stackhousia gunnii* were observed in June 1992, or at any of the several other brief visits made to examine this experiment. Although I do not know exactly what a seedling of this species looks like, seedlings of the closely related *S. monogyna* are distinctive and easily identifiable even at the cotyledonary stage. No seedlings that even vaguely resembled *S. monogyna* were observed at any time. In June 1992, there was nearly an order of magnitude more seedlings of *Vittadinia muelleri* on the dug plots compared with the controls, with totals of 173 and 22 seedlings respectively, summed over the 15 quadrats ( $P=0.009$ ; Fig. 6.12). The dug quadrats were still quite bare in June 1992, after 11 months, and had been disturbed by frost heaving of soil.

The counting of adult *S. gunnii* was complicated by the need to define an individual genet. The adults die back almost completely to rootstock each summer and resprout in the autumn and winter. Distinct clumps of shoots usually indicate a single individual, but sometimes the clumps are more diffuse. Stems of *S. gunnii* which were greater than 2 cm apart were arbitrarily considered to be separate individuals. On this basis, the counts of adult

plants did not change between the two sample dates on control quadrats, but declined significantly on the dug quadrats (Fig. 6.13).

*Odixia achlaena* pot germination experiment

The two-way analysis of variance indicated that whether or not the seed was heated made no difference to germination success. The length of time that the soil was heated (independent of the seeds) did have a significant effect on germination success (Table 6.3). Assuming that all the seeds that germinated were amongst the 30 added per pot, a back-transformed mean of 15.7% germinated on the pots heated for 2 h, compared with 6.4% on the pots heated for 0.5 h.

In the one-way ANOVA, all heated treatments produced more germinants than the unheated control. All three treatments that were heated for 2 h had more germinants than the two treatments that were heated for 0.5 h. There was no difference between the three treatments that were heated for 2 h (i.e. 100°C + seed heating; 80°C ± seed heating) (Table 6.3; Fig. 6.14).

**Table 6.1** The survival of seedlings of *Lasiopetalum micranthum* on the 29 dug (and unburnt) quadrats of the two simulated animal digging experiments at the Old Coach Road.

Digging strip	Total no. seedlings	Survival %	Survived partial $\chi^2$	Died partial $\chi^2$
0-10 cm (depression)	25	44.0	0.52	0.62
10-20 cm (mound)	30	56.7	0.02	0.03
20-30 cm (mound, highest area)	35	74.3	2.48	2.98
30-40 cm (mound)	29	37.9	1.48	1.78

**Table 6.2** Results of Friedman two-way analysis of variance by ranks for seedling counts of *Lepidium pseudotasmanicum* in the digging/watering experiment at Rosny Point.

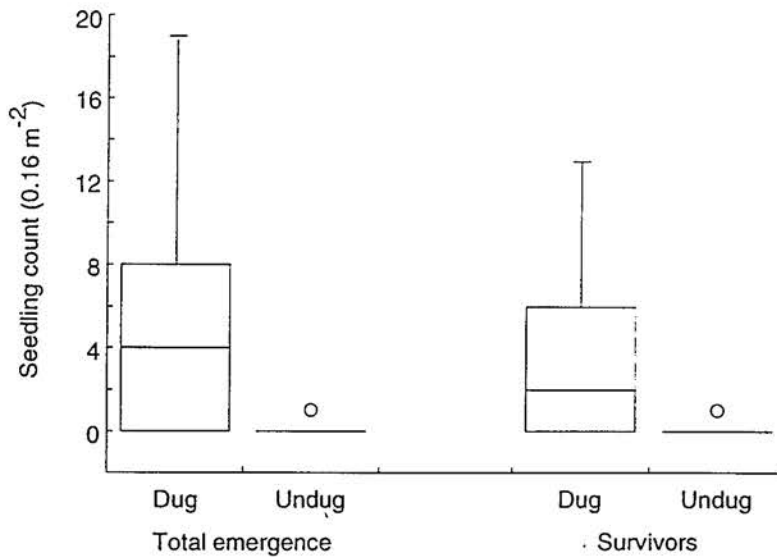
Sample time	No. blocks <sup>1</sup>	$\chi^2_r$	Prob.	Overall seedling density (m <sup>-2</sup> )
June 1991	6	8.55	0.036	53.6
July	9	9.33	0.025	90.3
August	8	3.83	0.28	84.2
October	9	4.57	0.21	106.4
January 1992	6	10.55	0.014	51.7

<sup>1</sup> Excludes blocks with no seedlings.

d.f. = 3 for all tests.

**Table 6.3** Results of analysis of variance on the germination of *Odixia achlaena* in a pot experiment.

Source of variation	d.f.	M.S.	F	P
Two-factor model (4 treatment combinations):				
Model	3	0.76	4.05	0.026
Error	16	0.19		
Heating of seed (+/-)	1	0.00	0.02	0.887
Time (0.5/2 h)	1	2.27	12.09	0.003
Heating x Time	1	0.01	0.05	0.826
One-way model (6 treatment combinations):				
Model	5	2.03	11.00	0.0001
Error	24	0.18		

**Fig. 6.2** The total seedling emergence of *Lasiopetalum micranthum* (over 23 months) and the count of survivors in April 1993, in the first simulated animal digging experiment at the Old Coach Road. The treatments are significantly different for both measures ( $P < 0.01$ ).

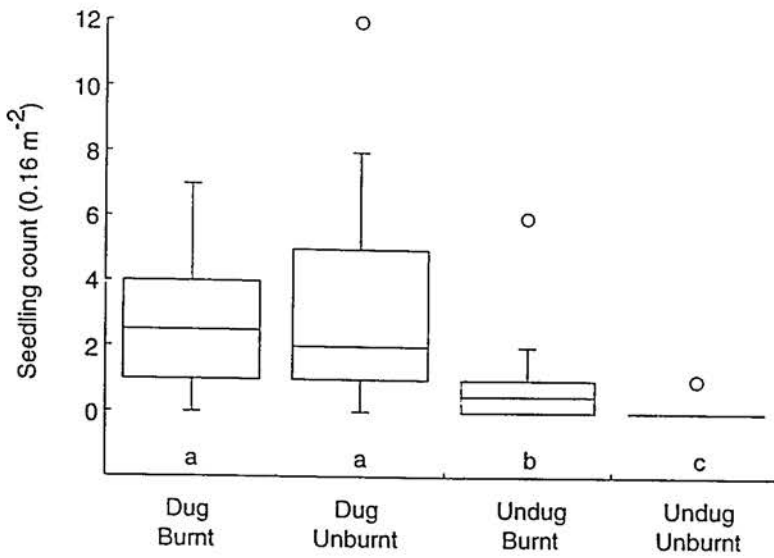


Fig. 6.3 The total seedling emergence of *Lasiopetalum micranthum* until 1 September 1992, in the second simulated animal digging experiment at the Old Coach Road. Treatments with the same letter are not significantly different ( $P < 0.05$ ).

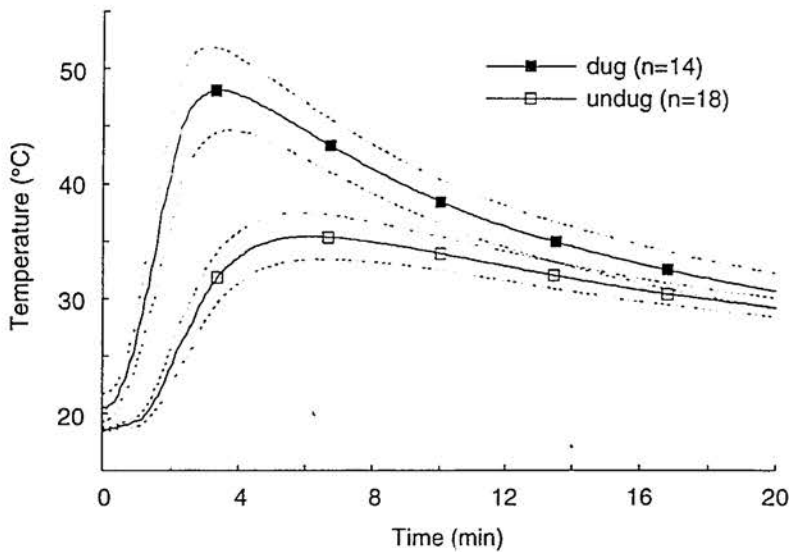
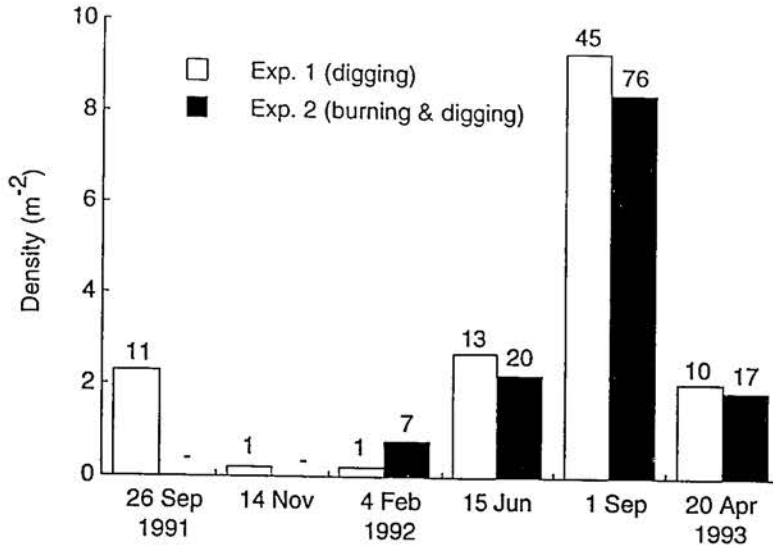
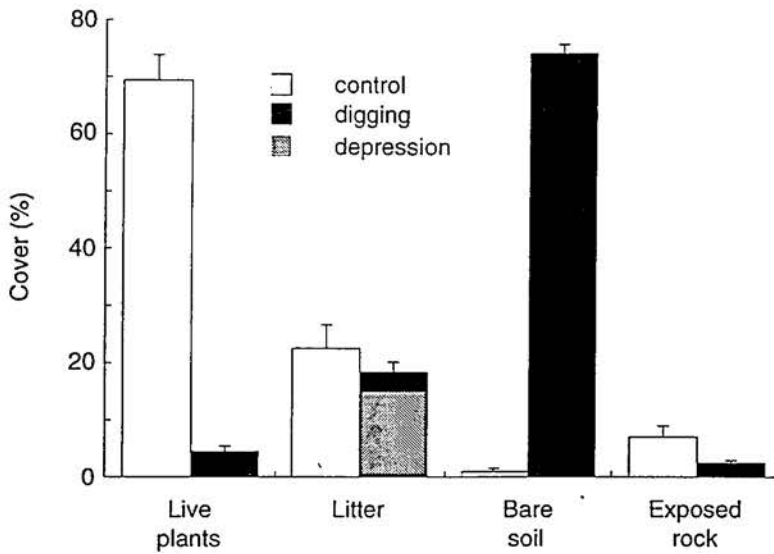


Fig. 6.4 Mean soil temperatures at 1 cm depth in the quadrats heated with a blowtorch for 2 min at the Old Coach Road (broken lines indicate s.e.m.).

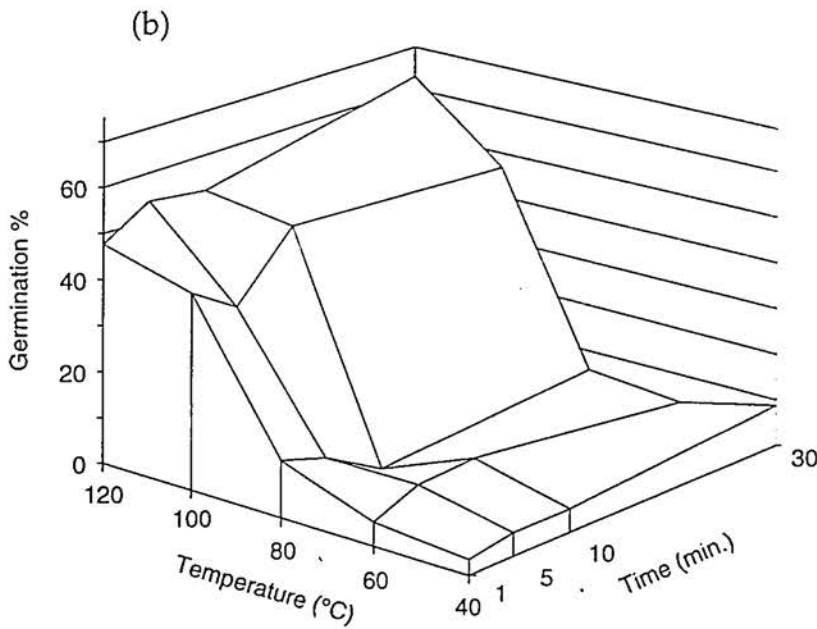
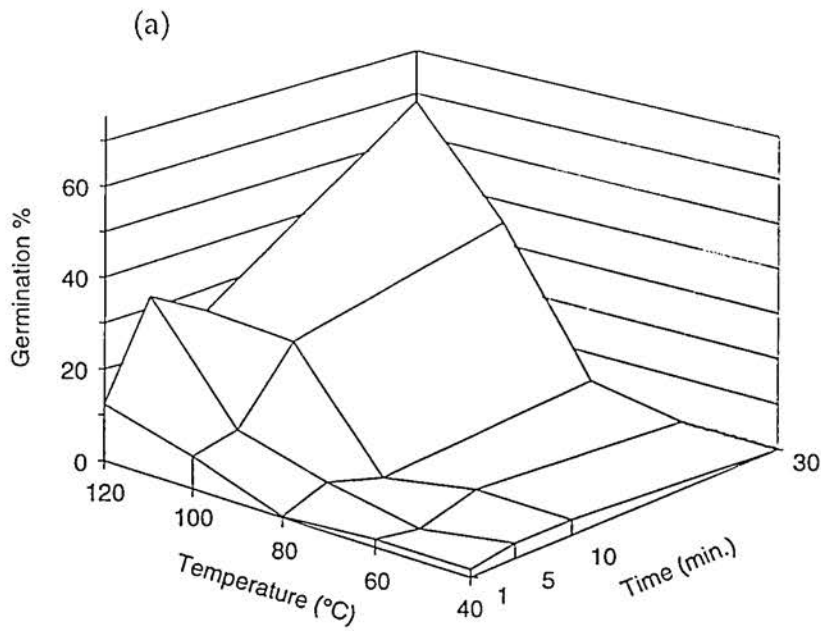


**Fig. 6.5** The total number of new germinants of *Lasiopetalum micranthum* recorded at successive visits in the Old Coach Road experiments, expressed as densities. Numbers above columns indicate actual counts of new seedlings (the April 1993 total for Exp. 2 excludes the undug/unburnt quadrats).



**Fig. 6.6** Mean cover ( $\pm$  s.e.m.) after 10 months in the 15 paired quadrats of the first simulated digging experiment at the Old Coach Road (the mean for litter cover on diggings indicates the proportion on mounds and depressions). Live plants include all understorey species.





**Figs 6.7** The percentage germination of seeds of *Lasiopetalum micranthum* in oven heating trials which varied both temperature and heating time. (a) after 207 days, (b) after 426 days.

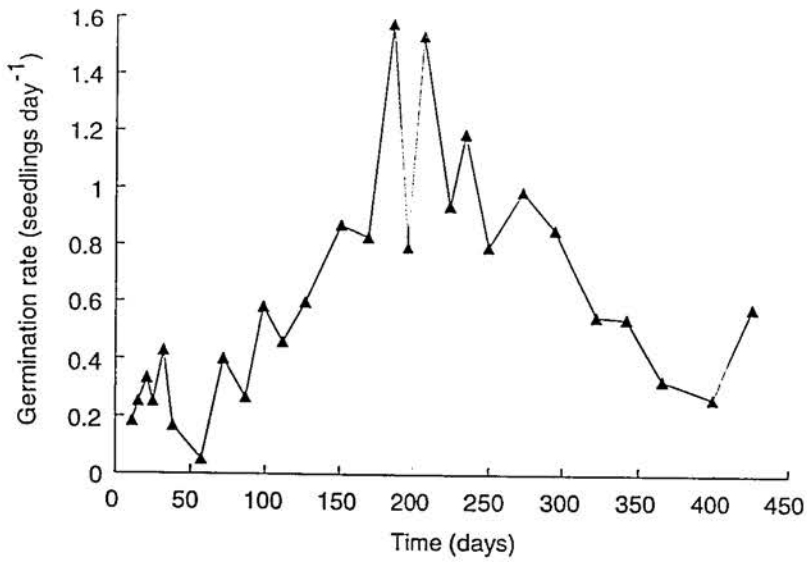


Fig. 6.8 The germination rate of seeds of *Lasiopetalum micranthum* in relation to time in Petri dishes in a dark incubator.

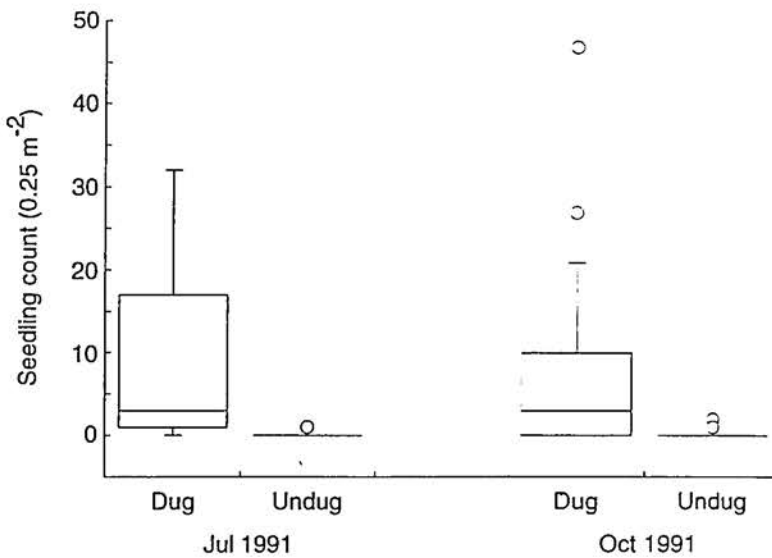


Fig. 6.9 Counts of seedlings of *Lepidium hyssopifolium* in the experiment at Bagdad. The treatments are significantly different at both times ( $P < 0.001$ ).

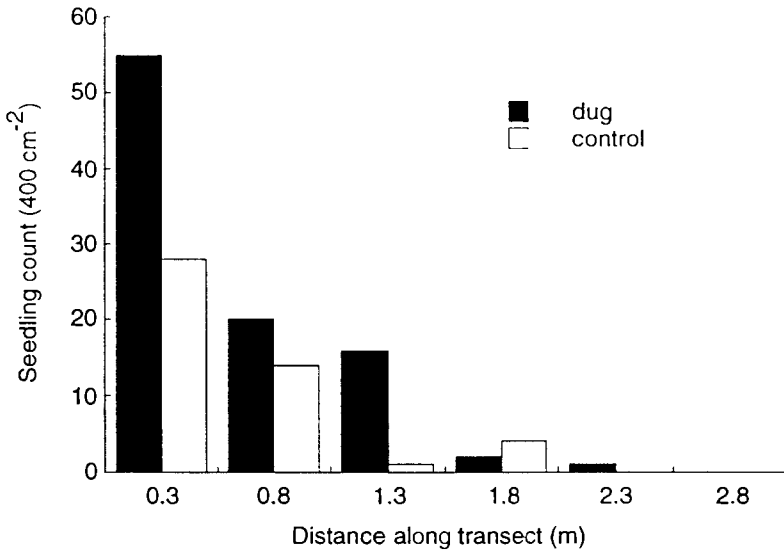


Fig. 6.10 The distribution of seedlings of *Lepidium pseudotasmanicum* along one of the transects from the first experiment at Rosny Point, at the final visit in February 1992. The distance along the transect also indicates the distance from the base of the nearest adult plant.

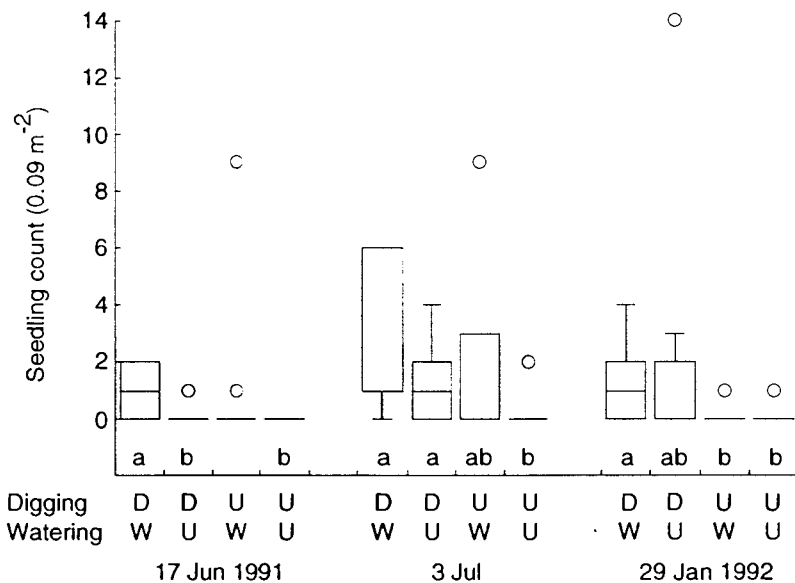


Fig. 6.11 Counts of seedlings of *Lepidium pseudotasmanicum* in the second experiment at Rosny Point. One extreme outlier is not shown for the DW treatment at each sample time. Within each time, treatments with the same letter are not significantly different ( $P < 0.05$ ), however, not all comparisons were testable (see text). D=dug; W=watered; U=undug or unwatered.

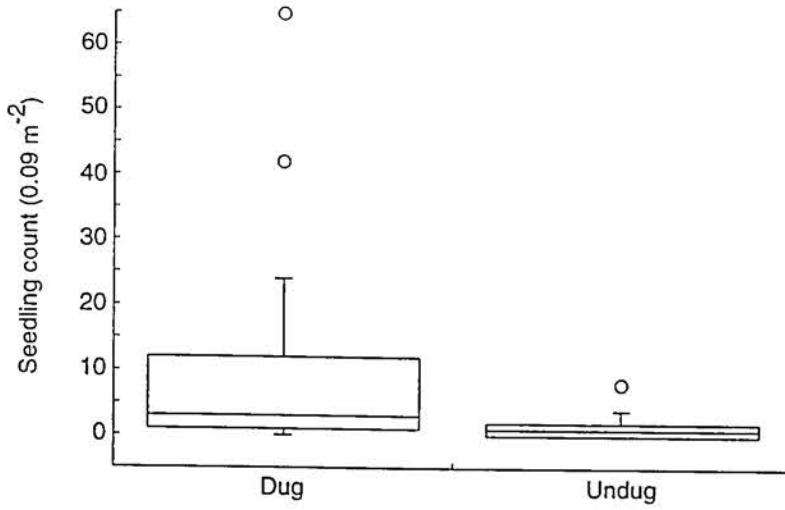


Fig. 6.12 Counts of seedlings of *Vittadinia muelleri* in the simulated animal digging experiment at the Tunbridge Tiers Road, in June 1992. The treatments are significantly different ( $P < 0.01$ ).

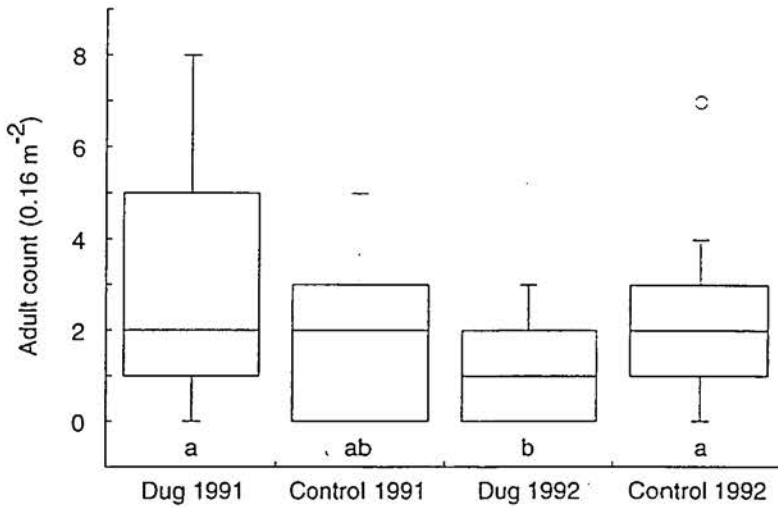


Fig. 6.13 The count of adult plants of *Stackhousia gunnii* in the experiment at the Tunbridge Tiers Road, in July 1991 and June 1992. Treatments and times with the same letter are not significantly different ( $P < 0.05$ ).

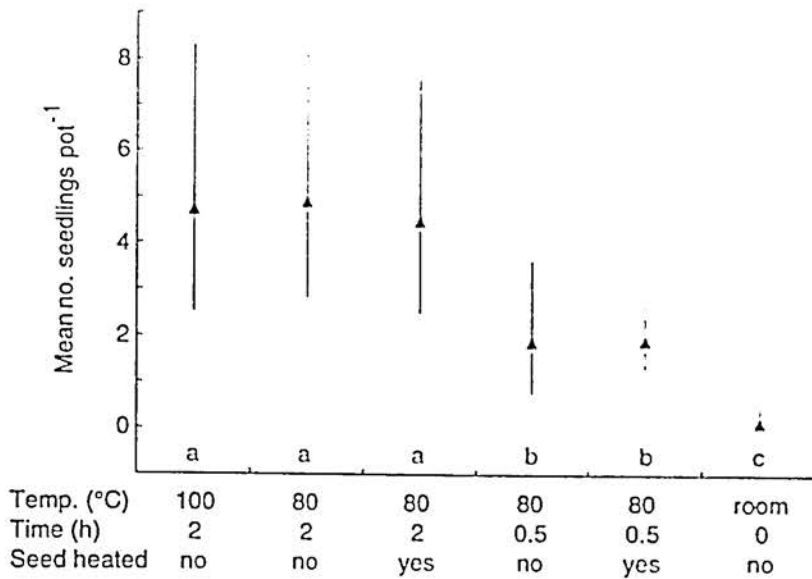


Fig. 6.14 The mean number of seedlings of *Odixia achlana* per pot in the glasshouse experiment (and 95% confidence limits, all back-transformed). Treatments with the same letter are not significantly different ( $P < 0.05$ ).

## Discussion

### *Lasiopetalum micranthum*

A pre-treatment at 100-120°C induced the highest level of germination of *Lasiopetalum micranthum* in oven heating trials, although some germination of unheated seeds did occur after a protracted period. These results indicate that this species is adapted to regenerate with the stimulus of fire. Interestingly, the highest levels of germination in the burning/digging experiment were induced by digging rather than burning. It could be argued that the soil temperatures generated by the blowtorch were well below those associated with a real wildfire. This may well be true of a hot fire in extreme weather conditions, but is probably not true of a relatively mild wildfire. A fire which burnt at least part of the Old Coach Road site in the late 1980s induced prolific seedling regeneration around a fallen tree, which would have burnt

for many hours and heated the soil to much higher temperatures than in most areas. There was little evidence of more widespread recruitment of the same density arising from this fire, although it is not clear how much of the area was burnt.

The literature provides an indication of soil temperatures during low intensity wildfires—such a fire would be expected at the Old Coach Road site because of the very low fuel loading (estimated at no more than 3 t ha<sup>-1</sup>). In Australia, temperatures of 50-75°C at 1 cm depth have been reported from fuel reduction burns (Humphreys & Craig, 1981) and up to 67°C at 2.5 cm depth (Beadle, 1940). In a low-intensity prescribed burn in *Eucalyptus pauciflora* forest, a mean temperature of 54°C was reported for 2 cm depth, with a maximum of 94°C (Raison *et al.*, 1986). In non-Australian grasslands, there was virtually no increase in soil temperature at 2 cm depth in one study (Sumrall *et al.*, 1991), while a temperature of 82°C at 2.5 cm was reported in another (West, 1965). Scotter (1970) demonstrated from theory and experiments that soil temperatures at 1 cm depth would reach a maximum of 37-47°C during a grassland fire with low fuel loading, with the range reflecting the influence of soil dryness. It is evident from these figures that soil temperatures reached during wildfires will vary considerably depending on the fuel loading, soil dryness and climate conditions. Because of the very low fuel loading, a wildfire at the Old Coach Road would most likely have soil temperatures akin to the lower values quoted here, except under the most extreme climatic conditions.

The soil temperatures produced by the direct solar heating of bare ground are considerably higher than under the grassy sward and were as high as 61°C at 0.5 mm depth at Bellerive on a hot day (see Chapter 3). Such temperatures may be responsible for inducing germination, although they are well below the optimum temperature found in the oven trials. The second series of oven trials, with long periods of seed heating at 50 and 60°C, produced virtually no germination after nearly 8 months. Given that shorter times or lower temperatures in the first series induced significantly more germination after the same period of time in the incubator, the second series may have suffered from some unknown experimental problem. It seems unlikely that

these oven heating conditions could have been lethal to seeds, because the same conditions appear not to be deleterious in the field.

The blowtorch burning is also unlikely to have been so hot as to kill seeds in the soil (except perhaps for seeds very close to or at the soil surface), because the burnt/dug and unburnt/dug treatments produced similar levels of germination. If solar heating alone is responsible for the germination on the dug quadrats, then the burnt/undug treatment should have had similar levels of germination to the dug treatments, because completely bare soil was created by the burning. It seems that the actual mechanical movement of the soil was also important, although it is not clear why. Perhaps the digging brought soil-stored seed to the surface and more readily available for germination. The loosening of this clay-rich soil, which is hard and compact, may have facilitated germination either by improving soil moisture conditions or making the soil more easily penetrated by shoots.

The quadrats of the dug/burnt treatment were dug before burning, resulting in higher soil temperatures during burning compared with the undug/burnt treatment (Fig. 6.4). This difference is presumably due to the higher thermal conductivity of the soil in the dug quadrats, as a result of the soil being drier. Had the dug/burnt quadrats been burnt before digging, then both dug/burnt and undug/burnt would have received the same amount of soil heating during burning. However, soil temperatures reached during either burning treatment did not appear to influence germination, relative to the effect of digging.

The creation of bare soil by mechanical disturbance is sufficient to stimulate germination and facilitate at least short-term survival of seedlings of *Lasiopetalum micranthum*. This much at least is established here. Given that this species is hard-seeded and germinates after heating, it seems likely that solar heating of soil is an important factor, although the laboratory experiment designed to test this hypothesis was inconclusive. It would be interesting to know how many hard-seeded species, particularly in the Fabaceae, are also likely to germinate in response to the soil temperatures associated simply with the creation of bare ground. Wildfires that are cool and cause little increase in soil temperatures during the burn (e.g. Raison *et al.*, 1986), may



nonetheless aid hard-seeded species by removing litter and understorey biomass. This is a hypothesis that may be worthy of further research.

The extremely slow rate of germination of *L. micranthum* in Petri dishes and the delay of the bulk of germination in the field experiments until 16 months (experiment 1, digging only) and 12 months (experiment 2, digging & burning) after setting up of the experiments, both suggest that the process of imbibition is very slow. In both field experiments and in other observations (see Fig. 5.21), there was little germination in early or mid-winter, even though soil moisture conditions should have been favourable. The poor germination in September 1991 in the first field experiment is consistent with the solar heating hypothesis, because the diggings had not yet been exposed to long, hot sunny days, with winter having just finished. Germination in the following September was considerably better, even though the best germination had been observed in September 1991 in other work (Fig. 5.21).

The depressions of the dug quadrats had the same density of seedlings as the mounds, even though by February 1992 litter accumulation had prevented high soil temperatures in the depressions. If the solar heating hypothesis is correct, then presumably sufficient solar heating of the depressions had occurred in the earlier summer months when there was less litter. This finding also suggests that at 5 cm soil depth, which was the depth of the depressions, there is a considerable store of seed. The better survivorship of seedlings at the highest points of the mounds may be related to the greater depth of loosened soil and possibly more favourable moisture conditions in this type of soil (cf. Chapter 3 for sandy soil). Interestingly, the seedlings in the depression did not have better survival rates, even though moisture presumably would accumulate there. The accumulated litter may have covered many seedlings and affected them by cutting out light and/or causing damping off.

### *Lepidium hyssopifolium*

Simple mechanical disturbance of the soil and removal of above ground biomass was sufficient to stimulate abundant germination of this species, and indicates that *Lepidium hyssopifolium* has a persistent seed bank in the

soil. The latter must be concluded because only two dug quadrats were within dispersal distance of extant adult plants and the plants which formerly grew where the experiment was set up had been gone since 1985. A maximum dispersal distance of 2.5 m can be deduced for seeds of *L. hyssopifolium* from the first experiment at the *L. pseudotasmanicum* study site. The seeds of the two species are very similar in size, weight and morphology and the plants have similar maximum heights (although the *L. hyssopifolium* plants at Bagdad were quite short). The seed bank of *L. hyssopifolium* is examined further in the next chapter.

Although some seedlings of *L. hyssopifolium* had survived on the dug plots until the conclusion of the field study, the long-term prospects for these remaining seedlings is probably not good. At least in the short-term, seedlings survived better where the overall productivity was higher and this was presumably related to soil moisture. But in the longer term, the remaining seedlings are very small and have to cope with the intense competition imposed by the dense and considerably taller sward of exotic grasses and forbs. They are unlikely to reach reproductive maturity. However, this site is atypical for *L. hyssopifolium* because it lacks tree cover which would normally suppress the grassy sward.

### *Lepidium pseudotasmanicum*

The experiments demonstrated that diggings which are within the dispersal range of a seed source, which is maximally 2.5 m from adult *Lepidium pseudotasmanicum*, can enhance the establishment of seedlings. The results of the first experiment also imply that no seed was stored in the soil at a greater distances than this. Plants were capable of establishing in the absence of digging, however, and therefore digging is probably not essential for the regeneration of *L. pseudotasmanicum* at this site. Therefore why is this species restricted to the margins of the new path? It is not known how large this population of *L. pseudotasmanicum* was before the creation of the path, or even if it existed at all. Rosny Point is typical habitat for *L. pseudotasmanicum*—it grows in a number of places along the Derwent River under *Allocasuarina*

*verticillata*—and bandicoot digging is still common amongst some of these populations (e.g. East Risdon).

The results of the second experiment suggest that digging facilitated germination at least in part by improving soil moisture conditions. The best evidence for this comes from the July count, when digging and watering treatments on their own were not significantly different from each other. However, the results are not conclusive because some treatment comparisons were not testable and some type II errors may have occurred in others. It is quite possible that the overall counts of seedlings on diggings were reduced by the tampering, thereby blurring differences with undug treatments.

Watering was only applied at the beginning of the experiment and by the end, the effect of this treatment had disappeared. This is not surprising, because germinants on all treatments had the benefit of substantial rainfall later in 1991, particularly in August (see Fig. 5.7: the Bellerive rainfall data is equally appropriate for Rosny Point, the station being less than 1 km away). The above average rainfall of November and December 1991 may have been responsible for the excellent success of the plants which had grown to reproductive maturity by January 1992.

#### *Stackhousia gunnii* and *Vittadinia muelleri*

The lack of germination of *Stackhousia gunnii* may be related to the extremely poor seed set that has been observed for this species in the Tunbridge area. There has also been no success at germinating this species in the glasshouse (Louise Gilfedder, pers. comm.). These issues are currently being investigated in another project funded by the Australian Nature Conservation Agency. Given the observations on germination of *S. monogyna* at Bellerive, it might have been predicted that germination of *S. gunnii* would not respond positively to simulated animal diggings. The counts of adult resprouts suggest that *S. gunnii* may have poor vegetative recovery after this amount and kind of disturbance. On the other hand, the vegetative recovery may simply be slower, because it is dependent on a disrupted root system.

*Vittadinia muelleri* germinated in greater abundance on the bare soil of the disturbances compared with the undisturbed herbaceous sward of the

control quadrats. Willis & Groves (1991) found in laboratory trials that a higher percentage of seeds of *V. muelleri* germinated in light compared with dark. Therefore, mechanical disturbance of the soil surface and the consequent removal of litter and living biomass probably enhance germination by exposing seeds to light.

### *Odixia achlaena*

The experiment established that heating of the soil alone provides the stimulus for the germination of *Odixia achlaena* and that the direct heating of seeds is not necessary. Virtually no germination was observed in the absence of soil heating, regardless of whether or not the seeds were heated.

It is beyond the scope of this work to determine the cause(s) of this result. Hypotheses have been proposed and tested for similar germination responses in Californian chaparral vegetation following fire (i.e. the breaking of dormancy of species which do not have hard seeds). These include: the removal of microbial inhibitors to germination from the soil (see Keeley & Pizzorno, 1986); the removal of chemical inhibitors to germination from the soil (see Gill & Groves, 1981; Keeley *et al.*, 1985); and the production of molecules by the heating of hemicellulose (from charring, but not ashing wood) which stimulates germination (Keeley & Pizzorno, 1986; Keeley, 1987). The latter is believed to be more widespread than the former two mechanisms in chaparral in California (Keeley & Pizzorno, 1986). The experiment on *O. achlaena* seems to preclude a charate stimulus because no wood was present in the pots. Chemical and microbial changes to soil following fire have been well documented in Australia (Humphreys & Craig, 1981; Warcup, 1981).

The experiment was intended to and did demonstrate that *O. achlaena* is unlikely to germinate simply as a result of mechanical soil disturbance. Although the experiment did not test whether soil temperatures induced by solar heating (i.e. 60-70°C for several hours) will also cause appropriate chemical or microbiological changes to the soil, field observations on the lack of germination in the absence of fire suggest that they do not (Chapter 5).

Although the heating treatments successfully germinated seeds, the germination rate was still quite low. There could be a number of reasons for

this result. Firstly, seeds could easily have been washed down the sides of pots by watering, thus removing them from the pool of potential germinants. Other factors which were not provided by the experiment may be necessary for the germination of this species. For example, the seed may require a period of some kind of environmental conditioning in the soil. The complexity of mechanisms which stimulate germination, identified by Keeley (1987) for a range of species from fire-prone vegetation, indicates the range of potential causes.

### Conclusions

The germination and/or establishment of a species was found to be enhanced by simulated animal digging in every field experiment. The cause of the response was probably related to the exposure of soil to more intense solar heating in the case of *Lasiopetalum micranthum*. Other species may benefit from the exposure of seeds to light (e.g. *Lepidium hyssopifolium* and *Vittadinia muelleri*) and/or the improved moisture conditions provided by the disturbed microsite.

In some ways, fire and mechanical soil disturbance provide similar changes to the surface soil environment. Both create bare mineral soil and expose the soil to direct solar heating. Therefore, species whose germination requirements are satisfied by light (e.g. *V. muelleri*) should benefit from both equally. The combined effect of low intensity burning and soil disturbance was not cumulative for *L. micranthum*; in fact, the effect of digging appeared to override the effect of burning. Species which are dependent on higher soil temperatures than those induced by solar heating to break seed dormancy (e.g. *Odixia achlaena*), will benefit from moderate to high intensity fires (or hot spots in low intensity fires), but not from mechanical soil disturbance.

## Chapter 7

### Seed Stored in the Soil at Various Depths in the Habitats of Rare and Endangered Species

#### Introduction

The process of digging by small mammals brings soil to the surface by effectively inverting the soil profile (see Chapter 3). Seed buried at depth is unlikely to germinate, but the inversion through digging may place this seed in a situation in which germination is more likely. In this chapter, the store of seed in the soil at various depths is investigated at five study sites. The aim is to examine which species have a pool of viable seeds buried in the soil and to assess the importance of this seed bank in relation to animal digging.

#### Methods

The quantity of viable seeds in the soil was determined using the seedling emergence method (Roberts, 1981; Gross, 1990). Soil cores were randomly taken from within designated areas, which were usually 10 x 10 m and located over a relatively dense population of the target rare or threatened species. With the exception of Hospital Creek, all sample areas were within 60 m of the permanent quadrats located over diggings (Chapter 5). At Hospital Creek, the soil samples were taken from an area which was not burnt in September 1990, some 400 m from the permanent quadrats. Three smaller areas were sampled at Annandale because of the patchy distribution of *Lepidium hyssopifolium*; these 5 x 5 m areas were approximately 50 m apart. Two areas were sampled at Bellerive—although these areas were only 30 m apart, they had very different vegetation, probably as a result of burning history. One area had a very open and low grassy sward with abundant *Velleia paradoxa*, and appeared to be frequently burnt; the other had a dense cover of *Lomandra longifolia* and *Acacia dealbata*, and no *V. paradoxa*, and appeared to have been less frequently burnt.

The cores were collected after scraping away surface litter and humus, using a metal tubular corer which was 29 cm long and 4.6 cm in diameter.



The intact soil cores were carefully removed from the corer with a plunger and divided into sections of the original profile, and bulked for each section. Table 7.1 gives a complete summary of the study sites, target species, sample dates, areas sampled, number of cores and division of cores into soil profile levels. The large number of cores (usually 100) was considered preferable to collecting a smaller number of larger samples, because of the spatial variability of seed density in the soil (Thompson, 1986; Benoit *et al.*, 1989). For each site, the cores were all taken to the same soil depth. This depth was the maximum that could generally be penetrated with relative ease and without constantly hitting rocks. The soil samples were stored in a refrigerator at 3.6-5.5°C until further processing.

The method of extracting the soil cores from the corer was a potential source of error in the estimates of germinable seed densities at various depths. The cores were removed from the corer by pushing from the bottom, so any contamination of different levels would go from the top of the profile into the deeper part. Therefore the contamination (if it occurred) would tend to increase the apparent density of seed in the deeper portion. There is good evidence to indicate that contamination of deeper levels did not occur to any great extent. For example, there was a very high density of *Cerastium glomeratum* seed in the top 5 cm of Annandale soil, in comparison with other data presented here, and yet very little seed germinated from the deeper soil layer. There are similar although less extreme examples from all sites (see Results).

At each study site except Annandale, a list was made of all vascular plant species in the sampled areas, and the projected foliage cover of each was estimated on the following scale: +=<1%; 1=<1-5%; 2=5-25%; 3=25-50%; 4=50-75%; 5=75-100%.

In the laboratory, the bulked soil samples were sieved through a 4 x 4 mm sieve to remove rocks and larger organic material (including tubers) and thoroughly mixed. The soil was then spread out in 34 x 28 cm trays on top of sand which had been sterilized at 120°C for 24 hours. The sieved soil was 1 cm thick in each tray on top of 2 cm of sand. Finally, a thin layer (2 mm) of sterilized sand was sprinkled evenly over the soil.



Trays were randomly arranged in a glasshouse and regularly watered. Several control trays of sterilized sand were randomly interspersed among the experimental trays, to help identify the species which came from seed originating in the glasshouse. Three taxa consistently contaminated trays: *Epilobium billardierianum*, *E. ciliatum* and perennial *Juncus* spp., all of which grow prolifically around the glasshouse. Perennial *Juncus* spp. are excluded from all results presented here and the other two species do not occur at any of the study sites.

At 2-3 week intervals, the germinants which could be identified were noted and removed from the trays and all remaining unidentified seedlings were counted. Very few seedlings died while very small and most were identified at least to genus level. The extremes of daily maximum and minimum temperatures in the glasshouse were 43°C and 7°C respectively in summer and 23°C and 10°C in winter, when the glasshouse was heated. In the autumn, no heating was applied and night temperatures dropped to 1°C.

To germinate hard-seeded species, trays were subjected to heating with a blowtorch. During burning, the trays were covered with a copper shield, which was lagged on the sides with asbestos to insulate the plastic trays from the heat. The Companion No. 74 blowtorch, which runs on liquid petroleum gas, produces a broad blue flame some 40 cm long. The flame was played over the trays for 4 min and the copper shield was left on top for a further 5 min. Trials with thermocouples were used to determine the temperatures reached in the soil. The 4 min heating regime was chosen because it raised the temperature of the soil to approximately 80°C at 1 cm depth (i.e. the bottom of the soil layer). This temperature was selected because in a recent study, it was found to be the overall optimum for germinating Fabaceae species (Auld & O'Connell, 1991).

The trays from Bellerive were all placed in the glasshouse, without blowtorch treatment, until all germination had ceased. After this time, which was 8 months for the majority of trays, but longer for some, all the trays then received the blowtorch treatment and germination was again observed until it had ceased. For the samples from East Risdon, Hospital Creek and the Old Coach Road, only half of the trays for each soil depth were heated initially

and all were placed in the glasshouse at the same time (for each sample site). The unheated trays from East Risdon were subsequently heated after all germination had ceased, as described for Bellerive, but with 3 min of blowtorch heating. No trays from Annandale received heat treatment.

Trays were only discarded after all germination had apparently ceased, which was after a maximum of 14 months for Bellerive samples, 15 months for the secondarily heated East Risdon samples and 6-11 months for all others. Seed bank data are usually presented as a density of viable seeds per m<sup>2</sup> (e.g. Harper, 1977; Roberts, 1981). To make the data comparable between study sites and soil depths, the results here are presented as densities of germinated seeds per unit volume of soil, based on the total soil volume extracted (i.e. volume of core section x no. cores). The unit volume used is cm<sup>3</sup> x 10<sup>4</sup>, which is equivalent to a ground area of 1 m<sup>2</sup>, to a depth of 1 cm. Therefore, the formula used for the density of germinated seed ( $D_s$ ) is as follows:

$$D_s = C \times 10^4 / \pi r^2 L n F$$

where      C=number of germinated seeds  
               r=radius of the core (2.3 cm)  
               L=length of core section (2-5 cm)  
               n=no. cores (mostly 100)  
               F=fraction of total sieved soil volume used (44-100%)

Selected comparisons were made between the densities of germinated seeds in different core sections using the one-sample  $\chi^2$  test.

Table 7.1 Details of the field sampling for seed banks.

Study site	Target species	Sample Date	Sample area (m)	No. cores	Core depth divisions (cm)
Annandale	<i>Lepidium hyssopifolium</i>	18/3/91	5 x 5 (x 3)	30+30+24 <sup>1</sup>	0-5, 5-10
Bellerive	<i>Velleia paradoxa</i>	8-9/11/90	10 x 10 (x2)	100 (x2) <sup>2</sup>	0-5, 5-10, 10-15
East Risdon	<i>Olearia hookeri</i>	18/4/91	10 x 10	100	0-5, 5-10
Hospital Creek	<i>Odixia achlaena</i>	30/10/91	10 x 10	100	0-2, 2-6, 6-10
Old Coach Road	<i>Lasiopetalum micranthum</i>	20/3/91	10 x 10	100	0-3, 3-6

<sup>1</sup> samples from different areas bulked.<sup>2</sup> samples from different areas not bulked.

## Results

Figure 7.1 gives a profile of soil temperatures reached in trays from Bellerive and the Old Coach Road, during and immediately after heating with the blowtorch for four minutes. The mean maximum temperatures were 79°C and 84°C respectively.

### Annandale

At least 48 species germinated from the Annandale soil, but 50% of the taxa were exotic (Table 7.2). *Lepidium hyssopifolium* had a higher density of germinated seed than any other native taxa and was only exceeded in total counts by two exotic species: *Cerastium glomeratum* and *Vulpia* spp. For the 5-10 cm soil depth, *L. hyssopifolium* had the highest density out of all taxa, although the density for this species was still significantly higher in the shallow soil zone ( $\chi^2_1=3.88$ ,  $P=0.049$ ). *Wahlenbergia* spp. and *Juncus bufonius* were two other native taxa with relatively high density values in the 5-10 cm zone, but overall, most taxa had more germinated seed in the shallow zone. The exotic *Chenopodium album* was the only species with a significantly higher density of germinated seed in the deeper zone compared with the shallow zone ( $\chi^2_1=10.76$ ,  $P=0.001$ ).

*Bellerive*

A total of 39 taxa germinated from the soil from the frequently burnt area at Bellerive and 90% of those were native. At least a further 27 native species had no seed germinate from the soil, but were present in the above ground vegetation (Table 7.3). From the infrequently burnt area, these figures were 41 soil seed bank taxa, with 83% native and 27 extra native species above ground. Although there was a large number of native taxa represented in the soil seed bank, most had very low numbers of germinants. Only four taxa exceeded 20 germinants  $\text{cm}^{-3} \times 10^4$  per depth section: *Wahlenbergia stricta*, *Hypericum gramineum*, *Bossiaea cinerea* and *Poa rodwayi*. These higher values are all from the infrequently burnt area. No seed of *Velleia paradoxa* germinated from either area.

A total of 16 native taxa germinated from the 10-15 cm soil zone from the frequently burnt area and 14 from infrequently burnt area. The Fabaceae species in the infrequently burnt area, treated together as a group, had a significantly higher density of germinated seeds in the 10-15 cm soil zone compared with the 0-5 cm zone ( $\chi^2_1=4.10$ ,  $P=0.043$ ). No other taxa, out of those that were represented by more than just a few germinants, had more seed at depth than in the shallow soil layer. The taxa which germinated mainly after the blowtorch heating and in low numbers before, were the Fabaceae species and *Dodonaea viscosa*.

*East Risdon*

Eighteen taxa emerged from the East Risdon soil, but two of these may have come from tuber(oid)s (Table 7.4). All of these taxa were native and the one with the most abundant germinated seed was *Stipa* spp. Eleven taxa germinated from the 5-10 cm soil depth zone, but all but two of these were present only in very low numbers (i.e.  $\leq 10 \text{ cm}^{-3} \times 10^4$ ). *Olearia hookeri* was present in the soil seed bank, but again, densities of germinants were very low at 8 and 5  $\text{cm}^{-3} \times 10^4$  for the two soil depths. A further 14 taxa had no seeds germinate from the soil, but were recorded from the sample area.

Substantially more seeds germinated from the trays that were heated after a period in the glasshouse without heating, than in the trays that were heated from the start. *Pultenaea pedunculata* was one species which germinated exclusively in heated trays.

### *Hospital Creek*

Twenty-one taxa germinated from the Hospital Creek soil and only one of these was not native (Table 7.5). A further 36 taxa, including four exotic species, were present in the sample area but did not germinate from the soil. *Wahlenbergia* spp. had the highest density of germinated seeds overall, and *Odixia achlaena* was the second most abundant taxon. Fourteen taxa germinated from the 2-6 cm depth range, but only seven germinated from the 6-10 cm zone. In the soil from 2-10 cm, only four taxa had more than 10 germinants  $\text{cm}^{-3} \times 10^4$ : *Wahlenbergia* spp., *O. achlaena*, *Schoenus apogon* and *Opercularia varia*. Most taxa were considerably more abundant in the top 2 cm of soil. Exceptions were *Schoenus apogon* and *Opercularia varia*, but the total counts of germinants for these species were too small for statistical comparison. There were 18 germinated seeds of *O. achlaena*  $\text{cm}^{-3} \times 10^4$  in the 2-6 cm depth zone.

Germination was better in heated trays compared with unheated trays only for *Pelargonium inodorum* (0-2 cm; 2-6 cm) and *O. achlaena* (0-2 cm). Germination of both these species was actually higher in unheated trays than heated trays of soil from the 6-10 cm depth, although the total numbers of germinants was very small.

### *Old Coach Road*

Thirty-two taxa germinated from the Old Coach Road soil (Table 7.6). Only two of these were exotic and they were a negligible component of the total soil seed bank in terms of numbers. A further 20 taxa were present in the vegetation in the sample area, but apparently not as seed stored in the soil. *Lasiopetalum micranthum* only germinated in the heated trays, but was relatively well represented in the soil seed bank, with 46 germinants  $\text{cm}^{-3} \times 10^4$  in the top 3 cm of soil and 26  $\text{cm}^{-3} \times 10^4$  in the 3-6 cm zone. Twenty-three

taxa germinated from 3-6 cm depth. Most of these taxa were more abundant in the shallow 3 cm, but several still had reasonably high numbers in the deeper zone. Only *Viola hederacea* had a significantly higher density of germinated seeds in the 3-6 cm zone compared with the 0-3 cm zone ( $\chi^2_1=5.65$ ,  $P=0.017$ ). Heating was necessary to germinate four other taxa besides *L. micranthum*: *Lepidosperma* spp., *Bossiaea prostrata*, *Acacia mearnsii* and *Dichondra repens*.

Table 7.2 The density and actual count of seeds germinated from the soil from Annandale.

Species	Density (cm <sup>-3</sup> x 10 <sup>4</sup> ) <sup>1</sup>		Count <sup>1</sup>	
	0-5 cm	5-10 cm	0-5 cm	5-10 cm
* <i>Cerastium glomeratum</i>	155	10	108	7
* <i>Vulpia</i> spp.	125	36	87	25
<i>Lepidium hyssopifolium</i>	80	53	56	37
<i>Crassula sieberana</i>	92	29	64	20
* <i>Bromus</i> spp.	86	24	60	17
* <i>Hypochoeris glabra</i>	87	19	61	13
<i>Wahlenbergia</i> spp.	47	50	33	35
<i>Juncus bufonius</i>	44	42	31	29
* <i>Dactylis glomerata</i>	43	36	30	25
* <i>Chenopodium album</i>	14	44	10	31
* <i>Rumex acetosella</i>	50	6	35	4
* <i>Briza minor</i>	33	20	23	14
* <i>Trifolium subterraneum</i>	36	11	25	8
* <i>Aira caryophylla</i>	39	3	27	2
* <i>Cirsium vulgare</i>	29	11	20	8
Monocotyledonae spp.	14	14	10	10
<i>Gnaphalium collinum</i>	16	11	11	8
<i>Isolepis marginata</i>	9	16	6	11
* <i>Sonchus oleraceus</i>	16	9	11	6
* <i>Stellaria media</i>	20	3	14	2
<i>Centrolepis strigosa</i>	10	9	7	6
Dicotyledonae spp.	10	9	7	6
Poaceae spp.	6	10	4	7
<i>Oxalis perennans</i>	10	4	7	3
<i>Cotula australis</i>	13	0	9	0
<i>Einadia nutans</i>	10	0	7	0
<i>Hydrocotyle callicarpa</i>	3	3	2	2
<i>Hypericum gramineum</i>	4	1	3	1
<i>Astroloma humifusum</i>	4	0	3	0
<i>Eucalyptus amygdalina</i>	4	0	3	0
<i>Luzula meridionalis</i>	3	1	2	1
* <i>Centaureum erythraea</i>	3	0	2	0
* <i>Hordeum</i> spp.	1	1	1	1
* <i>Moenchia erecta</i>	1	1	1	1
* <i>Plantago coronopus</i>	3	0	2	0
* <i>Solanum nigrum</i>	3	0	2	0
<i>Cymbonotus lawsonianus</i>	1	0	1	0
* <i>Cynosurus echinatus</i>	0	1	0	1
<i>Danthonia</i> spp.	0	1	0	1
<i>Dichondra repens</i>	1	0	1	0
<i>Drosera</i> spp.	0	1	0	1
<i>Gonocarpus tetragynus</i>	1	0	1	0
* <i>Holcus lanatus</i>	1	0	1	0
* <i>Lolium</i> spp.	1	0	1	0
<i>Lomandra longifolia</i>	0	1	0	1
# <i>Orchidaceae</i> spp.	0	1	0	1
* <i>Parentucellia viscosa</i>	1	0	1	0
<i>Schoenus apogon</i>	0	1	0	1
* <i>Senecio vulgaris</i>	1	0	1	0
<i>Stipa</i> spp.	0	1	0	1

<sup>1</sup> Viable seed density and actual counts of seeds germinated by soil depth.

\* denotes exotic species.

# possibly not a seedling.



Table 7.3 The density and actual count of seeds germinated from the soil and the above ground vegetation in two areas at Bellerive.

Species	Frequently Burnt Area						Infrequently Burnt Area					
	Density <sup>1</sup>			Count <sup>2</sup>			Density <sup>1</sup>			Count <sup>2</sup>		
	5	10	15	Uh	H	V <sup>3</sup>	5	10	15	Uh	H	V <sup>3</sup>
* <i>Centaurium erythraea</i>	721	95	42	336	0	1	7	9	5	8	1	
* <i>Aira</i> spp.	87	74	20	57	14	+	40	19	5	21	6	+
* <i>Briza maxima</i>	0	0	2	1	0	+	73	21	5	42	0	+
<i>Wahlenbergia stricta</i>	18	10	10	14	1	+	28	19	3	17	4	+
<i>Hypericum gramineum</i>	8	13	2	9	0		21	19	8	19	1	
Dicotyledonae spp.	13	3	10	10	0		12	9	13	11	3	
<i>Carex breviculmis</i>	13	13	2	11	0	+	5	14	5	10	0	+
<i>Bossiaea cinerea</i>	3	0	7	0	4		7	9	23	2	14	2
<i>Dichelachne</i> & <i>Deyeuxia</i> spp.	8	8	2	2	5		19	7	0	9	2	
Monocotyledonae spp.	8	13	15	13	1		0	7	0	3	0	
<i>Poa rodwayi</i>	3	0	0	0	1	+	26	2	10	8	8	
<i>Oxalis perennans</i>	5	8	0	5	0	+	14	7	3	7	3	+
<i>Bossiaea prostrata</i>	0	0	0	0	0	+	5	12	13	2	10	+
<i>Oxycarpus varia</i>	3	8	7	4	3	+	2	5	3	0	4	+
<i>Crassula sieberana</i>	13	8	0	7	1		5	0	0	2	0	
<i>Dodonaea viscosa</i>	0	0	0	0	0	1	5	19	0	1	9	+
<i>Gonocarpus tetragynus</i>	0	10	5	4	2	1	2	5	0	3	0	1
<i>Luzula meridionalis</i>	3	8	2	5	0		5	5	0	4	0	+
<i>Helichrysum apiculatum</i>	3	5	0	1	2	2	5	5	0	4	0	+
<i>Senecio quadridentatus</i>	0	5	5	4	0		5	2	0	3	0	
<i>Indigofera australis</i>	0	0	0	0	0		2	7	5	1	5	+
<i>Schoenus apogon</i>	0	3	2	1	1		2	7	0	3	1	
<i>Wahlenbergia multicaulis</i>	3	5	5	5	0		0	2	0	1	0	
<i>Juncus bufonius</i>	3	0	7	4	0		0	0	3	1	0	
<i>Stipa</i> spp.	5	0	0	1	1	2	5	2	0	2	1	+
* <i>Briza minor</i>	0	0	0	0	0		9	0	0	0	4	
<i>Centrolepis strigosa</i>	0	0	0	0	0		5	5	0	4	0	
<i>Danthonia</i> spp.	0	3	0	1	0	1	2	5	0	3	0	1
<i>Gnaphalium collinum</i>	3	0	0	1	0		7	0	0	3	0	
<i>Hibbertia riparia</i>	0	0	10	4	0	1	0	0	0	0	0	
* <i>Holcus lanatus</i>	0	0	0	0	0		5	2	3	4	0	
<i>Kennedia prostrata</i>	3	3	0	0	2	+	0	5	0	0	2	
<i>Themeda triandra</i>	10	0	0	4	0	3	0	0	0	0	0	1
<i>Astroloma humifusum</i>	5	3	0	0	3	+	0	0	0	0	0	+
* <i>Erica</i> spp.	0	8	0	3	0		0	0	0	0	0	
<i>Epacris impressa</i>	3	0	0	1	0		0	2	3	1	1	+
<i>Hovea linearis</i>	3	3	2	1	2	1	0	0	0	0	0	
<i>Lepidosperma</i> spp.	0	8	0	3	0		0	0	0	0	0	
<i>Lomandra longifolia</i>	3	3	0	2	0	2	0	0	3	1	0	3
* <i>Silene gallica</i>	0	0	0	0	0		5	0	3	3	0	
<i>Stackhousia monogyna</i>	0	0	2	0	1	+	5	0	0	1	1	
<i>Wahlenbergia gracilentia</i>	5	3	0	3	0		0	0	0	0	0	
<i>Pimelea humilis</i>	0	5	0	2	0	1	0	0	0	0	0	+
<i>Poa sieberiana</i>	0	3	0	0	1	+	0	2	0	0	1	+
Poaceae spp.	3	0	0	1	0		0	0	3	1	0	
<i>Stylidium graminifolium</i>	0	0	0	0	0		5	0	0	0	2	+
<i>Bulbine glauca</i>	0	3	0	1	0	1	0	0	0	0	0	+
<i>Carpobrotus rossii</i>	0	0	2	0	1	+	0	0	0	0	0	
* <i>Cerastium glomeratum</i>	0	0	0	0	0		2	0	0	1	0	
<i>Dianella revoluta</i>	0	0	0	0	0	1	0	0	3	1	0	+
<i>Dillwynia cinerascens</i>	0	0	0	0	0	1	2	0	0	0	1	+

(cont. next page)

Table 7.3 (cont.)

Species	Frequently Burnt Area						Infrequently Burnt Area					
	Density <sup>1</sup>			Count <sup>2</sup>			Density <sup>1</sup>			Count <sup>2</sup>		
	5	10	15	Uh	H	V <sup>3</sup>	5	10	15	Uh	H	V <sup>3</sup>
<i>Ehrharta stipoides</i>	0	0	0	0	0	1	0	0	3	0	1	+
<i>Gahnia radula</i>	3	0	0	0	1	2	0	0	0	0	0	2
<i>Lepidium pseudotasmanicum</i>	0	3	0	0	1		0	0	0	0	0	
<i>Scleranthus biflorus</i>	0	0	0	0	0		0	2	0	1	0	
<i>Senecio glomeratus</i>	0	0	0	0	0		2	0	0	1	0	
Species with no seedling emergence from soil:												
<i>Acacia dealbata</i>						2						3
<i>Acaena echinata</i>						+						+
<i>Allocasuarina littoralis</i>						+						+
<i>Allocasuarina verticillata</i>						2						+
<i>Arthropodium milleflorum</i>						+						+
<i>Brachyscome aculeata</i>						+						+
<i>Brachyscome spathulata</i>												+
<i>Bursaria spinosa</i>						+						+
<i>Cassitya pubescens</i>												2
* <i>Cirsium vulgare</i>												+
<i>Corybas incurvus</i>						+						+
<i>Craspedia glauca</i>						+						+
<i>Danthonia pilosa</i>						1						
<i>Dichelachne crinita</i>						+						
<i>Dichelachne inaequiglumis</i>						+						
<i>Diplarrena moraea</i>												3
<i>Diuris sulphurea</i>						+						
<i>Drosera peltata</i>												+
<i>Ehrharta distichophylla</i>												1
<i>Elymus scabrus</i>						+						+
<i>Eucalyptus amygdalina</i>												+
<i>Eucalyptus viminalis</i>												+
<i>Helichrysum scorpioides</i>						+						+
<i>Lepidosperma concavum</i>						+						+
<i>Lepidosperma lineare</i>						1						
<i>Leptorhynchus squamatus</i>						+						+
<i>Leucopogon virgatus</i>						1						
<i>Olearia myrsinoides</i>												+
<i>Plantago varia</i>						+						+
<i>Podolepis jaceoides</i>						1						+
<i>Pterostylis</i> spp.												1
<i>Ranunculus lappaceus</i>												+
<i>Stipa semibarbata</i>						2						
<i>Thelymitra pauciflora</i>						+						
<i>Thysanotus patersonii</i>						+						
<i>Velleia paradoxa</i>						2						

<sup>1</sup> Viable seed density per original volume of soil (cm<sup>-3</sup> × 10<sup>4</sup>), by soil depth (cm): 5=0-5; 10=5-10; 15=10-15.

<sup>2</sup> Actual count of seeds germinated in unheated trays (Uh) and heated trays (H).

<sup>3</sup> Species in above ground vegetation in 10 × 10 area, indicating projected foliage cover: +=<1%; 1=<1-5%; 2=5-25%; 3=25-50%.

\* denotes exotic species.

**Table 7.4** The density and actual count of viable seeds germinated from the soil and the above ground vegetation at East Risdon.

Species	Density ( $\text{cm}^{-3} \times 10^4$ ) <sup>1</sup>					Count <sup>2</sup>	Vegetation <sup>3</sup>
	0-5 cm			5-10 cm			
	Uh	H 1	H 2	Uh	H2		
<i>Stipa</i> spp.	60	3	3	8	0	27	1
<i>Poranthera microphylla</i>	32	14	3	10	0	22	
<i>Helichrysium obcordatum</i>	30	0	0	23	0	20	1
<i>Pultenaea pedunculata</i>	0	35	5	0	3	16	2
<i>Oxalis perennans</i>	16	0	0	23	0	15	
Dicotyledonae spp.	8	0	3	5	0	6	
<i>Billardiera procumbens</i>	5	0	0	8	0	5	
<i>Olearia hookeri</i>	8	0	0	5	0	5	2
<i>Opercularia varia</i>	5	0	3	5	0	5	
<i>Pomaderris pilifera</i>	0	8	3	3	0	5	1
<i>Dichelachne</i> spp.	0	0	0	0	5	2	
<i>Tetratheca labillardieri</i>	0	3	0	3	0	2	1
# <i>Thelymitra</i> spp.	5	0	0	0	0	2	
# <i>Thysanotus patersonii</i>	5	0	0	0	0	2	+
<i>Dianella revoluta</i>	3	0	0	0	0	1	2
<i>Dodonaea viscosa</i>	0	3	0	0	0	1	1
<i>Eucalyptus amygdalina</i>	3	0	0	0	0	1	2
Monocotyledonae spp.	0	3	0	0	0	1	
Poaceae spp.	3	0	0	0	0	1	
<i>Senecio</i> spp.	0	3	0	0	0	1	
<i>Stylidium graminifolium</i>	0	3	0	0	0	1	1

Species with no seedling emergence from soil.

<i>Acacia genistifolia</i>	+
<i>Acianthus</i> spp.	+
<i>Allocasuarina littoralis</i>	+
<i>Astroloma humifusum</i>	+
<i>Bursaria spinosa</i>	+
<i>Caladenia catenata</i>	+
<i>Cassytha pubescens</i>	+
<i>Comesperma volubile</i>	+
<i>Danthonia caespitosa</i>	+
<i>Eucalyptus amygdalina</i> x <i>risdonii</i>	2
<i>Exocarpos cupressiformis</i>	+
<i>Exocarpos strictus</i>	+
<i>Lepidosperma laterale</i>	+
<i>Pultenaea daphnoides</i>	+
* <i>Vulpia myuros</i>	+

<sup>1</sup> Viable seed density per original volume of soil, by soil depth in unheated trays (Uh), trays heated after a period in the glasshouse (H1) and trays heated from the start (H2).

<sup>2</sup> Actual count of seeds germinated.

<sup>3</sup> Species in above ground vegetation in 10 x 10 area, indicating projected foliage cover: +=<1%; 1=<1-5%; 2=5-25%; 3=25-50%.

\* denotes exotic species.

# possibly not all seedlings.

**Table 7.5** The density and actual count of seeds germinated from the soil and the above ground vegetation at Hospital Creek.

Species	Density (cm <sup>-3</sup> x 10 <sup>4</sup> ) <sup>1</sup>						Count <sup>2</sup>	Vegetation <sup>3</sup>
	0-2 cm		2-6 cm		6-10 cm			
	Uh	H	Uh	H	Uh	H		
<i>Wahlenbergia</i> spp.	211	24	52	3	28	3	67	+
<i>Odixia achlaena</i>	24	42	18	3	9	3	22	2
<i>Pelargonium inodorum</i>	0	54	0	3	9	6	15	
<i>Dichelachne rara</i>	54	6	6	0	0	0	12	1
<i>Schoenus apogon</i>	6	6	9	6	16	0	12	+
<i>Oxalis perennans</i>	12	12	6	6	6	0	10	+
<i>Gnaphalium collinum</i>	48	6	0	0	0	0	9	+
<i>Goodenia ovata</i>	12	12	9	6	0	0	9	+
<i>Opercularia varia</i>	6	6	9	0	12	0	9	+
<i>Poaceae</i> spp.	42	0	3	0	3	0	9	
<i>Lepidosperma</i> spp.	24	6	3	0	0	0	6	
<i>Danthonia</i> spp.	30	0	0	0	0	0	5	2
<i>Hypericum gramineum</i>	18	0	3	0	0	0	4	+
<i>Viola hederacea</i>	12	0	6	0	0	0	4	+
<i>Crassula</i> spp.	12	0	0	0	0	0	2	
<i>Galium australe</i>	12	0	0	0	0	0	2	
* <i>Juncus articulatus</i>	0	0	6	0	0	0	2	
Monocotyledonae spp.	6	0	3	0	0	0	2	
<i>Acacia dealbata</i>	0	0	0	3	0	0	1	+
Dicotyledonae spp.	0	0	3	0	0	0	1	
<i>Geranium solanderi</i>	6	0	0	0	0	0	1	+
<i>Ranunculus</i> spp.	6	0	0	0	0	0	1	
<i>Ehrharta stipoides</i>	0	0	3	0	0	0	1	2
<i>Stipa</i> spp.	6	0	0	0	0	0	1	+

Species with no seedling emergence from soil:

<i>Acacia genistifolia</i>	-
<i>Acaena echinata</i>	-
<i>Acaena novae-zelandiae</i>	+
<i>Acrotriche serrulata</i>	+
<i>Arthropodium milleflorum</i>	+
<i>Astroloma humifusum</i>	+
<i>Bossiaea prostrata</i>	+
<i>Bursaria spinosa</i>	+
<i>Callistemon pallidus</i>	1
<i>Carex breviculmis</i>	1
* <i>Centaurium erythraea</i>	+
* <i>Cirsium vulgare</i>	+
<i>Craspedia glauca</i>	+
<i>Diplarrena moraea</i>	+
<i>Eucalyptus cordata</i>	+
<i>Eucalyptus globulus</i>	+
<i>Eucalyptus pulchella</i>	2
<i>Gonocarpus tetragynus</i>	+
<i>Goodenia lanata</i>	+
<i>Helichrysum dendroideum</i>	+
<i>Helichrysum scorioides</i>	+
<i>Hydrocotyle hirta</i>	+
* <i>Hypochoeris radicata</i>	+
<i>Lagenifera stipitata</i>	+
<i>Lepidosperma lineare</i>	2
<i>Leptospermum scoparium</i>	+

(cont. next page)

Table 7.5 (cont.)

Species	Density (cm <sup>-3</sup> x 10 <sup>4</sup> ) <sup>1</sup>						Count <sup>2</sup>	Vegetation <sup>3</sup>
	0-2 cm		2-6 cm		6-10 cm			
	Uh	H	Uh	H	Uh	H		
<i>Olearia ramulosa</i>								+
<i>Picris</i> spp.								+
<i>Poa sieberiana</i>								1
<i>Poa tenera</i>								+
<i>Senecio</i> spp.								+
<i>Solenogyne</i> spp.								+
<i>Stipa aphylla</i>								+
<i>Stylidium graminifolium</i>								+
* <i>Taraxacum officinale</i>								+
<i>Veronica calycina</i>								+

<sup>1</sup> Viable seed density per original volume of soil, by soil depth in unheated trays (Uh) and heated trays (H).

<sup>2</sup> Actual count of seeds germinated.

<sup>3</sup> Species in above ground vegetation in 10 x 10 area, indicating projected foliage cover: +=<1%; 1=<1-5%; 2=5-25%; 3=25-50%.

\* denotes exotic species.



**Table 7.6** The density and actual count of seeds germinated from the soil and the above ground vegetation at the Old Coach Road.

Species	Density (cm <sup>-3</sup> × 10 <sup>4</sup> ) <sup>1</sup>				Count <sup>2</sup>	Vegetation <sup>3</sup>
	0-3 cm		3-6 cm			
	Uh	H	Uh	H		
<i>Schoenus apogon</i>	110	106	52	15	63	+
Dicotyledonae spp.	110	0	43	4	35	
<i>Gnaphalium collinum</i>	83	0	64	0	33	+
<i>Wahlenbergia gymnoclada</i>	92	9	34	0	30	
<i>Agrostis venusta</i>	74	0	13	0	19	
<i>Lasiopetalum micranthum</i>	0	46	0	26	17	1
<i>Wahlenbergia gracilis</i>	55	0	21	0	17	
<i>Viola hederacea</i>	9	5	47	4	15	1
<i>Hypericum gramineum</i>	37	0	26	0	14	1
<i>Stipa</i> spp.	51	0	9	0	13	1
<i>Wahlenbergia</i> spp.	37	5	13	0	12	+
<i>Carex breviculmis</i>	18	5	26	0	11	1
<i>Wahlenbergia gracilentia</i>	32	0	17	0	11	
Monocotyledonae spp.	32	5	9	0	10	
<i>Lepidosperma</i> spp.	0	18	0	15	8	
<i>Themeda triandra</i>	32	0	4	0	8	2
<i>Bossiaea prostrata</i>	0	18	4	8	7	1
<i>Opercularia varia</i>	5	9	9	8	7	
<i>Acacia mearnsii</i>	0	14	0	8	5	+
<i>Dichondra repens</i>	0	23	0	0	5	1
<i>Gonocarpus tetragynus</i>	9	9	4	0	5	1
<i>Poa rodwayi</i>	9	5	9	0	5	3
* <i>Centaurium erythraea</i>	9	0	4	0	3	+
<i>Dichelachne</i> spp.	14	0	0	0	3	
<i>Oxalis perennans</i>	14	0	0	0	3	+
<i>Poranthera microphylla</i>	5	5	0	4	3	
<i>Veronica calycina</i>	5	0	9	0	3	+
Poaceae spp.	0	0	9	0	2	
<i>Sebaea ovata</i>	9	0	0	0	2	
* <i>Cerastium glomeratum</i>	5	0	0	0	1	
<i>Danthonia</i> spp.	5	0	0	0	1	1
<i>Eucalyptus</i> spp.	5	0	0	0	1	
<i>Helichrysum apiculatum</i>	0	0	4	0	1	
<i>Plantago varia</i>	5	0	0	0	1	1
<i>Ranunculus</i> spp.	0	0	4	0	1	
<i>Senecio</i> spp.	5	0	0	0	1	

Species with no seedling emergence from soil:

<i>Acaena echinata</i>	
<i>Allocasuarina verticillata</i>	+
<i>Astroloma humifusum</i>	+
<i>Brachyscome aculeata</i>	+
<i>Bursaria spinosa</i>	+
<i>Chamaescilla corymbosa</i>	+
<i>Cheilanthes austrotenuifolia</i>	1
<i>Craspedia glauca</i>	+
<i>Ehrharta stipoides</i>	1
<i>Eucalyptus amygdalina</i>	+
<i>Galium</i> spp.	+
<i>Goodenia lanata</i>	+
<i>Helichrysum scorpioides</i>	+
<i>Hibbertia hirsuta</i>	+

(cont. next page)

Table 7.6 (cont.)

Species	Density (cm <sup>-3</sup> × 10 <sup>4</sup> ) <sup>1</sup>				Count <sup>2</sup>	Vegetation <sup>3</sup>
	0-3 cm		3-6 cm			
	Uh	H	Uh	H		
<i>Lepidosperma inops</i>						1
<i>Lepidosperma laterale</i>						2
<i>Lomandra longifolia</i>						+
<i>Pultenaea daphnoides</i>						+
<i>Thelymitra</i> spp.						+
<i>Thysanotus patersonii</i>						+

<sup>1</sup> Viable seed density per original volume of soil, by soil depth in unheated (Uh) and heated trays (H).

<sup>2</sup> Actual count of seeds germinated.

<sup>3</sup> Species in above ground vegetation in 10 x 10 area, indicating projected foliage cover: +=<1%; 1=<1-5%; 2=5-25%; 3=25-50%.

\* denotes exotic species.

Table 7.7 The presence in the sample areas of taxa which were postulated to be myrmecochorous by Berg (1975).

Species	Study sites											
	Bellerive			East Risdon			Hospital Creek			Old Coach Road		
	A	S	D	A	S	D	A	S	D	A	S	D
<i>Acacia dealbata</i>	+	-					+	+	y			
<i>Acacia genistifolia</i>				+	-		+	-				
<i>Acacia mearnsii</i>										+	+	n
<i>Bossiaea cinerea</i>	+	+	y									
<i>Bossiaea prostrata</i>	+	+	y				+	-		+	+	n
<i>Comesperma volubile</i>				+	-							
<i>Dillwynia cinerascens</i>	+	+	n									
<i>Goodenia lanata</i>							+	-		+	-	
<i>Goodenia ovata</i>							+	+	n			
<i>Hibbertia riparia</i>	+	+	y									
<i>Hovea linearis</i>	+	+	y									
<i>Kennedia prostrata</i>	+	+	y									
<i>Lasiopetalum micranthum</i>										+	+	n
<i>Lepidosperma</i> (4 spp.)	+	+	y				+	+	n	+	+	n
<i>Luzula meridionalis</i>	+	+	y									
<i>Opercularia varia</i>	+	+	y				+	+	y	+	+	y
<i>Pomaderris pilifera</i>				+	+	?						
<i>Pultenaea daphnoides</i>				+	-					+	-	
<i>Pultenaea pedunculata</i>				+	+	n						
<i>Tetratheca labillardieri</i>				+	+	y						
<i>Thysanotus patersonii</i>	+	-		+	+	n				+	-	
<i>Velleia paradoxa</i>	+	-										

A = presence or absence in above ground vegetation; S = presence or absence in soil seed bank; D = density of seed in deeper soil  $\geq$  density in shallower soil (y), or not (n), or not discernible (?).



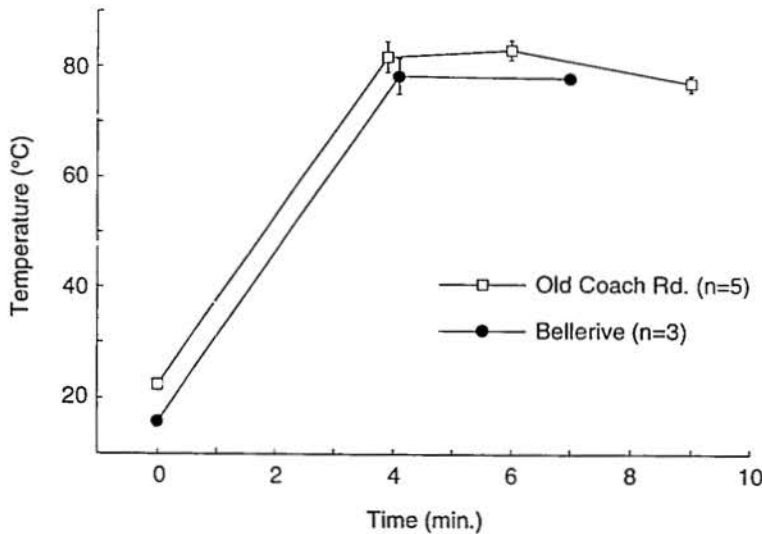


Fig. 7.1 Mean soil temperatures ( $\pm$  s.e.m.) at 1 cm depth in seedling trays during heating with a blowtorch for 4 min.

## Discussion

These data are consistent with other studies which have found a poor correlation between the composition of the soil seed bank and the composition of the above ground vegetation (e.g. Rabinowitz, 1981a; Lunt, 1990). The range of densities of native seeds which germinated from the soil in this study are similar to those found in other soil seed bank studies of drier native Australian ecosystems (e.g. Vlahos & Bell, 1986; Lunt, 1990; Gilfedder & Kirkpatrick, 1993). A comparison can be made between the mean densities found in Lunt (1990) for a species rich grassland and those from the 0-3 cm soil from the Old Coach Road, if the latter are multiplied by a factor of four (i.e. figures in Lunt, 1990 are given per  $\text{m}^2$  of 4 cm deep soil). The densities of *Themeda triandra* in this comparison are very similar (139 and 128  $\text{m}^{-2}$ ), while the density of *Wahlenbergia* spp. is higher at the Old Coach Road (864  $\text{m}^{-2}$  and

208 m<sup>-2</sup>). While there are many differences between these sites and the methods used, the comparison does indicate a general similarity in the size and diversity of soil seed banks in native and grassy plant communities in temperate Australia.

The seedling emergence method can only give a reasonable estimate of the densities of viable seeds stored in the soil for species which are readily germinable (Roberts, 1981; Gross, 1990). Species which do not germinate cannot be presumed to have no store of viable seed in the soil—the experiment may simply have failed to provide the right conditions for germination. The range of glasshouse temperatures, the long period of time that trays spent in the glasshouse and the heating of some trays, ensured that a wide range of environmental conditions were made available for the germination of seeds in this study. Several species had quite different densities in the two series of heated trays from East Risdon, demonstrating how important different experimental conditions can be (Table 7.4). This difference may have been a result of variation in soil temperatures reached during heating.

The time of year that the soil samples are collected will have some bearing on the amount of seed that germinates in the glasshouse, at least for some species (Thompson & Grime, 1979). The vast majority of native shrub and herb species at the sites in this study flower in spring or summer and disperse their seed in the summer months. At the time that the soil samples were collected at Bellerive, in early November 1990, *Luzula meridionalis* was the only taxon from Table 7.3 that had commenced dispersing the current season's seed (Pyrke, unpublished data). The germination of most species occurs in the autumn and winter, with little taking place in spring and summer (Chapter 5). Since spring and autumn were the two times when the soil samples were collected, it may be predicted that more seeds will germinate from soil collected in autumn compared with soil collected in spring, particularly amongst species which have only a transient soil seed bank (Thompson & Grime, 1979). This difference would arise because in the spring collected sites, there would be less seed in the soil as result of germination and mortality; but at each of the autumn collected sites, germination had barely commenced for the year.

The data from the Old Coach Road and Hospital Creek are worthy of comparison, because they are consistent with the prediction made above. The Old Coach Road soil was collected in March and 60% of the 50 native taxa germinated from the soil; while Hospital Creek was sampled in October, but only 38% of the 52 native taxa germinated. The density of seeds of a number of taxa common to both sites was higher at the Old Coach Road, but these could be attributable to differences in the abundance of mature plants (e.g. *Schoenus apogon*, *Gnaphalium collinum*, *Hypericum gramineum*, *Stipa* spp.). Standardization of seed bank densities, relative to the densities of the species in the above ground vegetation, could provide a better basis for comparing sites, but this would require a more detailed account of abundances in the vegetation than was recorded in this study.

It appears that *Velleia paradoxa* does not have a persistent store of viable seed in the soil. This species germinates readily every year in the field and has no special germination requirements (Chapter 5), so it should have germinated in the glasshouse if any viable seed was present. The size and shape of diaspores and the particle size of the soil are both factors which influence the incorporation of seeds into the soil profile. Generally, smaller seeds are more likely to move down a soil profile than larger ones, and coarser sandy soils allow more movement of seeds down the profile than finer clay soils (Chambers *et al.*, 1991). The smaller and rounder a seed is, as opposed to large, elongated or flat, the more likely it is to persist in the soil for a long time (Thompson *et al.*, 1993). *Velleia paradoxa* has very large, flat seeds, which are probably too big to move down the soil profile, even on a sandy soil such as was sampled at Bellerive. The soil at Bellerive was collected at the end of spring, which was before *V. paradoxa* had flowered and past the end of the germination period. Therefore it seems likely that this species has only a transient and short-lived seed bank at the soil surface, which has been completely depleted by late spring.

*Lepidium hyssopifolium* on the other hand, appears to be a species which does have a reasonably substantial store of buried viable seed, even below 5 cm soil depth. However, there is a problem in determining whether individual seeds in the soil are in fact short- or long-lived. The soil at Annandale is quite

sandy and the seeds are very small, so seeds are possibly able to move down the profile very quickly—seeds can move down a soil profile to a depth of 5 cm within a matter of weeks (Chambers *et al.*, 1991). Therefore generally, the time of collection will probably also influence the nature of the soil seed bank observed at depth, as well as near the surface. But *Lepidium hyssopifolium* disperses seed nearly all year round, which means that the time of sampling is more or less irrelevant for this species. Fortunately, the Bagdad experiment in Chapter 6 confirms that seeds of *L. hyssopifolium* remain viable in the soil for at least several years. Although animal digging probably brings seed of *L. hyssopifolium* to the soil surface, this process may be of limited importance where mature plants are present, because fresh seed is constantly being dispersed. However, such soil disturbance may resurrect populations where adult plants are no longer present.

*Olearia hookeri* appeared to have very little soil stored seed, but may have been one species whose germination requirements were not met by the experimental treatments. The soil was collected in April, which is at most four months after the dispersal of seed from the previous spring flowering, so natural seed mortality should not have occurred to any great extent by this time. Although *O. hookeri* regenerates prolifically after fire (Jamie Kirkpatrick, pers. comm.), the heating treatments which were applied may not have been appropriate for this species. The trays that were heated at the start may have reached temperatures high enough to kill *O. hookeri* seed. The seed may have perished in the soil before the second series of heating was applied, which was some 10 months after the soil was collected.

*Odixia achlaena* appeared to have a modest density of soil stored seed at 2-6 cm depth, relative to other densities reported in this study. However, this density may be an under-estimate of the true level of viable seed in the soil at that depth. *Odixia achlaena* does not germinate freely in the field and was found to require soil heating to break dormancy (Chapter 6). The exact cause of this dormancy is not known and more seed germinated from the unheated than the heated trays in the 2-6 cm and 6-10 cm soil, although the overall numbers were quite low. These conflicting findings suggest that the nature of the seed dormancy in *O. achlaena* may be complex, as has been identified for other species of fire-prone vegetation (see Keeley, 1987).

*Lasiopetalum micranthum* has a moderate level of viable soil stored seed at 3-6 cm depth. Again, this density may be an underestimate because of the need to break dormancy. The soil temperature in heated trays was less than the optimum found in oven heating trials of *L. micranthum* seeds (Chapter 6). Regardless of this difference, the seed density found in the soil seed bank study is comparable with that found in the digging experiments (Chapter 6); the density was 26 m<sup>-2</sup> of 1 cm depth of soil in the soil seed bank trial, while the median density of seedlings in the first simulated animal digging experiment was 25 m<sup>-2</sup> on the dug quadrats (Fig. 6.2). Although the density of soil stored seed of *L. micranthum* is still very low in comparison with northern hemisphere examples (e.g. see Roberts, 1981), combined with the high survival rate of seedlings which germinate in the field, at least in the short term (Chapter 6), the soil seed bank may still be of ecological importance to this species.

The seeds of *L. micranthum* are relatively large in comparison with the average grain size of the clay-rich soil at the Old Coach Road and would seem unlikely to move down the soil profile simply by gravity alone (see Chambers *et al.*, 1991). It is possible that they are transported by seed-harvesting ants, as happens with Fabaceae seeds (e.g. Auld 1986a). In fact, on the basis of seed morphology, all 35 *Lasiopetalum* species in Australia are postulated to be myrmecochorous (Berg, 1975).

On the basis of Berg (1975), 22 taxa from the five study sites reported on here are possibly myrmecochorous, including *Velleia paradoxa* and *Lasiopetalum micranthum*. Eighteen of these 22 taxa germinated from soil from at least one site, and for 10 of these 18, the density of seed in the deeper soil was greater than or equal to the density in the shallower soil, in at least one site (Table 7.7). Although the numbers of germinants were very small for many of these species, the greater densities of seeds at depth presumably reflect the transportation of seeds down the profile by ants, at least for Fabaceae species at Bellerive. *Viola* is not included by Berg (1975) as a potentially myrmecochorous genus, but *Viola hederacea* seeds were much more common at depth than near the surface at the Old Coach Road and other species of *Viola* are myrmecochorous (Culver & Beattie, 1980).

Although the soil stored seed of newly formed mounds was not directly examined in my study, there is little reason to doubt the potential for bandicoot digging to bring seeds to the surface, where such seeds are known to be present. The affect of bandicoot digging inverting the soil profile on to mounds was described in Chapter 3. Novoplansky (1984, reported in Heth, 1991) found that mounds from mole rat diggings had negligible seed at formation compared with the number of seeds dispersing on to them later. However, the soils of the mole rat study site possibly have no seed at depths greater than 5 cm (Heth, 1991). Besides the ant dispersed species, there are examples in my study of other species which do have seed buried at depth (e.g. *Wahlenbergia* spp.). The bare soil surface of fresh diggings will not have any input of seed until after the following flowering season and the seed brought to the soil surface may be an important component of the pool of germinants in the first autumn and winter.

### Conclusions

These data demonstrate that some species have a persistent store of seed in the soil at depths of up to 10-15 cm. Examples are *Lepidium hyssopifolium*, *Lasiopetalum micranthum*, *Odixia achlaena*, *Wahlenbergia* spp. and native Fabaceae spp. Digging by small mammals presumably brings this seed to the surface, which is then more likely to germinate (e.g. Auld, 1986b). This process may have particular importance for species which are otherwise removed from the active soil layer. The Fabaceae species from Bellerive are a good example, because much of the seed is presumably buried too deep to germinate, even after a stimulus such as fire.



## Chapter 8

# The Relationship Between Bandicoot Diggings, Exotic Species and the Survival of Native Seedlings

### Introduction

The invasion of native vegetation by exotic plant species in southern Australia is facilitated by various kinds of disturbance, particularly mechanical soil disturbance (Buchanan, 1989; Hobbs & Atkins, 1988; Hobbs, 1989). The Bellerive study site is an urban bush remnant which has varying degrees of degradation from exotic weed invasion. The most weedy areas are around the perimeter and along vehicular tracks and species such as *Ulex europaeus* and *Chrysanthemoides monilifera* are largely confined to such areas. Other exotic species are more pervasive at this site, particularly annual grasses such as *Aira* spp. and *Briza maxima*.

Soil disturbance by gophers was found to facilitate invasion of exotic annual grasses in a serpentine grassland in California (Hobbs & Mooney, 1985; 1991). Given the large amount of mechanical soil disturbance created by bandicoots on the sandstone soil at Bellerive, it is of interest to know first whether exotics are being encouraged by this disturbance and second, whether they are having an effect on the native species.

The third aim of this chapter is to test the effectiveness of hand weeding of *B. maxima* and therefore to determine the contribution of the persistent soil seed store (*sensu* Thompson & Grime, 1979) to yearly germination of this species. All the data are from experiments and observational studies at Bellerive.

### Methods

#### *Exotic species removal experiment on bandicoot mounds*

An experiment was set up on 19 July 1990 to test the effect of exotic species upon the recruitment of native species. Thirty large and recently



formed bandicoot mounds were marked and half of these were randomly assigned the weeding treatment. The other half of the diggings were unweeded controls. All diggings were within an area of 150 m<sup>2</sup>. A 40 x 40 cm grid was placed over each digging and two opposite corners were marked with large nails. These nails were subsequently stolen and were replaced with less conspicuous wire markers. The actual digging areas did not fill the entire grid, but the boundaries were drawn on to a graphical representation of the quadrat and the actual treatment areas were determined by counting grid cells. The mean ( $\pm$  s.d.) areas of the weeded and control diggings were 0.100 m<sup>2</sup> ( $\pm$  0.026) and 0.106 m<sup>2</sup> ( $\pm$  0.025) respectively.

The weeded quadrats had all exotic species removed at the start of the experiment and then again in July 1991, October 1991, May 1992 and October 1992. Removal was performed by cutting with scissors to ground level. This method was chosen to minimise further disturbance to the quadrats (Aarssen & Epp, 1990). The most abundant exotic species were *Briza maxima* and *Aira* spp. (*A. caryophylllea* and *A. elegantissima*), but *B. maxima* was by far the most important species in terms of biomass and cover. Other less abundant exotic species which were removed were (in descending order of abundance) *Holcus lanatus*, *Vulpia myuros*, *Rumex acetosella*, *Silene gallica* and *Hypochoeris radicata*. Seedlings and resprouted plants were mapped on to graph paper in January 1991, October 1991, March 1992 and finally in December 1992 (see Chapter 5 for mapping methods). Exotic species and *Ehrharta stipoides* were not mapped, but the projected foliage cover of the former was estimated using the 5 x 5 cm grid cells as a guide.

#### *Briza maxima* density on bandicoot diggings and competition effects

In Chapter 5, some data were presented from 19 permanent quadrats on bandicoot diggings, which were each paired with a control quadrat on adjacent undisturbed vegetation. More data are presented here for these quadrats, involving counts of individuals of *B. maxima* which were made in the winter visits, as well as densities and survival of native seedlings.

*Briza maxima* removal experiment

An experiment was set up on 29 November 1990 to test the effectiveness of hand weeding *B. maxima* in reducing germination from the persistent soil seed bank in subsequent years. A set of 30 contiguous quadrats, which were 2 x 2 m, were laid out in three rows by 10 columns as the basis of a randomised block design. The layout of the blocks accommodated an obvious gradient in density of *B. maxima*. The quadrats were marked with large nails. Three treatments were randomly allocated within each block: *B. maxima* removed by pulling; *B. maxima* removed by cutting near ground level with scissors; and no *B. maxima* removal (i.e. a control). The two removal treatments aimed to test whether the soil disturbance created by pulling stimulated more germination from the soil seed bank relative to cutting.

Removal was performed over the entire 2 x 2 m area, aiming to prevent the seed rain of *B. maxima* outside the quadrat from falling on a core area of 0.4 x 0.4 m in the centre. A literature search failed to reveal any information on the dispersal distance of *B. maxima* seed, although the broad, papery margins of the lemmas probably help carry the seeds in the wind. The tallest plants at this site were 0.4 m, but the vast majority were less than 0.3 m tall. Therefore, after the removal of *Briza maxima*, the core areas were at least two times the distance from the nearest seed source. To save time, individuals of *B. maxima* which were less than 10 cm tall and beyond an inner 1 x 1 m area were not removed, but weeding was comprehensive inside this zone. Dispersal of *B. maxima* seed from the current cohort had not commenced when removal was performed and care was taken not to drop inflorescences on to the core areas.

At the start of the experiment, individuals of *B. maxima* were counted in the core areas before removal. This procedure was repeated in November 1991. The comparison of counts from November 1991 revealed that there was no difference between the pulling and cutting treatments (see Results). Consequently, all removal in 1991 was by pulling, because it was quicker. A final count was made in November 1992. Only flowering individuals were counted at each census.

### Data Analysis

In the removal experiment on bandicoot mounds, the differences between densities of surviving native seedlings and the proportion of native seedlings surviving were tested by the Mann-Whitney *U* test. Native Poaceae and Orchidaceae species were excluded from these analyses because seedlings could not be reliably distinguished from plants resprouting from under bandicoot mounds. Only one species (*Lomandra longifolia*) had seedlings in sufficient abundance to be tested alone. Therefore densities and survival proportions were pooled across all native species. *Crassula sieberana* (an annual species) and unidentified monocotyledons were also excluded from survival proportions. Densities were standardised to a unit area of 1000 cm<sup>2</sup>.

Comparisons between the densities of *Briza maxima* on mounds, holes and controls in the paired permanent quadrats were tested by the Wilcoxon signed-rank test. Tests were performed between years for the same microsites and between microsites for the same years. Parametric tests were not performed for the reasons outlined in Chapter 5. Data from the removal experiment on digging mounds and the paired quadrats are presented in the form of 'box plots', which indicate the 25th and 75th percentiles (the box), the median (the bar inside the box) and the range of values (lines with bars beyond the box, with circles indicating outliers).

In other analyses for the paired quadrats, Spearman's rank-order correlations were performed between *B. maxima* densities, the proportions of native seedlings surviving, the total cover of understorey plants, litter, bare soil and tree canopy cover. To try to resolve cause and effect relationships, Spearman's partial rank-order correlations were performed using the CORR procedure in SAS (SAS, 1988a). Insufficient data were available to examine the survival of individual native species in relation to *B. maxima* density and therefore the data were pooled. The data included seedlings of native dicotyledons (except for the annual *Crassula sieberana*) and native monocotyledons (except for Poaceae, Orchidaceae and individuals which could not be identified at least to family level). Seedling survival was calculated until December 1992, with 1991 and 1992 germinants treated as separate

cohorts (the 1992 cohort excluded germinants recorded for the first time in December 1992; see Appendix 3 for data summary).

In the *B. maxima* removal experiment, counts were tested by parametric analysis of variance for randomised block designs, with two factors, removal treatment and year. The data satisfactorily met the homoscedasticity and normality requirements after log transformation. Pairwise comparisons were made with paired *t* tests. Linear regression was used to describe changes in abundance relative to initial abundances.

## Results

### *Exotic species removal experiment on bandicoot mounds*

There were no significant differences between the weeded and unweeded controls for any of the parameters tested: densities of surviving *Lomandra longifolia* seedlings at December 1992; densities of surviving native seedlings at December 1992; and the proportion of native seedlings surviving at December 1992 (out of the seedlings mapped in March 1992 or earlier) (Fig. 8.1). Survival proportions were based on a range of 2-38 germinants per quadrat, with a mean of 10.9. The mean ( $\pm$  s.d.) projected foliage cover of exotic species in the unweeded quadrats was 18.6% ( $\pm$  7.7) at the conclusion of the study in December 1992. The annual exotic grasses had partially cured at this time.

### *Briza maxima density on bandicoot diggings and competition effects*

The density of *Briza maxima* in the paired permanent quadrats in July 1990 (when diggings were newly formed) was higher on controls compared with mounds and higher on mounds compared with holes. In August 1991, the densities on holes and controls were both higher than on mounds, but were not significantly different from each other. By August 1992, the density was still higher on controls compared with mounds, but the other two comparisons were not significantly different (Fig. 8.2). Comparing years within the same microsite category, *B. maxima* density increased between 1990 and

1992 on the control quadrats; increased after the first year but not the second on holes; and increased slightly between 1990 and 1992 on mounds (Fig. 8.2).

For the 1992 cohort on the control quadrats, there was a highly significant, negative correlation between the density of *B. maxima* and the proportion of native seedlings surviving (Table 8.1; Fig. 8.3). These survival proportions were based on a range of 2-44 germinants per quadrat, with a mean of 13.7. *Briza maxima* density was also positively correlated with the amount of exposed bare soil. A partial correlation between *B. maxima* density and the survival of the 1992 seedlings was still significant after the inclusion of bare soil as a partial constant ( $R=-0.72$ ,  $n=18$ ,  $P=0.001$ ; cf. Table 8.1). A reciprocal partial correlation between seedling survival and bare soil, with *B. maxima* density as the partial constant, was considerably different from the simple correlation ( $R=0.33$ ,  $n=18$ ,  $P=0.20$ ; cf. with Table 8.1 where  $R=-0.37$ ).

The proportion of native seedlings surviving in 1991 on controls was not correlated with the density of *B. maxima*, but it was negatively correlated with the amount of bare soil (Table 8.1).

Seedling survival on mounds was not correlated with any variable for the 1991 cohort. However, for the 1992 cohort there were positive correlations with understorey cover and litter, a negative correlation with bare soil, but no correlation with *B. maxima* density. Unlike the control quadrats, on mounds there was no correlation between *Briza maxima* density and bare soil. On holes, there were no significant correlations between seedling survival or *B. maxima* density and any variables (Table 8.1).

The actual densities of surviving native seedlings in December 1992 were not correlated with the density of *B. maxima* on any microsite category. There were no significant correlations between the survivor densities and any other variables on mounds or holes. On controls, there were significant correlations between survivor densities and total understorey cover in 1991, and with litter, bare soil and tree cover in 1992 (Table 8.2).

#### *Briza maxima* removal experiment

Overall, there was a highly significant effect of weeding (i.e. removal of *Briza maxima*) and a weak interaction between weeding and the year of the

experiment (Table 8.3). At the beginning of the experiment, before treatments were applied, there was a small difference in the abundance of *B. maxima* between two of the three sets of quadrats (Fig. 8.4). One year later in 1991, and also in 1992, there was considerably less *Briza maxima* in the plots which received the removal treatments in comparison with the controls. The pulled and cut treatments were not significantly different from each other in 1991, nor in 1992 after both had received the pull treatment in the second year. The abundance of *B. maxima* increased between 1990 and 1991 in the control plots ( $P=0.035$ ), but declined in the weeded plots. The latter effect is best described by a regression of the change in density of *B. maxima* on the initial density. This regression, for the pooled pulled and cut treatments, indicates a reduction in density of 63.7% in 1991 (Fig. 8.5a). At the end of the second year, this reduction was only 46.0% (Fig. 8.5b).

**Table 8.1** Spearman rank-order correlations between the proportion of native seedlings surviving and other variables in the permanent paired quadrats at Bellerive.

	<i>Briza</i> density	Underst. cover	Litter	Bare soil	Tree cover
<i>Control quadrats 1991 cohort:</i>					
Seedling survival prop.	-0.39	0.13	0.37	-0.56 *	0.15
<i>Briza maxima</i> density		-0.23	-0.48 *	0.63 **	-0.17
Understorey cover			0.32	0.02	0.00
Litter				-0.70 ***	0.31
Bare soil					0.14
<i>Control quadrats 1992 cohort:</i>					
Seedling survival prop. <sup>1</sup>	-0.73 ***	0.44	0.27	-0.37	-0.13
<i>Briza maxima</i> density		-0.28	-0.56 *	0.65 **	-0.04
<i>Mounds 1991 cohort:</i>					
Seedling survival prop.	-0.11	0.19	0.21	-0.17	0.02
<i>Briza maxima</i> density		-0.50 *	-0.16	0.34	-0.04
Understorey cover			0.24	-0.45	-0.10
Litter				-0.90 ***	0.19
Bare soil					-0.15
<i>Mounds 1992 cohort:</i>					
Seedling survival prop.	-0.18	0.46 *	0.48 *	-0.51 *	0.12
<i>Briza maxima</i> density		-0.38	-0.23	0.34	0.10
<i>Holes 1991 cohort:</i>					
Seedling survival prop. <sup>2</sup>	-0.06	0.28	-0.20	0.04	0.09
<i>Briza maxima</i> density		-0.38	-0.29	0.43	-0.19
Understorey cover			0.56 *	-0.65 **	-0.12
Litter				-0.91 ***	0.02
Bare soil					0.03
<i>Holes 1992 cohort:</i>					
Seedling survival prop. <sup>2</sup>	-0.32	0.20	0.37	-0.26	0.26
<i>Briza maxima</i> density		-0.37	-0.22	0.33	0.09

<sup>1</sup> n=18

<sup>2</sup> n=15 (n=19 for all other comparisons)

\* 0.01 < P < 0.05; \*\* 0.001 < P < 0.01; \*\*\* P < 0.001.



Table 8.2 Spearman rank-order correlations between the density of surviving native seedlings and other variables in the permanent paired quadrats at Bellerive.

	<i>Briza maxima</i> density	Underst. cover	Litter	Bare soil	Tree cover
Control quadrats 1991 cohort:	-0.13	0.50 *	0.03	0.11	-0.41
Control quadrats 1992 cohort:	0.19	0.16	-0.47 *	0.69 **	-0.53 *
Mounds 1991 cohort:	-0.29	0.32	0.16	-0.16	-0.12
Mounds 1992 cohort:	-0.14	0.34	0.26	-0.26	-0.11
Holes 1991 cohort:	0.06	0.09	-0.25	0.07	-0.03
Holes 1992 cohort:	0.02	-0.04	-0.03	0.16	0.17

n=19 for all comparisons.

\* 0.01<P<0.05; \*\*0.001<P<0.01; \*\*\*P<0.001.

Table 8.3 Results of analysis of variance on the counts of individuals of *Briza maxima* in the removal experiment at Bellerive.

Source of variation	d.f.	M.S.	F	P
Model	17	10.33	15.90	0.0001
Error	72	0.65		
Block	9	13.71	21.09	0.0001
Removal treatment	2	21.63	33.27	0.0001
Year	2	1.19	1.83	0.168
Treatment x Year	4	1.66	2.56	0.046

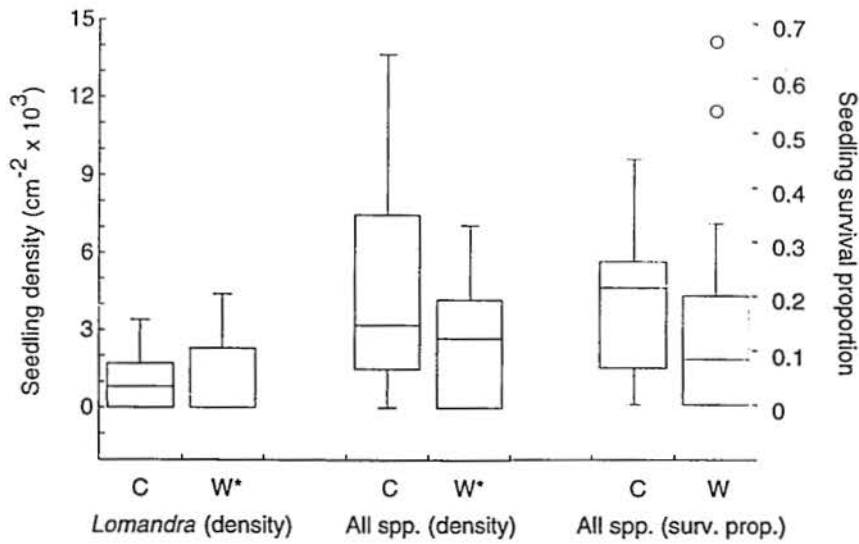


Fig. 8.1 Results of the exotic species removal experiment on bandicoot digging mounds at Bellerive. No comparisons were significantly different. C=unweeded controls; W=exotic species removed.  $n=15$  for all plots, except the survival proportion on controls ( $n=13$ ). \* one outlier not shown in these plots.

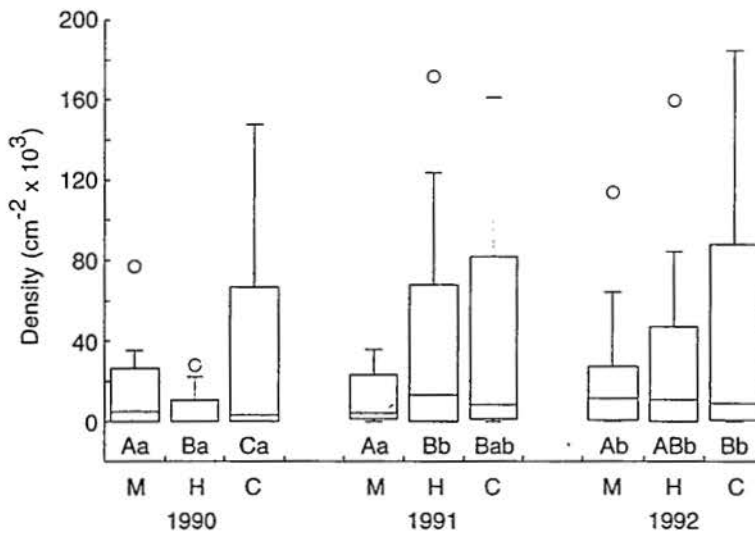


Fig. 8.2 The density of individuals of *Briza maxima* in the permanent quadrats at Bellerive in July (1990) or August (1991, 1992). Treatments with the same letter are not significantly different: capital letters compare microsites within years; lowercase letters compare years within microsites ( $P<0.05$ ). M=mounds; H=holes; C=controls.  $n=19$  for all plots.

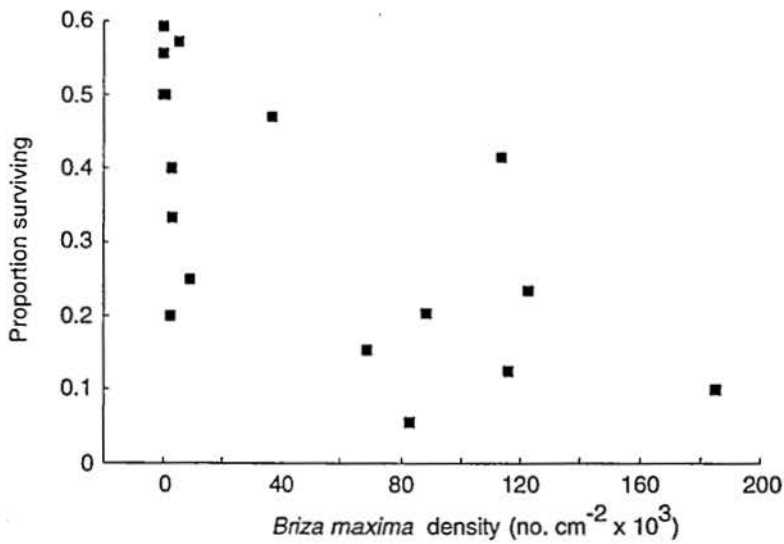


Fig. 8.3 The relationship between the proportion of native seedlings surviving (1992 cohort) and the density of *Briza maxima* in the control plots from the paired permanent quadrats at Bellerive.

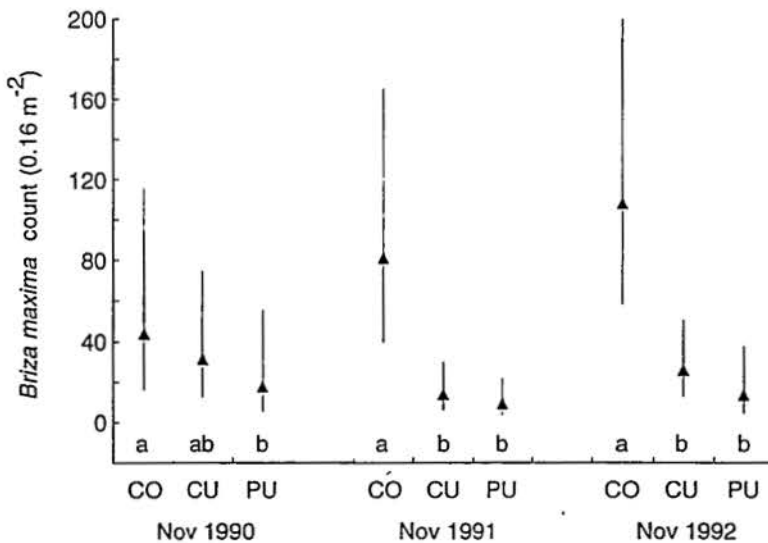
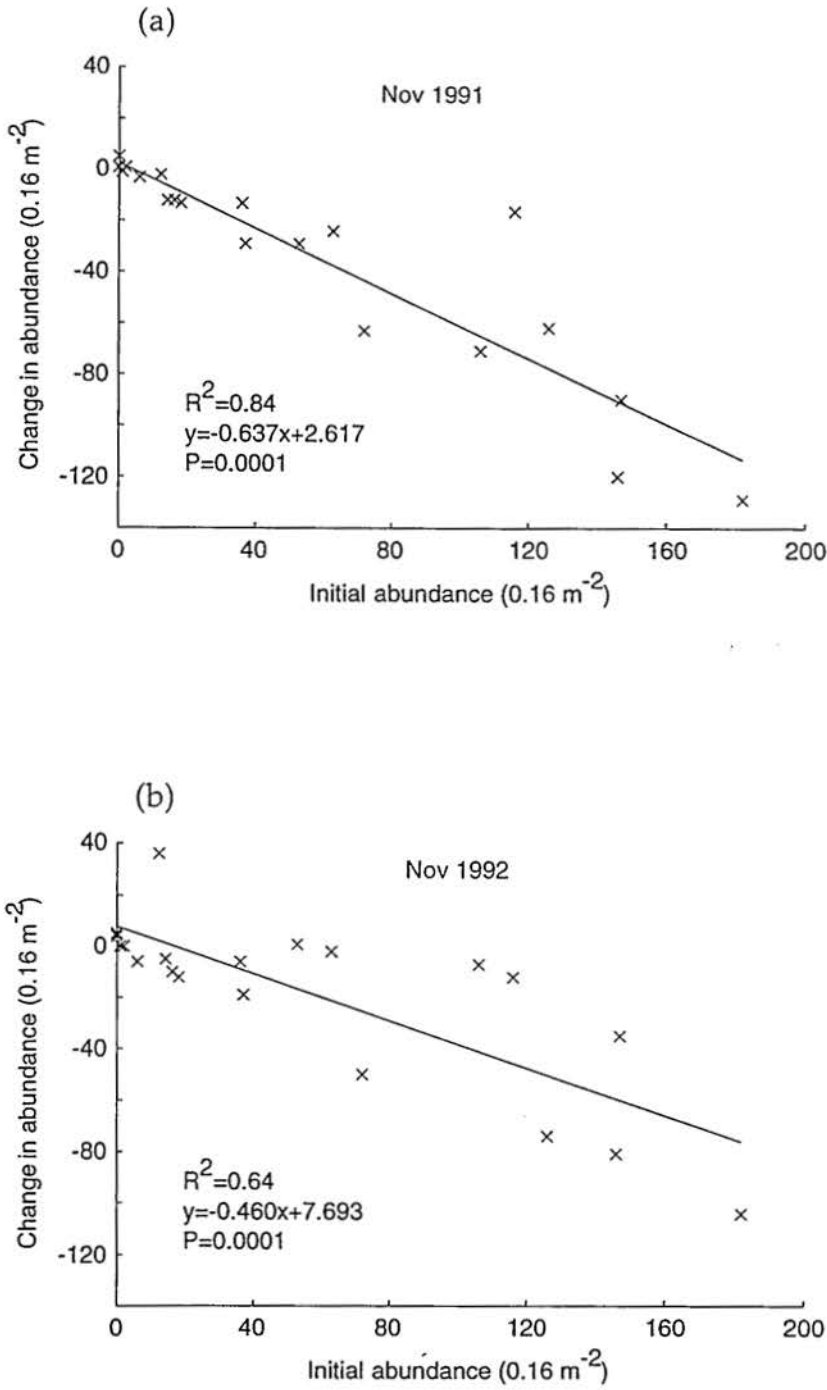


Fig. 8.4 The counts of individuals of *Briza maxima* in the removal experiment at Bellerive, indicating means and 95% confidence limits (both are back-transformed). Treatments with the same letter are not significantly different (comparing within years only,  $P < 0.05$ ). CO=controls; CU=cut; PU=pulled.



**Figs 8.5** The change in abundance of *Briza maxima* in the pulled and cut treatments of the removal experiment at Bellerive, between November 1990 and (a) November 1991; (b) November 1992.

## Discussion

### *Competition between exotic species and native seedlings*

Removing exotic species from bandicoot mounds appeared to make no difference to the survival or density of native seedlings. Therefore, there was no evidence from *this* experiment to support the hypothesis that competition from exotic species is a cause of mortality amongst native seedlings. There are good reasons, however, why competition from exotics may not be important in this experiment, relative to other factors. The density of surviving native seedlings was quite low and the result may not reflect the true disposition of all species. A few species dominated the total pool of survivors (e.g. *Lomandra longifolia*), and mortality in general was so high amongst smaller seeded species that the effect of competition from exotics may have been masked. The sampling was infrequent in this experiment and was more suited to examining survival densities than surviving proportions, because seedlings were not mapped in late autumn and winter when the most germination occurs (see Chapter 5). It is also possible that the abundance of exotic species on digging mounds in this weeding experiment was too low to have much effect on native species (see later discussion).

The results from the paired quadrats, however, do provide evidence of a competition effect from exotics—but not on digging mounds. *Briza maxima* density appeared to have an influence on the survival of native seedlings on undisturbed control quadrats, but not on the mounds where the density of *B. maxima* was lower. The latter result is consistent with the weeding experiment discussed above. The influence of *B. maxima* on undisturbed areas was only evident in the 1992 cohort of native seedlings, which had not yet been exposed to summer water stress in December 1992. The influence of *B. maxima* on the survival until December 1992 of native seedlings of the 1991 cohort, if evident earlier, had presumably been concealed by mortality over the summer of 1991/1992. *Briza maxima* is usually dead by the end of December and therefore no longer a consumer of resources such as water and nutrients.

The results of the partial correlations suggest that *B. maxima* density is having a direct influence on the survival of native seedlings in undisturbed

areas, rather than indirectly reflecting the influence of bare soil on native seedling survival. Bare soil was not correlated with seedling survival for the 1992 cohort on control quadrats. However, the counts of individuals of *B. maxima* represent a more accurate measure of an ecological influence than the estimates of bare soil cover. Bare soil was negatively correlated with the survival of native seedlings from the 1991 cohort on control quadrats (also the 1992 cohort on mounds). This possibly indicates that barer areas do have an effect on seedling survival, by causing greater stress on seedlings through higher evapotranspiration over the summer months.

*Briza maxima* may be affecting native seedlings by competing for soil moisture. Soil water potential has been shown to be directly related to densities of annual grasses in pot experiments (Gordon & Rice, 1993). The phenology of native seedlings and *B. maxima* coincide—germination of both occurs in the late autumn and winter months. It is also possible that there is an allelopathic effect from *B. maxima* on the survival of native seedlings.

The results indicate that there is a strong interplay of factors causing mortality of native seedlings. Competition from exotics may be a factor, in some microsites and at certain times of the year, but other factors, such as density independent mortality (e.g. summer drought) and density dependent mortality may be more important in many years.

#### *Digging disturbance and Briza maxima density*

There was no evidence from the paired quadrats to suggest that the disturbance created by bandicoot digging was facilitating *B. maxima* invasion, at least not within the first three years of the formation of larger bandicoot diggings. The densities on mounds and holes were at no time higher than on the control areas, although the holes acted as a seed trap and had a *B. maxima* density akin to the controls after one year. The density of *B. maxima* was higher on the mounds than on the holes in the first year, presumably because the amount of seed stored in the soil which formed the mound was higher than at the depth of the holes (Chapter 7).

*Briza maxima* density was positively correlated with the amount of bare soil on the control quadrats but not on mounds. This indicates that it is

not just the availability of bare soil that is controlling *B. maxima* density on mounds. Perhaps the yearly germination of this species has a large component coming from the persistent soil seed bank, with only a fraction coming from the most recent input of seed from seed rain. If this is true, it may take much more than three years for the soil seed bank on bandicoot mounds to build up to the numbers that are present in the undisturbed areas (see Chapter 7 and later discussion). Another possibility is that the surface soil temperatures reached on mounds (Chapter 3) are lethal for *B. maxima* seeds. Temperatures of 34°C or greater have been found to be lethal for *B. maxima* seeds in laboratory trials (Rayner, 1989).

The relationship between disturbance, resource availability and weed invasion has been the subject of a number of papers by Hobbs and co-workers (Hobbs & Mooney, 1985; 1991; Hobbs & Atkins, 1988; Hobbs *et al.*, 1988; Hobbs, 1989; Hobbs & Huenneke, 1992). While soil disturbance has the capacity to encourage weed invasion, it may not do so unless levels of resources such as nutrients are increased (see also Heddle & Specht, 1975). In experiments from Western Australia, fertilisation rather than mechanical soil disturbance was more important for the invasion of some weed species, particularly in plant communities with very infertile soils (Hobbs & Atkins, 1988; Hobbs, 1989). Hobbs *et al.* (1988) found that gopher disturbance actually promoted native forbs over exotics in the absence of fertilisation. Hobbs (1989) predicted that echidna disturbances would not enhance invasion, because they do not increase nutrient availability. Hobbs (1989) also predicted that rabbit scrapings would enhance weed invasion because they are associated with the fertilization effect of faeces.

The greater weediness of rabbit scrapings compared with bandicoot diggings is readily discernible at Bellerive, reflecting the difference in nutrient availability. The nutritional impoverishment of bandicoot digging mounds compared with undisturbed areas (Chapter 3) may be a factor limiting the success of *B. maxima* on the considerable bare soil available on these areas (Chapter 5). It is of course possible that all three of the hypotheses mentioned thus far are operating to keep mounds free of *B. maxima*, i.e. less soil stored seed, lethal soil temperatures and low nutrient availability.



The question still remains, however, as to why *B. maxima* is so abundant and widely distributed in this vegetation. Perhaps disturbance associated with earlier management of the area is responsible, for example, heavy grazing, trampling and nutrient input from cattle. Alternatively, perhaps the *smaller* bandicoot diggings facilitated the invasion of *B. maxima*. All the data presented in this chapter have involved larger mounds formed from bandicoot diggings of at least 15 cm depth. Shallower diggings which produce smaller mounds are likely to have a very different effect on weeds. The majority of diggings are less than 3 cm deep (from Figs 3.2 and 4.4a) and create bare ground without reducing nutrient levels or burying seed to any appreciable extent. In fact, there is evidence from other data that areas with numerous smaller diggings are associated with higher densities of the exotic species *B. maxima*, *Aira* spp. and *Silene gallica* (Chapter 4). Finally, it is possible that smaller diggings acted as 'invasion nuclei' initially and *B. maxima* has subsequently spread out so widely in the rest of the community that digging disturbance is no longer important.

#### *Hand weeding of Briza maxima*

The *B. maxima* removal experiment indicated that hand weeding will more than halve the density of individuals that reach reproductive maturity in the following year. The linear regression indicated that the reduction was uniform across the range of densities of *B. maxima* present in the quadrats receiving the removal treatments (i.e. 0 to  $\approx 1100$  flowering individuals  $m^{-2}$ ). If this was a typical year, these data indicate that nearly 50% of the yearly germinants may come from the persistent soil seed bank, with the balance coming from the most recent year's seed rain. The seed bank figure could actually be smaller than this, because it is not known how effective the experimental design was in stopping seed rain from falling on the core areas of the quadrats. However, the linear relationship (Fig. 8.5a) would presumably be much weaker if a substantial component was drawn from seed rain from a much larger area.

The removal of *B. maxima* in the second year apparently had no impact on the densities in these plots; in fact they increased on the previous year's

level. It is not possible to determine whether this increase was a result of unwanted input from seed rain or increased germination from the persistent soil seed store. Strong wind conditions at a critical time may have increased the distances that dispersing seed could cover, thus thwarting the attempt to stop seed rain on the core areas of the quadrats which received the removal treatments. It seems improbable that the persistent seed bank could alone produce more seedlings in 1992 than in 1991, if no new input of seed had been received since December 1989/January 1990. However, the longevity of viable *B. maxima* seed in the soil is not known and 1992 appeared to be the best year for this species on control areas (Figs 8.2, 8.4).

Therefore, the experimental design may have been unable to identify the true level of germination from the persistent seed bank in the second year, or perhaps even the first. Despite this, there is good evidence from other data to indicate that a persistent store does exist for *B. maxima*. A substantial amount of seed germinated in the glasshouse from soil collected in November 1990 (Chapter 7). An autumn germinating species with a transient seed bank would be expected to have no seed in the soil by November (Thompson & Grime, 1979). The data do suggest that hand pulling can reduce *B. maxima* density considerably, and that the soil disturbance created by pulling does not itself facilitate germination of this species. However, the results indicate the importance of long-term monitoring of this kind of experiment and the need to repeat treatments over a sufficient number of years, because of the large year to year variation in results.

### Conclusion

*Briza maxima* appears to be having an effect on the survival of native seedlings at Bellerive on sandstone. The data suggest that rather than encouraging *B. maxima* invasion and consequently the out-competing of native seedlings, larger diggings may be acting as refuges for the establishment of native species by providing areas with reduced *B. maxima* density. There is still some evidence, however, that smaller diggings are encouraging exotic species.

## Chapter 9

### Synthesis and Conclusions

#### Microscale succession and plant growth on simulated and natural diggings

A common theme which emerges from all of the various studies in this thesis is that the colonisation of animal disturbances in drier forests and woodlands in Tasmania is a very slow process. At Bellerive, bandicoot digging mounds had very little cover of recruits, even three years after their formation. Similarly slow colonisation was evident on natural animal disturbances at Hospital Creek and on artificial disturbances at the Old Coach Road and Tunbridge Tiers Road. At Annandale, faster colonisation was completely attributable to exotic annual species and not to the native flora. The small amount of biomass of native species which did develop on animal disturbances was largely attributable to vegetative recovery from underneath mounds. Establishment from seedlings was negligible for many species because of high mortality (e.g. *Lepidium hyssopifolium* at Annandale; and *Wahlenbergia stricta*, *Helichrysum apiculatum* at Bellerive), or else growth was very slow and individuals were years away from reproductive maturity (e.g. *Odixia achlaena* at Hospital Creek; *Velleia paradoxa* at Bellerive; and *Lasiopetalum micranthum* at the Old Coach Road).

The dynamics on small-scale animal disturbances in Tasmania are very different from some described in the literature. Platt (1975) found that equilibrium plant communities developed on badger mounds after an initial non-interactive period of less than a year. The species composition of the plant associations which developed on the mounds was a result of interspecific interactions. Collins (1989) found that small-scale disturbances were colonised completely within two years in an Oklahoma tallgrass prairie. Watt (1974) described succession on mole hills in a chalk grassland, where the initial colonists (mostly annuals) were replaced by perennial forbs which were in turn out-competed by perennial grasses.

At the Bellerive study site, if microscale succession does occur on bandicoot digging mounds, the rate is too slow to be observed over a three

year period. In fact, even the process of initial colonisation was too slow to be observed over the three years of this study, although such colonisation may be more rapid in years with better climatic conditions. Disturbances eventually become obscure in the landscape, which limits the capacity to identify successional patches, even if they do exist. I suggest that successional sequences of floristic replacement do not actually exist on bandicoot and bettong diggings, although this not to say that these disturbances are not having an influence on community dynamics.

The slow rate and/or intermittent nature of seedling establishment and slow rate of plant growth on diggings meant that in most cases, biological attributes of established plants on disturbed and undisturbed microsites could not be compared. For example, in other studies, plants have been found to have improved growth and reproduction on digging mounds compared with undisturbed areas as a result of reduced competition (e.g. Hobbs & Mooney, 1985; Martinsen *et al.*, 1990). *Lepidium pseudotasmanicum* at the Rosny study site reached reproductive maturity on disturbances within 12 months, but insufficient seedlings survived in undisturbed areas to make statistical comparisons of growth and reproduction. There were no differences in growth rate for *Odixia achlaena* or *Dodonaea filiformis* at Hospital Creek, but sample sizes may again have been limiting. *Crassula sieberana* did flower on some digging mounds at Bellerive, but dispersal and senescence of this diminutive annual species occurred too rapidly to be measured.

### Germination on simulated and natural diggings

A conspicuous similarity to other studies which have examined small-scale disturbances, is the life-history characteristics of many of the plant species which germinated more prolifically on digging mounds. Both annuals (e.g. *Crassula sieberana*) and short-lived perennials (e.g. *Senecio* spp.) were found, which has been a common finding elsewhere (Watt, 1974; Platt, 1975; Bonham & Lerwick, 1976; Burggraaf - van Nierop & van der Meijden, 1984; Collins, 1989; Gibson, 1989). In other studies, these have been labelled as 'fugitive' species which are often unable to germinate in undisturbed areas (e.g. Platt, 1975).

Longer-lived perennials such as *Wahlenbergia stricta*, *Vittadinia muelleri* and *Helichrysum apiculatum* germinated more prolifically on soil disturbances. These species also have characteristics, such as small-seededness and a light requirement for germination (as does *C. sieberana*), which are recognised as disturbance-dependent or weedy traits (Grime, 1979; Gross, 1984; McIntyre, 1990). However, in the unproductive environment at Bellerive, the conditions suitable for the germination of these species were not unique to disturbance mounds, so the advantage was a matter of degree rather than kind (cf. Watt, 1974; Platt, 1975). Several species which germinated in greater densities on diggings compared with undisturbed areas appear to respond simply to the availability of bare soil, since there is a relationship between bare soil and seedling density, exclusive of diggings (e.g. *Crassula sieberana*, *Helichrysum apiculatum*, *Wahlenbergia stricta*).

*Lepidium* species are small-seeded and dependent on soil disturbance for germination in the absence of adult plants. Although the light requirements for germination have not been tested in the laboratory, the results of the Bagdad experiment suggest that seeds only germinate when exposed to light. The germination densities of *L. hyssopifolium* were similar on and off diggings at Annandale, but this was in a situation where seed rain was continuous for much of the year. In such circumstances, providing no other dormancy mechanism is present, seeds can presumably germinate immediately if soil moisture conditions are suitable. Germinated seeds would then not move beyond the surface zone.

Generally, species with larger seeds did not germinate more prolifically on soil disturbances. This reflects the larger energy store in the seed, a lack of a light requirement for germination and therefore an ability to germinate under litter. Examples of these species include *Arthropodium milleflorum*, *Bulbine glauca*, *Brunonia australis* and *Stackhousia monogyna*. Field data for these species come from my study and the germination requirements have been tested in the laboratory (Hitchmough *et al.*, 1989; McIntyre, 1990; Willis & Groves, 1991). *Velleia paradoxa* was a notable exception to this schema, with better germination on diggings, a light requirement for germination and very large seeds. The reason for this anomaly is not known, but a large reserve of



energy in the seed and an ability to utilise gaps are very useful traits for this species, because it often grows in dense grassy swards. *Lasiopetalum micranthum* is another exception, but as a hard-seeded species, it may represent another group of species which is able to benefit from solar heating of bare soil to break dormancy.

The time of year when a particular disturbance was formed has been found to determine which species were the most successful colonists in an annual grassland (Hobbs & Mooney, 1985). Because diggings remain bare for so long, the time of year in which they are formed is probably not a critical factor in Tasmania. Many plant species will utilise the resource by germinating from seed rain which has fallen well after the diggings were formed. The timing of digging may be important for the germination of seed brought to the surface, if this seed germinates readily as soon as moisture conditions are suitable. Digging was generally more prolific in the winter months, which is the time when most seedlings emerge.

### Survival of seedlings on simulated and natural diggings

Conditions suitable for germination represent one component of the regeneration niche (Grubb, 1977) or safe site (Harper, 1977). The next stage is an ability to survive after germination and this will depend on the environmental conditions of a given microsite. Microsites created by animal disturbances have been shown to provide better conditions for seedling survival for some species in some circumstances (e.g. Gutterman, 1988 cited in Gutterman *et al.*, 1990; Hobbs & Mooney, 1985), or worse in others (e.g. Reichman, 1988).

The abundance of litter was one of the environmental factors which was found to affect early seedling survival in my study. The amount of litter on digging mounds was lower compared with undisturbed areas, but holes acted as litter traps and had more litter than undisturbed areas in some circumstances. Survivorship has again been found to be both favoured (e.g. Fowler, 1986) and disfavoured (e.g. Fowler, 1988; Pierson & Mack, 1990) with increasing litter cover. The effect of litter will depend on whether it reduces desiccation of seedlings by helping to retain soil moisture, or increases

mortality by preventing roots from reaching moister soil or by causing damping off (Fowler, 1988).

To summarise these effects, the importance of survival success of seedlings on microsites provided by animal diggings, relative to undisturbed areas, depends primarily on three factors: the size of the seed of the species in question; the degree of competition exerted in the undisturbed vegetation; and physical differences (e.g. soil moisture, fertility and temperature) if these are important relative to competition (Gross & Werner, 1982; Goldberg & Werner, 1983; Gross, 1984; Ryser, 1993). Larger-seeded species will be more resilient to differences in both abiotic and biotic factors compared with smaller-seeded species.

It is not surprising, therefore, that a variety of survival responses was found in this thesis, with the range of species and environments under study. There was evidence of survival being worse on undisturbed areas compared with digging mounds because of the effect of greater litter cover isolating roots from the soil (e.g. *Lepidium hyssopifolium* at Annandale). Deeper litter on holes possibly had a damping off effect on *Odixia achlaena* seedlings at Hospital Creek, thus causing higher mortality. The greater litter cover in undisturbed areas relative to digging mounds at Bellerive appeared to cause better survival percentages, particularly amongst small-seeded species, presumably because the soil was moister. Survival of one large-seeded species was unrelated to litter cover or disturbance microsite (*Velleia paradoxa* at Bellerive), while a small-seeded species appeared only to be affected at certain times of the year (e.g. *L. hyssopifolium* at Annandale).

In my study, survivorship was mostly assessed in situations where competitive effects in the undisturbed vegetation appeared to be small compared with the influence of the physical environment; hence litter cover is important. These environments have infertile and unproductive soils and the understorey cover is discontinuous (e.g. Bellerive, Annandale). Study sites on dolerite are more productive environments and small-scale disturbances in these areas may be expected to provide relief from competition from the dominant grasses (*Poa rodwayi* and *Themeda triandra*). The seedlings of *Lasiopetalum micranthum* appear to benefit from this relief. Seedlings of the



small-seeded *Vittadinia muelleri* at the Tunbridge Tier Road on dolerite may also be expected to survive better on simulated diggings in comparison with those amongst the undisturbed sward, but survivorship was not recorded.

In the three years of the study, the survival rate of seedlings of many species was extremely low, regardless of microsite differences. This low rate may or may not be typical of most years, as discussed in Chapter 5. There are many fluctuating variables which produce different conditions from year to year, including rainfall, temperature, wind, fire, predation and grazing. These variables may converge in the occasional year to produce conditions suitable for the germination and establishment of certain species. Fluctuations in the populations of digging mammals and consequential changes in digging frequency may also be one of those factors.

There may be species from this study which have a syndrome of establishing in the occasional year, but for which a good year was not sampled. Examples include *Helichrysum apiculatum*, *Wahlenbergia stricta*, *Scleranthus biflorus* and *Senecio* spp. at Bellerive and *Lepidium hyssopifolium* at Annandale. It is difficult to make definitive conclusions on the importance of diggings for these species. All had either higher levels of germination or very short-term survival on diggings compared with undisturbed ground, but ultimately, little or no survival on either. While there is some evidence that diggings are important for the regeneration of these species from seed, the data are not conclusive because the ultimate measure that counts is the number of individuals which become reproductive adults.

It is conceivable that for some small-seeded species at Bellerive higher mortality on diggings may neutralise the advantage of greater emergence densities, in a play-off between lower soil moisture and fertility on the one hand and better light conditions for germination on the other. The balance of this play-off could only be determined by examining survivorship over a sufficient number of years to encompass the range of rainfall variability. Survival prospects of seedlings on digging mounds are probably better if they have survived the first summer and roots have penetrated to the undisturbed soil profile below the mound. Other studies have identified the lack of net advantage of gaps (Ryser, 1993) or animal disturbances

(Novoplansky, 1984 reported in Heth, 1991) because of the worsening of drought effects in such areas.

One possible advantage provided by diggings for native seedlings is relief from competition from weeds. There is evidence from this study that larger digging mounds at Bellerive remain relatively free of cover of the exotic *Briza maxima* for several years. There is also evidence that this weed is responsible for early mortality of native seedlings. This of course presupposes that the native seedlings in question are capable of surviving on diggings in at least some years, as discussed above. The reasons why the density of *B. maxima* is lower on larger digging mounds are not clear, but may be related to the predisposition that exotics have for nutrient-rich soils (Heddle & Specht, 1975; Hobbs, 1989). Smaller diggings on nutrient-poor soils may not have the same resource-limiting effect, because the mounds have a higher fertility than those associated with larger diggings. Similarly, disturbances of all sizes on the more fertile dolerite soils may not be too infertile for the establishment of exotic species.

#### A comparison of fire and mechanical soil disturbance

My data indicate that a bare soil surface is critical for the germination of many native species in dry forests in Tasmania, even on infertile soils which tend to be less productive and have a discontinuous ground cover of plants. The exact means by which the bare ground is created may not in itself be very important, except that different natural mechanisms such as fire and animal disturbance tend to have a very different total impact on the community. Fire tends to affect an entire area at once, removing large amounts of biomass and litter. A relatively rapid recovery of ground cover takes place after fire, particularly on fertile soils or if tree-scorch causes leaf fall. In contrast, digging by mammals tends to occur in small patches within the community and diggings tend to stay bare for much longer than burnt areas.

A group of species is probably favoured by both kinds of disturbance (e.g. *Velleia paradoxa*, *Helichrysum apiculatum*, *Wahlenbergia stricta*, *Crassula sieberana*, *Senecio* spp.), but digging will often provide more years per disturbance patch in which the bare surface is available. Thus, diggings provide

a regeneration niche which is abundant in time, but limited in space, and fire provides a regeneration niche which is abundant in space, but limited in time. However, fire is probably a more important agent of disturbance because more ground surface is exposed overall. For example, the Bellerive site on sandstone currently has a burning frequency of 3-8 years. Assuming that an 80-90% bare surface is only present after fire for one year, this still produces more bare ground than the digging frequency of 2.9% per year. On dolerite at the Old Coach Road, the closure rate after fire is much faster, but probably still creates more bare ground, even by the time that seed produced post-fire is able to germinate, than the extremely low digging rate at this site. Given the sporadic nature of seedling germination density and survival on a year to year basis, both mechanisms may tend to enhance recruitment when the availability of the niche coincides with suitable climatic conditions.

Fire disturbance and animal disturbance are only analogous to a certain extent and where they differ is in the degree of soil heating, but this may only apply to fires of moderate or greater intensity. There is evidence from this study that mechanical soil disturbance will enable solar soil heating to occur to the same temperatures as a low intensity fire (Scotter, 1970; Raison *et al.*, 1986; Auld & O'Connell, 1991). Thus, animal disturbance is sufficient to enable germination of some hard-seeded species such as *Lasiopetalum micranthum*. However, even for hard-seeded species that will germinate at temperatures generated by solar soil heating on diggings (i.e. 60°C), the responses and therefore the maintenance of populations may be better after hotter fires (Auld & O'Connell, 1991). The data in this thesis suggest that this may be true for *L. micranthum*. Some hard-seeded species will not germinate at all at the temperatures induced by solar heating, because they require higher temperatures (Auld & O'Connell, 1991). Other species, such as *Odixia achlaena*, require higher soil temperatures to break other kinds of dormancy mechanisms and their germination will not benefit from animal disturbance.

In environments where both fire and animal disturbance are common, the combination of regenerative opportunities will enhance regeneration prospects and species richness (Collins & Barber, 1985; Gibson, 1989).

## Influence of trees on the spatial patterns of digging and understorey

Most of my study sites are woodlands or open forests, thus distinguishing them from the treeless communities of many other studies which have examined the effects of small-scale animal disturbance on vegetation. Trees are another variable that must be considered, because the spatial distribution of both understorey and diggings are influenced by trees in Tasmania, at the scale related to tree size and density (Chapter 4; Robertson, 1985; Taylor, 1992a; Chris Johnson, pers. comm.). The influence of trees is certainly a direct one, where the purpose of digging is to extract sporocarps of hypogeal fungi growing along tree roots (Claridge *et al.*, 1993a). Trees will also have an influence on the species composition of the understorey, because of shading and reduction of soil moisture relative to inter-canopy gaps (Chapter 3; Ian Lunt, pers. comm., Robertson, 1985; Vetaas, 1992).

The question remains as to whether or not trees have an indirect influence on understorey composition, via the effect of a small-scale disturbance regime which is determined by the trees. This is a chicken and egg problem which is difficult to resolve. *Lepidium hyssopifolium* is only found beneath tree canopies at the Annandale study site, where animal disturbances are similarly distributed. But in other places, this species is found only beneath canopies, even when animal diggings are absent. Therefore the relationship probably does not depend on diggings, although it may well be reinforced by them.

The larger winter bandicoot diggings at Bellerive tend to be spatially associated with trees, while smaller diggings and those dug in the summer months show no such association. The understorey composition is strongly affected by trees, with the maximum alpha diversity occurring at intermediate levels of tree influence. Therefore, diggings are to be found across the full range of understorey variation, from the middle of large canopy gaps to directly under canopies, but with an apparent peak of digging frequency which tends to be close to trees, but possibly not at minimum distances. The understorey diversity was higher where digging appeared to be most intense, although this was not established directly. This relationship may, however, be coincidental because higher diversity in this 'halo' zone has been reported

in similar vegetation in the complete absence of any native animal digging (Robertson, 1985).

Of the individual species which were found to have a higher density of seedlings emerging on diggings, only one occurs solely in the higher tree influence zone—*Wahlenbergia stricta*. Other species which also germinated preferentially on diggings were found across the full range of tree influence, and therefore of understorey variation and digging intensity (e.g. *Helichrysum apiculatum*, *Velleia paradoxa*). Therefore, while diggings increase the germination potential of these species, this is not then manifest as a spatial association, as might be expected if the relationship were one of at least some degree of dependence. If such a relationship does exist for any individual species, it was not identified in this study. For many species at Bellerive, however, the sampling was probably not intense enough to be conclusive.

The Bellerive data highlight that, in a woodland, the availability of the animal disturbance niche is not equal for all understorey plant species. The propensity for diggings to be located near trees is even stronger in places with bettong and potoroo diggings, in comparison with those areas which have only bandicoot diggings.

### Digging intensity and soil fertility

The intensity of digging, in other words the percentage of ground surface which is turned over each year, will have a large bearing on how relevant such disturbance is to the population dynamics of plant species, that is, to those species whose establishment will benefit from such disturbance. The intensity of digging is relatively high on soils formed from sedimentary parent materials such as sandstone, mudstone and alluvium. Such soils are relatively nutrient-poor in this study. More productive soils, such as those formed on dolerite or basalt, tend to have considerably lower digging intensities. It has been suggested that an inverse relationship between growth rates of mycorrhizal fungi and soil fertility may be responsible for this trend in digging intensity (Taylor, 1992a). However, bandicoots do not dig exclusively for hypogeal fungi and the looseness of the soil may be another

factor (Taylor, 1992a). The loose soils formed on granite in eastern Tasmania also have high levels of bettong digging.

An interesting aspect of the fertility/digging relationship is the implication for disturbance-related seedling establishment. Plant competition is greater on more productive soils, therefore gaps created by digging are more important for the establishment of less competitive plant species than they are on less productive soils. But the gaps created by animal disturbance are less frequent in the more productive and competitive environments. However, the fewer gaps that are created on more fertile soils are still of benefit for seedling establishment and are intense locally. There is also evidence that soil disturbance created by indigenous Australians, while digging up underground storage organs of plants, may have once been prolific, even on fertile soils (Gott, 1982; 1983). Therefore, mechanical soil disturbance may once have been a more prominent feature of grasslands, woodlands and open-forests on dolerite soils.

### Digging and soil stored seed

Digging may play an important role in bringing soil stored seed to the surface. In this study, this was not tested by directly sampling from newly formed mounds, but the seed store at various soil depths was described for a wide range of species. Bandicoot diggings effectively invert the soil profile. Several species have seed stored at depth in the soil which will be more likely to germinate at the surface of a digging mound (e.g. *Lasiopetalum micranthum*, *Lepidium hyssopifolium*, *Wahlenbergia stricta*). The relevance of this process for population dynamics will depend on the relative contribution to recruitment made by fresh seed rain compared with seed 'recovered' from depth by digging.

This recovery may be of particular benefit for plant species which are myrmecochorous. This is because seeds can be rapidly removed by ants to nests at depths where germination is unlikely to occur (Auld, 1986a; Westoby *et al.*, 1991). The recovered seeds will have had the elaiosome removed, thus removing their attractiveness for disperser ants (Westoby *et al.*, 1991). Larger seeds will be unlikely to move back down the soil profile by gravity (Thompson



*et al.*, 1993), but the principle of recovery should provide some benefit for species with smaller seeds. This benefit may be improved for species with a fire-related dormancy mechanism by the passage of a fire soon after digging, but some such species (e.g. *L. micranthum*) may benefit without a fire, as discussed earlier.

There are many myrmecochorous species in the floras of grasslands, woodlands and dry forests of south-eastern Australia (Berg, 1975), and many of these have hard, large seeds. All known myrmecochorous species have persistent seed banks (Thompson *et al.*, 1993). Although the discussion here is largely speculative, it is likely that research aimed specifically at myrmecochorous species in areas where digging is prolific will find that a relationship exists between the two. A prediction would be that in areas where digging is associated with tree roots, some myrmecochorous species will display a similar spatial pattern (this thesis did not focus specifically on these questions and the sampling strategies targeted rare species rather than myrmecochorous species *per se*). It is interesting that ant-dispersed plant species are more prevalent on infertile soils (Westoby *et al.*, 1991), which is where diggings are also more frequent in Tasmania.

## Conclusions

*Can a guild of species be recognised which is adapted to colonise mammal diggings and do these species have common attributes (i.e. strategies)?*

The evidence suggests that the germination and/or establishment of some species may be enhanced by disturbance caused by mammal digging. A group of these species seem to be characterised by having small seeds, with larger-seeded species generally not showing any response to diggings. There were exceptions to this generalisation and hard-seeded species, which often have larger seeds, may be another group which benefits from the bare soil created by mammal digging. This last supposition has been demonstrated experimentally for one species (*Lasiopetalum micranthum*), but not with real mammal diggings.



*Are some plant species rare because of a dependence on a specialised regeneration niche which involves animal disturbance?*

There are no examples from this study of species which are dependent exclusively on the disturbance created by small mammals to enable them to regenerate from seed. Therefore, in the typology of rarity of Rabinowitz (1981), there are no examples of species which are widespread but constantly sparse because of a dependence on animal disturbance. However, even if such species do not exist, the regeneration from seeds of many species will be enhanced by such disturbance (e.g. *Lepidium hyssopifolium*, *L. pseudotasmanicum*, *Velleia paradoxa*, *Lasiopetalum micranthum*).

For specific sites, animal disturbance may be important in the population dynamics of some species because other disturbances (such as fire) have not been of appropriate intensity or frequency. Animal disturbance has the potential to resurrect some populations of some species from soil stored seed when adults or seed rain are no longer present (e.g. *Lepidium hyssopifolium*).

*How important is animal disturbance for plant species in Tasmania?*

The extent of the enhancement of regeneration of plant species will largely be determined by the frequency of digging in the habitats of these species. For example, digging probably does provide a regeneration niche for *Lasiopetalum micranthum*, but the overall digging rate in the habitat of this species is very low. Therefore digging is probably not as important overall for this species, relative to other disturbances such as fire.

Digging is more importance for species such as *Velleia paradoxa*, *Lepidium hyssopifolium*, *Helichrysum apiculatum* and *Wahlenbergia stricta*. However, it is not possible to conclude from these data what percentage of the total recruitment to the breeding population occurs on diggings, because establishment was generally very limited over the period of the study. The data suggest that there are many species which appear to have the potential to benefit from digging disturbance.

## Recommendations for future research

This study provided many snippets of data which suggest the importance of digging disturbance for maintaining populations of both rare and common plant species, but did not provide definitive evidence. There is good reason to continue to pursue this research, particularly for those plant species which appear to benefit from digging. The true importance of digging disturbance may yet be revealed and become recognised as an ecological process that must be considered in conservation management.

The results indicate how difficult it can be to get meaningful ecological answers within a limited time, because of the fluctuations of climate and other factors. Future study can concentrate on the species identified here as being suitable, but monitoring must be spread over many more years. A strategy which is appropriate for a site such as Bellerive is give as follows:

(a) Set up a series of random permanent plots, not associated with digging disturbance, to monitor the year to year variation in seedling establishment. These plots need only be sampled twice a year in late winter (to map new germinants so that they can be recognised as such later) and late summer (to pick up survivors after the summer soil moisture deficit). Only map specific target species (e.g. *Velleia paradoxa*, *Helichrysum apiculatum* and *Wahlenbergia stricta*).

(b) Establish a new set of permanent quadrats over randomly selected new diggings every year in early autumn. Map seedlings twice a year as above. Permanent plots over diggings can be abandoned after a set number of years (perhaps three) to maintain a constant total number.

It is only from this kind of sampling strategy, over at least 10 years, that it can be determined whether diggings are important in the long term, or only under the occasional set of coincident conditions.

The issue of small scale soil disturbance being applied as a management tool in grasslands and grassy woodlands needs further investigation. There are several important questions here. First, in which situations will such disturbance also encourage weeds and in which ones will it not? Experiments comparing the importance of disturbances on sites of differing productivity

could be tied in here. A closely related question is what disturbance design (i.e. depth, size) will favour natives over exotics? Second, in which situations does it need to be applied at all? It is also worth following up the work on *Briza maxima* and *Aira* spp. to see if smaller animal disturbances are helping maintain the populations of these species, and are therefore likely to thwart weed control efforts.

Another area of future study is to examine the effects of digging on the physical and chemical properties of soils of varying fertility and texture. Only one reasonably infertile soil type was examined in this study — more fertile clay soils may have very different characteristics after disturbance. Also, the dynamics of soil moisture and temperature over various time scales could be investigated by data-logging on and off disturbances. In relation to digging disturbance, such research is a more academic topic which need only follow work that substantiates the importance of diggings to plant population dynamics. However, it has more general application for understanding the 'window' of suitable soil moisture and temperature conditions for the establishment of seedlings.

Finally, the question of whether digging brings seed of myrmecochorous species to the surface may be worth pursuing, perhaps in conjunction with burning experiments.

## References

- Aarssen, L.W. & Epp, G.A. (1990) Neighbour manipulations in natural vegetation: a review. *J. Veg. Sci.* **1**, 13-30.
- Armesto, J.J. & Pickett, S.T.A. (1985) Experiments on disturbance in old-field plant communities: Impacts on species richness and abundance. *Ecology* **66**, 230-240.
- Augee, M.L. (1983) Short-beaked echidna. *Complete book of Australian mammals*. (ed. by R. Strahan), pp. 8-9. Angus & Robertson, London.
- Auld, T.D. (1986a) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Dispersal and the dynamics of the soil seed-bank. *Aust. J. Ecol.* **11**, 235-254.
- Auld, T.D. (1986b) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Fire and the transition to seedlings. *Aust. J. Ecol.* **11**, 373-385.
- Auld, T.D. & O'Connell, M.A. (1991) Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Aust. J. Ecol.* **16**, 53-70.
- Barker, P.C.J. (1992) Autecology of *Phyllocladus* and *Anodopetalum* in Tasmania. Tasmanian NRCP Technical Report No. 10. Forestry Commission, Tasmania, and Dept. of the Arts, Sport, Env., Tourism and Territories, Canberra.
- Battaglia, M. & Reid, J.B. (1993) The effect of microsite variation on seed germination and seedling survival of *Eucalyptus delegatensis*. *Aust. J. Bot.* **41**, 169-181.
- Beadle, N.C.W. (1940) Soil temperatures during forest fires and their effect on the survival of vegetation. *J. Ecol.* **28**, 180-192.
- Belsky, A.J. (1986) Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. I. Colonization of grazed and ungrazed plots. *J. Ecol.* **74**, 419-437.
- Bennett, A.F. & Baxter, B.J. (1989) Diet of the long-nosed potoroo, *Potorous tridactylus* (Marsupialia: Potoroidae), in south-western Victoria. *Aust. Wildl. Res.* **16**, 263-271.
- Benoit, D.L., Kenkel, N.C. & Cavers, P.B. (1989) Factors influencing the precision of soil seed bank estimates. *Can. J. Bot.* **67**, 2833-2840.
- Berg, R.Y. (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Aust. J. Bot.* **23**, 475-508.

- Bonham, C.D. & Lerwick, A. (1976) Vegetation changes induced by prairie dogs on shortgrass range. *J. Range Management* **29**, 221-225.
- Briggs, J.D. & Leigh, J.H. (1988) *Rare or threatened Australian plants*. Australian National Parks and Wildlife Service Special Publication No. 14., Canberra.
- Buchanan, A.M., McGeary-Brown, A. & Orchard, A.E. (1989) *A census of the vascular plants of Tasmania*. Tasmanian Herbarium occasional publication No. 2., Hobart.
- Buchanan, R.A. (1989) *Bush regeneration : recovering Australian landscapes*. TAFE Student Learning Publications, Sydney.
- Burggraaf - van Nierop, Y.D. & van der Meijden, E. (1984) The influence of rabbit scrapes on dune vegetation. *Biol. Conserv.* **30**, 133-146.
- Calder, D.M., Cropper, S.C. & Tonkinson, D. (1989) The ecology of *Thelymitra epipactoides* F.Muell. (Orchidaceae) in Victoria, Australia, and the implications for management of the species. *Aust. J. Bot.* **37**, 19-32.
- Carson, W.P. & Pickett, S.T.A. (1990) Role of resources and disturbance in the organization of an old-field plant community. *Ecology* **71**, 226-238.
- Chambers, J.C., MacMahon, J.A. & Haefner, J.H. (1991) Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. *Ecology* **72**, 1668-1677.
- Claridge, A.W. (1992) Comment: is the relationship among mycophagous marsupials, mycorrhizal fungi and plants dependent on fire? *Aust. J. Ecol.* **17**, 223-225.
- Claridge, A.W., Robinson, A.P., Tanton, M.T. & Cunningham, R.B. (1993a) Seasonal production of hypogaeal fungal sporocarps in a mixed-species eucalypt forest stand in south-eastern Australia. *Aust. J. Bot.* **41**, 145-167.
- Claridge, A.W., Tanton, M.T. & Cunningham, R.B. (1993b) Hypogaeal fungi in the diet of the long-nosed potoroo (*Potorous tridactylus*) in mixed-species and regrowth eucalypt forest stands in south-eastern Australia. *Wildl. Res.* **20**, 321-337.
- Claridge, A.W., Tanton, M.T., Seebeck, J.H., Cork, S.J. & Cunningham, R.B. (1992) Establishment of ectomycorrhizae on the roots of two species of *Eucalyptus* from fungal spores contained in the faeces of the long-nosed potoroo (*Potorous tridactylus*). *Aust. J. Ecol.* **17**, 207-217.
- Collins, S.L. (1987) Interaction of disturbances in tallgrass prairie: A field experiment. *Ecology* **68**, 1243-1250.

- Collins, S.L. (1989) Experimental analysis of patch dynamics and community heterogeneity in tallgrass prairie. *Vegetatio* 85, 57-66.
- Collins, S.L. & Barber, S.C. (1985) Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64, 87-94.
- Cox, D.R. & Oakes, D. (1984) *Analysis of survival data*. Chapman and Hall, London.
- Cropper, S. (1987) Ecological notes and suggestions for conservation of a recently discovered site of *Lepidium hyssopifolium* Desv. (Brassicaceae) at Bolwarrah, Victoria, Australia. *Biol. Conserv.* 41, 269-278.
- Culver, D.C. & Beattie, A.J. (1980) The fate of *Viola* seeds dispersed by ants. *Amer. J. Bot.* 67, 710-714.
- Daubenmire, R. (1968) *Plant communities*. Harper & Row, New York.
- Davis, M.A., Villinski, J., Banks, K., Buchman-Fifield, J., Dicus, J. & Hofmann, S. (1991a) Combined effects of fire, mound-building by pocket gophers, root loss and plant size on growth and reproduction in *Penstemon gradiflorus*. *Am. Midl. Nat.* 125, 150-161.
- Davis, M.A., Villinski, J., McAndrew, S., Scholtz, H. & Young, E. (1991b) Survivorship of *Penstemon gradiflorus* in an oak woodland: combined effects of fire and pocket gophers. *Oecologia (Berlin)* 86, 113-118.
- Dean, W.E. (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *J. Sediment. Petrol.* 44, 242-248.
- Driessen, M.M., Hocking, G.J. & Beukers, P. (1990) *Habitat, conservation status and management of the Tasmanian bettong, Bettongia gaimardi*. Department of Parks, Wildlife and Heritage, Hobart.
- Espigares, T. & Peco, B. (1993) Mediterranean pasture dynamics: the role of germination. *J. Veg. Sci.* 4, 189-194.
- Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57-68.
- Fensham, R.J. (1989) The pre-European vegetation of the Midlands, Tasmania: a floristic and historical analysis of vegetation patterns. *J. Biogeog.* 16, 29-45.
- Fensham, R.J. & Kirkpatrick, J.B. (1989) The conservation of original vegetation remnants in the Midlands, Tasmania. *Pap. Proc. R. Soc. Tasm.* 123, 229-246.



- Fowler, N.L. (1986) Microsite requirements for germination and establishment of three grass species. *Am. Midl. Nat.* **115**, 131-145.
- Fowler, N.L. (1988) What is a safe site?: neighbour, litter, germination date, and patch effects. *Ecology* **69**, 947-961.
- Gibson, D.J. (1989) Effects of animal disturbance on tallgrass prairie vegetation. *Am. Midl. Nat.* **121**, 144-154.
- Gilfedder, L. & Kirkpatrick, J.B. (1993) Germinable soil seed and competitive relationships between a rare native species and exotics in a semi-natural pasture in the midlands, Tasmania. *Biol. Conserv.* **64**, 113-119.
- Gill, A.M. & Groves, R.H. (1981) Fire regimes in heathlands and their plant-ecological effects. *Ecosystems of the World 9B. Heathlands and related shrublands*. (ed. by R.L. Specht), pp. 61-84. Elsevier, Amsterdam.
- Gill, A.M. & Nicholls, A.O. (1989) Monitoring fire-prone flora in reserves for nature conservation. *Fire management on nature conservation lands: proceedings of a national workshop, Busselton, Western Australia, October 1987*. (ed. by N. Burrows, L. McCaw & G. Friend), pp. 137-151. Department of Conservation and Land Management, Perth, WA.
- Goldberg, D.E. & Gross, K.L. (1988) Disturbance regimes of midsuccessional old fields. *Ecology* **69**, 1677-1688.
- Goldberg, D.E. & Werner, P.A. (1983) The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia (Berlin)* **60**, 149-155.
- Gordon, D.R. & Rice, K.J. (1993) Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* **74**, 68-82.
- Gott, B. (1982) Ecology of root use by the Aborigines of southern Australia. *Archaeology in Oceania*. **17**, 59-67.
- Gott, B. (1983) Murnong-*Microseris scapigera*: a study of a staple food of Victorian Aborigines. *Aust. Aboriginal Studies* **2**, 2-18.
- Grime, J.P. (1979) *Plant strategies and vegetation processes*. John Wiley & Sons, Chichester.
- Gross, K.L. (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J. Ecol.* **72**, 369-387.
- Gross, K.L. (1990) A comparison of methods for estimating seed numbers in the soil. *J. Ecol.* **78**, 1079-1093.



- Gross, K.L. & Werner, P.A. (1982) Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology* 63, 921-931.
- Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107-145.
- Grubb, P.J. (1986) Problems posed by sparse and patchily distributed species in species-rich plant communities. *Community ecology* (ed. by J. Diamond & T.J. Case), pp. 207-225. Harper & Row, New York.
- Gutterman, Y. (1988) An ecological assessment of porcupine activity in a desert biome. *Ecophysiology of desert vertebrates*. (ed. by P.K. Ghosh & I. Prakash), pp. 289-372. Scientific Publishers, Jodhpur, India.
- Gutterman, Y., Golan, T. & Garsani, M. (1990) Porcupine diggings as a unique ecological system in a desert environment. *Oecologia (Berlin)* 85, 122-127.
- Harkness, R.D. & Isham, V. (1983) A bivariate spatial point pattern of ants' nests. *Appl. Statist.* 32, 293-303.
- Harper, J.L. (1977) *Population biology of plants*. Academic Press, London.
- Hedde, E.M. & Specht, R.L. (1975) Dark Island heath (Ninety-mile Plain, South Australia). VIII The effect of fertilizers on composition and growth, 1950-1972. *Aust. J. Bot.* 23, 151-164.
- Heinsohn, G.E. (1966) Ecology and reproduction of the Tasmanian bandicoots (*Perameles gunnii* and *Isodon obesulus*). *Univ. Calif. Publ. Zool.* 80, 1-96.
- Heth, G. (1991) The environmental impact of subterranean mole rats (*Spalax ehrenbergi*) and their burrows. *The environmental impact of burrowing animals and animal burrows. Symp. Zool. Soc. Lond. No. 63* (ed. by P.S. Meadows & A. Meadows), pp. 265-280. The Zoological Society of London, Oxford.
- Hitchmough, J., Berkeley, S. & Cross, R. (1989) Flowering grasslands in the Australian landscape. *Landscape Aust.* 4/89, 394-403.
- Hobbs, R.J. (1989) The nature and effects of disturbance relative to invasions. *Biological invasions: a global perspective. Scope* 37. (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek & M. Williamson), pp. 389-405. John Wiley & Sons, Chichester.
- Hobbs, R.J. & Atkins, L. (1988) Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Aust. J. Ecol.* 13, 171-179.

- Hobbs, R.J., Gulmon, S.L., Hobbs, V.J. & Mooney, H.A. (1988) Effects of fertiliser addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia (Berlin)* 75, 291-295.
- Hobbs, R.J. & Hobbs, V.J. (1987) Gophers and grassland: a model of vegetation response to patchy soil disturbance. *Vegetatio* 69, 141-146.
- Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* 6, 324-337.
- Hobbs, R.J. & Mooney, H.A. (1985) Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia (Berlin)* 67, 342-351.
- Hobbs, R.J. & Mooney, H.A. (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* 72, 59-68.
- Humphreys, F.R. & Craig, F.G. (1981) Effects of fire on soil chemical, structural and hydrological properties. *Fire and the Australian biota* (ed. by A.M. Gill, R.H. Groves & I.R. Noble), pp. 177-200. Australian Academy of Science, Canberra.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187-211.
- Inouye, R.S., Huntly, N.J., Tilman, D. & Tester, J.R. (1987) Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. *Oecologia (Berlin)* 72, 178-184.
- Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (1987) *Data analysis in community and landscape ecology*. Pudoc, Wageningen.
- Kalbfleisch, J.D. & Prentice, R.L. (1980) *The statistical analysis of failure time data*. John Wiley and Sons, New York.
- Keeley, J.E. (1987) Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68, 434-443.
- Keeley, J.E., Morton, B.A., Pedrosa, A. & Trotter, P. (1985) Role of allelopathy, heated and charred wood in the germination of chaparral herbs and suffrutescents. *J. Ecol.* 73, 445-458.
- Keeley, S.C. & Pizzorno, M. (1986) Charred wood stimulated germination of two fire-following herbs of the California chaparral and the role of hemicellulose. *Amer. J. Bot.* 73, 1289-1297.
- Kirkpatrick, J.B. & Brown, M.J. (1984) The palaeogeographic significance of local endemism in Tasmanian higher plants. *Search* 15, 112-113.

- Kirkpatrick, J.B., Gilfedder, L., Hickie, J. & Harris, S. (1991) Reservation and conservation status of Tasmanian native higher plants. Wildlife Division Scientific Report No 91/2. Department of Parks, Wildlife and Heritage, Tasmania.
- Klinkhamer, P.G.L. & De Jong, T.J. (1988) The importance of small-scale disturbance for seedling establishment in *Cirsium vulgare* and *Cynoglossum officinale*. *J. Ecol.* **76**, 383-392.
- Kruskal, J.B. & Wish, M. (1978) *Multidimensional scaling*. Sage, Beverly Hills.
- Lamont, B.B., Ralph, C.S. & Christensen, P.E.S. (1985) Mycophagous marsupials as dispersal agents for ectomycorrhizal fungi on *Eucalyptus calophylla* and *Gastrolobium bilobum*. *New Phytol.* **101**, 651-656.
- Leeper, G.W. (1964) *Introduction to soil science*. (4th ed.) Melbourne University Press, Melbourne.
- Leigh, J.H., Wimbush, D.J., Wood, D.H., Holgate, M.D., Slee, A.V., Stanger, M.G. & Forrester, R.I. (1987) Effects of rabbit grazing and fire on a subalpine environment. I. Herbaceous and shrubby vegetation. *Aust. J. Bot.* **35**, 433-464.
- Lorimer, C.G. (1983) Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manag.* **6**, 343-360.
- Lotwick, H.W. & Silverman, B.W. (1982) Methods for analysing spatial processes of several types of points. *J. R. Statist. Soc. B* **44**, 406-413.
- Loucks, O.L., Plumb-Mentjes, M.L. & Rogers, D. (1985) Gap processes and large-scale disturbances in sand prairies. *The ecology of natural disturbance and patch dynamics*. (ed. by S.T.A. Pickett & P.S. White), pp. 71-83. Academic Press, Orlando.
- Lunt, I.D. (1990) The soil seed bank of a long-grazed *Themeda triandra* grassland in Victoria. *Proc. R. Soc. Vic.* **102**, 53-57.
- Malajczuk, N., Trappe, J.M. & Molina, R. (1987) Interrelationships among some ectomycorrhizal trees, hypogeous fungi and small mammals: Western Australian and northwestern American parallels. *Aust. J. Ecol.* **12**, 53-55.
- Martinsen, G.D., Cushman, J.H. & Whitman, T.G. (1990) Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. *Oecologia (Berlin)* **83**, 132-138.
- McConnaughay, K.D.M. & Bazzaz, F.A. (1987) The relationship between gap size and performance of several colonizing annuals. *Ecology* **68**, 411-416.

- McIlroy, J.C. (1983) Common wombat. *Complete book of Australian mammals*. (ed. by R. Strahan), pp. 117-119. Angus & Robertson, London.
- McIntyre, S. (1990) Germination in eight native species of herbaceous dicot and implications for their use in revegetation. *Vict. Nat.* 107, 154-158.
- McIntyre, S., Huang, Z. & Smith, A.P. (1993) Patterns of abundance in grassy vegetation of the New England Tablelands: identifying regional rarity in a threatened vegetation type. *Aust. J. Bot.* 41, 49-64.
- McLendon, T. & Redente, E.F. (1990) Succession patterns following soil disturbance in a sagebrush steppe community. *Oecologia (Berlin)* 85, 293-300.
- Mielke, H.W. (1977) Mound building by pocket gophers (Geomyidae): their impact on soils and vegetation in North America. *J. Biogeogr.* 4, 171-180.
- Miller, T.E. (1987) Effects of emergence time on survival and growth in an early old-field plant community. *Oecologia (Berlin)* 72, 272-278.
- Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. John Wiley & Sons, New York.
- Novoplansky, A. (1984) Annual plant colonization on mole rats' mounds, as a case study in the ecology of micro-disturbance. M.Sc. thesis, University of Jerusalem (in Hebrew).
- Nunez, M. (1988) A regional lapse rate for Tasmania. *Pap. Proc. R. Soc. Tasm.* 122, 53-57.
- Peart, D.R. (1989) Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonization. *J. Ecol.* 77, 267-289.
- Pickett, S.T.A. & White, P.S. (eds) (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando.
- Pierson, E.A. & Mack, R.N. (1990) The population biology of *Bromus tectorum* in forests: effect of disturbance, grazing, and litter on seedling establishment and reproduction. *Oecologia (Berlin)* 84, 526-533.
- Platt, W.J. (1975) The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecol. Monogr.* 45, 285-305.
- Quin, D.G. (1985) Observations on the diet of the southern brown bandicoot, *Isodon obesulus* (Marsupialia: Peramelidae), in southern Tasmania. *Aust. Mammal.* 11, 15-25.

- Rabinowitz, D. (1981a) Buried viable seeds in a North American tall-grass prairie: the resemblance of their abundance and composition to dispersing seeds. *Oikos* 36, 191-195.
- Rabinowitz, D. (1981b) Seven forms of rarity. *The biological aspects of rare plant conservation*. (ed. by H. Synge), pp. 205-217. John Wiley & Sons, Chichester.
- Rabinowitz, D. & Rapp, J.K. (1985a) Colonization and establishment of Missouri prairie plants on artificial soil disturbances. II. Detecting small-scale plant-to-plant interactions and separating disturbance from resource provision. *Amer. J. Bot.* 72, 1629-1634.
- Rabinowitz, D. & Rapp, J.K. (1985b) Colonization and establishment of Missouri prairie plants on artificial soil disturbances. III. Species abundance distributions, survivorship, and rarity. *Amer. J. Bot.* 72, 1635-1640.
- Raison, R.J., Woods, B.V., Jakobsen, B.F. & Bary, G.A.V. (1986) Soil temperatures during and following low-intensity prescribed burning in a *Eucalyptus pauciflora* forest. *Aust. J. Soil Res.* 24, 33-47.
- Rapp, J.K. & Rabinowitz, D. (1985) Colonization and establishment of Missouri prairie plants on artificial soil disturbances. I. Dynamics of forb and graminoid seedlings and shoots. *Amer. J. Bot.* 72, 1618-1628.
- Rayner, G. (1989) Aspects of the biology and population ecology of the environmental weed *Briza maxima*. Honours thesis, Monash University, Melbourne.
- Read, J. & Hill, R.S. (1988) The dynamics of some rainforest associations in Tasmania. *J. Ecol.* 76, 558-584.
- Reader, R.J. & Buck, J. (1991) Community response to experimental soil disturbance in a midsuccessional, abandoned pasture. *Vegetatio* 92, 151-159.
- Reed, R.A., Peet, R.K., Palmer, M.W. & White, P.S. (1993) Scale dependence of vegetation-environment correlations: A case study of a North Carolina piedmont woodland. *J. Veg. Sci.* 4, 329-340.
- Reichman, O.J. (1988) Comparison of the effects of crowding and pocket gopher disturbance on mortality, growth and seed production of *Berteroa incana*. *Am. Midl. Nat.* 120, 58-69.
- Robertson, D. (1985) Interrelationships between kangaroos, fire and vegetation dynamics at Gellibrand Hill Park, Victoria. PhD Thesis, University of Melbourne.



- Roberts, H.A. (1981) Seed banks in soil. *Adv. Appl. Biol.* 6, 1-55.
- Rounsevell, D.E., Taylor, R.J. & Hocking, G.J. (1991) Distribution records of native terrestrial mammals in Tasmania. *Wildl. Res.* 18, 699-717.
- Ryser, P. (1993) Influences of neighbouring plants on seedling establishment in limestone grassland. *J. Veg. Sci.* 4, 195-202.
- SAS (1988a) *SAS Procedures Guide, Release 6.03 Edition*. SAS Institute Inc., Cary, NC.
- SAS (1988b) *SAS/STAT user's guide, Release 6.03 Edition*. SAS Institute Inc., Cary, NC.
- SAS (1989) *SAS/STAT user's guide. Version 6*. SAS Institute Inc., Cary, NC.
- Scott, J.J. (1985) Effects of feral rabbits on the revegetation of disturbed coastal slope sites, Macquarie Island. MA thesis, Monash University, Melbourne.
- Scotter, D.R. (1970) Soil temperatures under grass fires. *Aust. J. Soil Res.* 8, 273-279.
- Shachak, M., Brand, S. & Gutterman, Y. (1991) Porcupine disturbances and vegetation pattern along a resource gradient in a desert. *Oecologia (Berlin)* 88, 141-147.
- Sigleo, W.R. & Colhoun, E.A. (1982) Terrestrial dunes, man and the late Quaternary environment in southern Tasmania. *Palaeogeog., Palaeoclimat., Palaeoecol.* 39, 87-121.
- Slankis, V. (1974) Soil factors influencing the formation of mycorrhizae. *Ann. Rev. Phytopath.* 12, 4-37.
- Smith, A.P., Wellham, G.S. & Green, S.W. (1989) Seasonal foraging activity and microhabitat selection by echidnas (*Tachyglossus aculeatus*) on the New England Tablelands. *Aust. J. Ecol.* 14, 457-466.
- Sokal, R.R. & Rohlf, F.J. (1969) *Biometry. The principles and practice of statistics in biological research*. Freeman, San Francisco.
- Specht, R.L. (1981) Heathlands. *Australian Vegetation*. (ed. by R.H. Groves), pp. 253-275. Cambridge University Press, Cambridge.
- Spencer, S.R., Cameron, B.D.E., Cooper, L.C. & Williams, L.R. (1985) Influence of pocket gopher mounds on a Texas coastal prairie. *Oecologia (Berlin)* 66, 111-115.
- Strahan, R. (ed.) (1983) *Complete Book of Australian Mammals*. Angus & Robertson, London.

- Stuwe, J. & Parsons, R.F. (1977) *Themeda australis* grasslands on the Basalt Plains, Victoria: floristics and management effects. *Aust. J. Ecol.* **2**, 467-476.
- Sumrall, L.B., Roundy, B.A., Cox, J.R. & Winkel, V.K. (1991) Influence of canopy removal by burning or clipping on emergence of *Eragrostis lehmanniana* seedlings. *Int. J. Wildland Fire* **1**, 35-40.
- Taylor, R.J. (1991) Plants, fungi and bettongs: A fire-dependent co-evolutionary relationship? *Aust. J. Ecol.* **16**, 409-411.
- Taylor, R.J. (1992a) Distribution and abundance of fungal sporocarps and diggings of the Tasmanian bettong, *Bettongia gaimardi*. *Aust. J. Ecol.* **17**, 155-160.
- Taylor, R.J. (1992b) Fire, mycorrhizal fungi and management of mycophagous marsupials. *Aust. J. Ecol.* **17**, 227-228.
- Taylor, R.J. (1992c) Seasonal changes in the diet of the Tasmanian bettong (*Bettongia gaimardi*), a mycophagous marsupial. *J. Mammal.* **73**, 408-414.
- Thompson, K. (1986) Small-scale heterogeneity in the seed bank of an acidic grassland. *J. Ecol.* **74**, 733-738.
- Thompson, K., Band, S.R. & Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Funct. Ecol.* **7**, 236-241.
- Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* **67**, 893-921.
- Tilman, D. (1983) Plant succession and gopher disturbance along an experimental gradient. *Oecologia (Berlin)* **60**, 285-292.
- Upton, G. & Fingleton, B. (1985) *Spatial data analysis by example. Volume 1 Point pattern and quantitative data*. John Wiley and sons, Chichester.
- Vetaas, O.R. (1992) Micro-site effects of trees and shrubs in dry savannas. *J. Veg. Sci.* **3**, 337-344.
- Vlahos, S. & Bell, D.T. (1986) Soil seed-bank components of the northern jarrah forest of Western Australia. *Aust. J. Ecol.* **11**, 171-179.
- Warcup, J.H. (1981) Effect of fire on the soil micro-flora and other non-vascular plants. *Fire and the Australian biota*. (ed. by A.M. Gill, R.H. Groves & I.R. Noble), pp. 203-214. Australian Academy of Science, Canberra.
- Watt, A.S. (1974) Senescence and rejuvenation in ungrazed chalk grassland (grassland B) in Breckland: the significance of litter and of moles. *J. Appl. Ecol.* **11**, 1157-1171.



- Webb, L.J., Tracey, J.G. & Williams, W.T. (1972) Regeneration and pattern in the subtropical rain forest. *J. Ecol.* 60, 675-695.
- West, O. (1965) *Fire in vegetation and its use in pasture management with special reference to tropical and subtropical Africa*. Commonwealth Agricultural Bureaux, Buckinghamshire.
- Westoby, M., French, K., Hughes, L., Rice, B. & Rodgerson, L. (1991) Why do more plant species use ants for dispersal on infertile compared with fertile soils? *Aust. J. Ecol.* 16, 445-455.
- White, P.S. (1979) Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45, 229-299.
- White, P.S. & Pickett, S.T.A. (1985) Natural disturbance and patch dynamics: an introduction. *The ecology of natural disturbance and patch dynamics*. (ed. by S.T.A. Pickett & P.S. White), pp. 3-13. Academic Press, Orlando.
- Williams, L.R. & Cameron, G.N. (1986) Effects of removal of pocket gophers on a Texas coastal prairie. *Am. Midl. Nat.* 115, 216-224.
- Williams, R.J. (1992) Gap dynamics in subalpine heathland and grassland vegetation in south-eastern Australia. *J. Ecol.* 80, 343-352.
- Williams, R.J. & Ashton, D.H. (1987) Effects of disturbance and grazing by cattle on the dynamics of heathland and grassland communities on the Bogong High Plains, Victoria. *Aust. J. Bot.* 35, 413-431.
- Willis, A.J. & Groves, R.H. (1991) Temperature and light effects on the germination of seven native forbs. *Aust. J. Bot.* 39, 219-228.
- Wilson, S.D. & Zammit, C.A. (1992) Tree litter and the lower limits of subalpine herbs and grasses in the Brindabella Range, ACT. *Aust. J. Ecol.* 17, 321-327.

## Appendix 1 Summary of the survey of mammal digging in the habitats of rare plants.

Plant nomenclature follows Kirkpatrick *et al.* (1991). National conservation status is given, or else for Tasmania only. Status follows Kirkpatrick *et al.* (1991), which has some changes from Briggs & Leigh (1988) because of the incorporation of more recent knowledge. To identify localities, the 1:100 000 series map and 6 figure grid references are given, using the Australian Map Grid (Zone 55). Digging abundance categories are as follows: abundant =  $\geq 5\%$ ; moderate =  $\geq 1$  but  $< 5\%$ ; sparse =  $< 1\%$ . # denotes a population/species included in the initial survey.

### 1. *Aphelia gracilis* (Centrolepidaceae, annual graminoid)

Status: rare (Tas only)

Populations examined: # Powranna (8314 South Esk 212848)

Geology: Quaternary alluvial gravels and sands

Habitat & vegetation: wet drainage line dominated by sedges

Digging: none observed

### 2. *Bertya rosmarinifolia* (Euphorbiaceae, shrub)

Status: vulnerable (Tas only)

Populations examined: Westwood (8215 Tamar 971104)

Geology: Tertiary alluvial sands

Habitat & vegetation: grassy eucalypt woodland

Digging: abundant bettong digging

### 3. *Brunonia australis* (Brunoniaceae, perennial forb)

Status: vulnerable (Tas only)

Populations examined: 1.# Powranna (8314 South Esk 212848); 2. Westwood (8215 Tamar 971105)

Geology: 1. Quaternary alluvial gravels and sands, Tertiary alluvial sands; 2. Tertiary alluvial sands

Habitat & vegetation: grassy eucalypt woodland

Digging: 1. & 2. abundant bettong digging

### 4. *Caesia calliantha* (Liliaceae, perennial forb)

Status: rare (Tas only)

Populations examined: Cranbrook (8513 Freycinet 878442)

Geology: Jurassic dolerite

Habitat & vegetation: grassy eucalypt woodland

Digging: none observed

### 5. *Caladenia caudata* (Orchidaceae, perennial forb)

Status: vulnerable

Populations examined: 1. Pittwater (8412 Prosser 413584); 2. Bellerive (8312 Derwent 310535); 3. Austins Ferry (8312 Derwent 209640)

Geology: 1. Quaternary sand; 2. Triassic quartz sandstone; 3. Triassic quartz mudstone  
 Habitat & vegetation: 1., 2. & 3. grassy woodland  
 Digging: 1. abundant rabbit scrapings; 2. abundant diggings by eastern barred & southern brown bandicoot; 3. abundant bandicoot diggings, also some rabbit scrapings

6. *Carex tasmanica* (Cyperaceae, perennial sedge)

Status: vulnerable

Populations examined: 1.# Kingston (8312 Derwent 267420); 2.# Queens Domain, Hobart (8312 Derwent 266538); 3. Waddamana Rd. (8213 Shannon 905216); 4. Austins Ferry (8312 Derwent 206642)

Geology: 1. Triassic quartz sandstone; 2. Jurassic dolerite; 3. unknown; 4. Triassic quartz mudstone

Habitat & vegetation: 1. & 3. grassy road verges of mostly native species; 2. grassy shallow gully, heavily weed invaded; 4. edges of creek dominated by sedges & exotic species

Digging: none observed at any population

7. *Colobanthus curtisiae* (Caryophyllaceae, perennial forb)

Status: rare (Tas only)

Populations examined: 1.# Tunbridge (8313 Lake Sorell 320363); 2. "Hermitage" (8213 Shannon 846184); 3. Woodbury (8313 Lake Sorell 274322)

Geology: 1. Jurassic dolerite; 2. Jurassic dolerite; 3. Triassic quartz sandstone

Habitat & vegetation: 1. grassy eucalypt woodland on road verge; 2. grassy eucalypt open-forest; 3. grassy open-forest

Digging: 1. sparse rabbit scrapings; 2. & 3. none observed

8. *Danthonia popinensis* (Poaceae, perennial grass)

Status: endangered

Populations examined: # Kempton (8312 Derwent 929156)

Geology: Triassic quartz sandstone

Habitat & vegetation: grassy road verge of mostly native species

Digging: none observed, remnant too small to support native mammals

9. *Dianella longifolia* (Liliaceae, perennial forb)

Status: rare (Tas only)

Populations examined: Gagebrook (8312 Derwent 217652)

Geology: Tertiary basalt

Habitat & vegetation: grassy woodland

Digging: none observed

10. *Eryngium ovinum* (Apiaceae, perennial forb)

Status: endangered (Tas only)

Populations examined: "Kingston" (8414 St Pauls 518786)

Geology: Triassic quartz sandstone

Habitat & vegetation: grassland

Digging: none observed

11. *Euphrasia scabra* (Scrophulariaceae, annual forb)

Status: vulnerable

Populations examined: # Dukes Marshes (8514 Break O'Day 946803)

Geology: Quaternary alluvium

Habitat &amp; vegetation: wet grassland

Digging: sparse rabbit digging

12. *Euphrasia semipicta* (Scrophulariaceae, perennial forb)

Status: vulnerable

Populations examined: # Fortescue Bay (8411 Storm Bay 788227)

Geology: Jurassic dolerite

Habitat &amp; vegetation: heathy woodland

Digging: none observed

13. *Gahnia rodwayi* (Cyperaceae, perennial sedge)

Status: rare

Populations examined: 1. # Chimney Pot Hill (8312 Derwent 223481); 2. Hospital Creek (8412 Prosser 671657)

Geology: 1. &amp; 2. Jurassic dolerite

Habitat &amp; vegetation: 1. &amp; 2. shrubby eucalypt woodland

Digging: 1. moderate levels of digging by bandicoots and echidnas; 2. moderate levels of digging by bettongs

14. *Glycine latrobeana* (Fabaceae, perennial forb)

Status: rare

Populations examined: # Powranna (8314 South Esk 212848)

Geology: Quaternary alluvial gravels and sands

Habitat &amp; vegetation: grassy eucalypt woodland

Digging: moderate levels of bettong digging

15. *Haloragis heterophylla* (Haloragaceae, perennial forb)

Status: rare (Tas only)

Populations examined: Gagebrook (8312 Derwent 221663)

Geology: Jurassic dolerite

Habitat &amp; vegetation: grassy woodland

Digging: none observed

16. *Helichrysum costatifructum* (Asteraceae, shrub)

Status: rare

Populations examined: 1. Birchs Bay (8311 D'Entrecasteaux 192176); 2. Bicheno (8514 Break O'Day 050653)

Geology: 1. &amp; 2. Jurassic dolerite

Habitat &amp; vegetation: 1. shrubby eucalypt woodland; 2. grassy woodland

Digging: 1. sparse bandicoot digging; 2. none observed

17. *Helichrysum lycopodioides* (Asteraceae, shrub)

Status: rare

Populations examined: # Lake Leake Rd. (8413 Little Swanport 809480)

Geology: Jurassic dolerite

Habitat &amp; vegetation: shrubby eucalypt woodland

Digging: very sparse echidna digging

18. *Lasiopetalum micranthum* (Sterculiaceae, prostrate shrub)

Status: vulnerable

Populations examined: 1.# Old Coach Rd. (8514 Break O'Day 874605); 2.# Lake Leake Rd. (8413 Little Swanport 810480); 3. Cranbrook (8513 Freycinet 878442)

Geology: 1., 2. &amp; 3. Jurassic dolerite

Habitat &amp; vegetation: 1., 2. &amp; 3. grassy woodland on shallow rocky soil

Digging: 1. &amp; 2. sparse echidna digging; 3. none observed.

19. *Lepidium hyssopifolium* (Brassicaceae, perennial forb)

Status: endangered

Populations examined: 1.# "Annandale" (8313 Lake Sorell 288387); 2.# Bagdad (8312 Derwent 190842); 3.# Bagdad (8312 Derwent 181831); 4.# Granton (8312 Derwent 180649); 5. Waddamana Rd. (8213 Shannon 898220); 6. Fingal (8414 St Pauls 804897)

Geology: 1. Quaternary ferruginous &amp; siliceous alluvium; 2. &amp; 4. Triassic quartz sandstone; 3. Quaternary alluvium; 5. &amp; 6. Permian mudstone

Habitat & vegetation: 1. beneath *Acacia dealbata* & *E. amygdalina* in grassy woodland; 2. beneath *E. viminalis* on very weedy road verge; 3. mainly beneath exotic *Cupressus* sp. in paddock; 4. beneath *E. viminalis* on weedy road verge; 5. beneath exotic *Populus* sp. on road verge; 6. beneath exotic *Cupressus* sp. on road verge

Digging: 1. abundant bettong digging &amp; possibly bandicoot digging; 2., 3., 4., 5. &amp; 6. none observed, remnants either too small or too disturbed to support digging mammals

20. *Lepidium pseudotasmanicum* (Brassicaceae, perennial forb)

Status: rare (Tas only)

Populations examined: 1.# "Annandale" (8313 Lake Sorell 288387); 2. Bagdad (8312 Derwent 190842); 3. Granton (8312 Derwent 180649); 4.# Rosny Point (8312 Derwent 288528); 5.# Risdon (8312 Derwent 263580); 6. Gagebrook (8312 Derwent 218662); 7.# Bellerive (8312 Derwent 312535)

Geology: 1. Quaternary ferruginous &amp; siliceous alluvium; 2., 3. &amp; 7. Triassic quartz sandstone; 4. &amp; 6. Jurassic dolerite; 5. Permian siltstone

Habitat & vegetation: 1. beneath *Acacia mearnsii* and *Eucalyptus amygdalina* in grassy woodland; 2. beneath *E. viminalis* on very weedy road verge; 3. beneath *E. viminalis* on weedy road verge; 4. *Allocasuarina verticillata* low forest on edge of new foot track; 5. *A. verticillata* low forest; 6. grassy woodland; 7. weedy sites & beneath exotic *Pinus* sp.

Digging: 1. abundant bettong digging &amp; possibly bandicoot digging; 2., 3. &amp; 4.

none observed, remnants either too small or too disturbed to support digging mammals; 5. abundant bandicoot digging; 6. none observed; 7. abundant bandicoot digging, except under *Pinus* sp.

21. *Melaleuca pustulata* (Myrtaceae, shrub)

Status: rare

Populations examined: Swan River (8514 Break O'Day 882579)

Geology: Jurassic dolerite

Habitat & vegetation: grassy woodland

Digging: sparse echidna or bettong digging

22. *Millotia tenuifolia* (Asteraceae, annual forb)

Status: rare (Tas only)

Populations examined: Old Coach Rd. (8514 Break O'Day 874605)

Geology: Jurassic dolerite

Habitat & vegetation: shallow rocky depressions & bare soil in grassy woodland

Digging: none observed

23. *Monotoca linifolia* (Epacridaceae, shrub)

Status: rare

Populations examined: # Grey Mountain (8311 D'Entrecasteaux 095280)

Geology: Triassic quartz sandstone

Habitat & vegetation: wet scrubby woodland

Digging: none observed

24. *Odixia achlaena* (Asteraceae, shrub)

Status: rare

Populations examined: 1.# Hospital Creek (8412 Prosser 671657); 2.# Kellevie Road (8412 Prosser 642666); 3. Jacob Hill (8412 Prosser 713718)

Geology: 1., 2. & 3. Jurassic dolerite

Habitat & vegetation: 1. shrubby eucalypt woodland; 2. grassy eucalypt woodland; 3. recently clear-felled & burnt dry sclerophyll forest

Digging: 1. moderate levels of bettong digging; 2. abundant bettong digging; 3. none observed

25. *Odixia angusta* (Asteraceae, shrub)

Status: rare

Populations examined: # Hospital Creek (8412 Prosser 673658)

Geology: Jurassic dolerite

Habitat & vegetation: margin of wet sclerophyll forest on rocky substrate

Digging: none observed in vicinity of population

26. *Olearia ericoides* (Asteraceae, shrub)

Status: rare

Populations examined: 1.# Chimney Pot Hill (8312 Derwent 223481); 2.# Ridgeway (8312 Derwent 237474)



Geology: 1. & 2. Jurassic dolerite

Habitat & vegetation: 1. & 2. shrubby eucalypt woodland

Digging: 1. moderate levels of bandicoot and echidna digging; 2. very sparse digging

27. *Olearia hookeri* (Asteraceae, shrub)

Status: rare

Populations examined: # Risdon (8312 Derwent 265583)

Geology: Permian siltstone

Habitat & vegetation: shrubby eucalypt woodland

Digging: abundant bettong digging & possibly bandicoot digging

28. *Olearia lanceolata* (Asteraceae, shrub)

Status: rare

Populations examined: 1. # Hospital Creek (8412 Prosser 673658); 2. Jacobs Hill (8412 Prosser 717710)

Geology: 1. & 2. Jurassic dolerite

Habitat & vegetation: 1. & 2. shrubby eucalypt open-forest on very rocky substrate

Digging: none observed, too rocky

29. *Prasophyllum buftonianum* (Orchidaceae, perennial forb)

Status: rare

Populations examined: Coles Bay (8513 Freycinet 061360)

Geology: Quaternary windblown sand

Habitat & vegetation: coastal heathland on sandy soil, in mowed area

Digging: none observed in immediate vicinity, but echidna digging common in nearby unmowed heathland

30. *Pultenaea humilis* (Fabaceae, perennial shrub)

Status: endangered (Tas only)

Populations examined: Powranna (8314 South Esk 194833)

Geology: Tertiary alluvial sands

Habitat & vegetation: dry eucalypt open-forest with a grassy & low shrubby understorey

Digging: abundant bettong digging

31. *Schoenus absconditus* (Cyperaceae, perennial sedge)

Status: rare

Populations examined: 1. Mt. Direction (8312 Derwent 260600); 2. Knopwood Hill (8312 Derwent 324540)

Geology: Jurassic dolerite

Habitat & vegetation: grassy woodland

Digging: none observed at either population

32. *Schoenus latelaminatus* (Cyperaceae, perennial sedge)

Status: vulnerable (Tas only)



Populations examined: # Powranna (8314 South Esk 212848)  
 Geology: Quaternary alluvial gravels and sands  
 Habitat & vegetation: wet sedge dominated drainage lines  
 Digging: none observed

33. *Scleranthus diander* (Caryophyllaceae, perennial forb)

Status: vulnerable (Tas only)

Populations examined: "Annandale" (8313 Lake Sorell 288387)

Geology: Quaternary ferruginous & siliceous alluvium

Habitat & vegetation: grassy woodland

Digging: abundant bettong digging & possibly bandicoot digging

34. *Stackhousia gummii* (Stackhousiaceae, perennial forb)

Status: endangered

Populations examined: Tunbridge Tier Rd. (8313 Lake Sorell 333360)

Geology: Jurassic dolerite

Habitat & vegetation: grassy eucalypt woodland on road verge

Digging: sparse echidna digging

35. *Stenanthemum pimeleoides* (Rhamnaceae, prostrate shrub)

Status: vulnerable

Populations examined: Epping Forest (8314 South Esk 273758)

Geology: Quaternary alluvial ferruginous gravel

Habitat & vegetation: grassy open-forest

Digging: abundant bettong digging

36. *Taraxacum aristum* (Asteraceae, perennial forb)

Status: rare

Populations examined: # Woods Lake Rd. (8213 Shannon 975465)

Geology: Jurassic dolerite

Habitat & vegetation: montane grassy woodland

Digging: none observed

37. *Velleia paradoxa* (Goodeniaceae, perennial forb)

Status: vulnerable (Tas only)

Populations examined: 1. # Bellerive (8312 Derwent 310535); 2. Flagstaff Gully (8312 Derwent 314555); 3. Risdon (8312 Derwent 261582); 4. Bagdad (8312 Derwent 192842)

Geology: 1. Triassic quartz sandstone mainly, but also Jurassic dolerite; 2. Jurassic dolerite; 3. Permian siltstone; 4. Triassic quartz sandstone

Habitat & vegetation: 1. grassy woodland on sandy soil on sandstone, shallow clay loam on dolerite; 2. grassy eucalypt woodland; 3. low *Allocasuarina verticillata* grassy forest; 4. grassy road verge of mostly native species, but also on a bare road batter

Digging: 1. very abundant bandicoot digging on sandstone, very sparse bandicoot digging on dolerite; 2. moderate levels of bandicoot digging; 3. abundant bandicoot digging; 4. none observed

38. *Vittadinia cuneata* (Asteraceae, perennial forb)

Status: rare (Tas only)

Populations examined: 1. Gagebrook (8312 Derwent 214656); 2. Bellerive (8312 Derwent 310538); 3. Mornington (8312 Derwent 324540)

Geology: 1. Tertiary basalt; 2. &amp; 3. Jurassic dolerite

Habitat &amp; vegetation: 1., 2. &amp; 3. grassy woodland

Digging: none observed at any population

39. *Vittadinia gracilis* (Asteraceae, perennial forb)

Status: vulnerable (Tas only)

Populations examined: Gagebrook (8312 Derwent 214656)

Geology: Tertiary basalt

Habitat &amp; vegetation: grassy woodland with mostly native species

Digging: none observed

40. *Vittadinia muelleri* (Asteraceae, perennial forb)

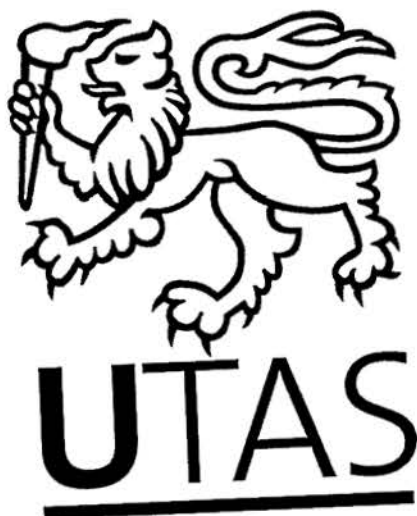
Status: rare (Tas only)

Populations examined: Tunbridge Tier Rd. (8313 Lake Sorell 333360)

Geology: Jurassic dolerite

Habitat &amp; vegetation: grassy eucalypt woodland on a road verge

Digging: sparse echidna digging



**Appendix 2** Complete floristic data from the 1 x 1 m grid quadrats at Bellerive. Abundance values are shown (understorey) or cover (trees) (see text for details). \* denotes exotic species.

Cluster group	unclassif.	1	2	3	4	5	6
	1	1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1
	122355667890	177 44344	114477104001315253771117111	13366992933433	1826612332582229332033632	5253566883999527060009902233	4788448512288112
	79367259138263	135484352239106	284524096786891467162437156	135684875750895	54945704610023533481012063	3476490892012830270467955891	7931896280257971
<i>Lissanthe strigosa</i>	---	1-	---	---	---	---	---
<i>Acacia mearnsii</i>	---	---	1-1-	---	---	---	---
<i>Lepidosperma laterale</i>	2-	2-32-	33-	---	---	---	---
<i>Drosera peltata</i>	---	121-122-11111	1-21-	1-1	---	---	---
<i>Chamaecilla corymbosa</i>	---	2-	---	---	---	---	---
<i>Poa hookeri</i>	---	23-	22-1	1-1	---	---	---
<i>Hypericum gramineum</i>	---	2-	1-	---	---	---	---
<i>Agrostis capillaris</i>	---	---	1-332-	---	---	---	---
<i>Dichelachne</i> spp.	1-2-	2-	1-	---	1-1-	---	---
<i>Vulpia myuros</i>	---	---	2-	---	---	---	---
<i>Centaureum erythraea</i>	---	1-	2311-33343313-	22-433323312-1-121-1-11-	21-1-	11-1-	2-211-1-2-
<i>Schoenus apogon</i>	1-1-	23221-311232-322-	1221-21-221-111-22213221-	1-	2-21-1-2-1-2-11-1-	21-1-	1-1-1-11-1-2-
<i>Daviesia ulicifolia</i>	---	---	---	1-	---	---	---
<i>Bossiaea prostrata</i>	2-1-	11-21112222212112-	112-2-2-2122221-1-1-	1-1-	22-222-	212-1-11-22121-1-	1-1-1-
<i>Deyeuxia quadriseta</i>	---	1-2-2-1-1-	1-11-11-	1-1-	1111-	1-	2-
<i>Diplarrena moraea</i>	---	1-	1-	1-121-1-	---	---	---
<i>Agrostis aemula</i>	1-1-	1-2-	1111-1-	1-1-12-	2-1-1-	---	11-1-1-
<i>Themeda triandra</i>	21-13-	231-	3322233332321-	3333333323332333123333323-	11-	22-32222221-233212323-223-	1112-22-1-1-22-2-1221-2-
<i>Carpobrotus rossii</i>	---	---	---	1-	---	22-1221-	11-22-1121-
<i>Lepidosperma lineare</i>	12-21-	21111-2112111-	1-2-1122221-111-12-	---	22-1221-	11-22-1121-	1-11121-1-11-
<i>Galium australe</i>	---	---	---	1-	---	---	---
<i>Cynosurus echinatus</i>	23-221-2-1-	23333321-321333-	2121322-12221-3212222222-	3233311-2-1	22333-321-223-11223222-	221121-	1-1-332-1121-2-
<i>Poa rodwayi</i>	---	---	---	---	---	---	---
<i>Chrysanthemoides monilifera</i>	---	---	---	---	---	---	---
<i>Elymus scabrus</i>	1-1-	2-	2-	1-	1-1-2122-	1-	2-
<i>Carex breviculmis</i>	21-2-1-2-	111-1-111-	11-12-223-	2-221-	1-	22-2-3-2-	321-1-2-12-
<i>Ehrharta distichophylla</i>	---	1-	21-	12-1211-	21-222332333213-	1-	2-2-
<i>Kennedia prostrata</i>	1-	---	12-	1-	21-22-	1-	2-
<i>Goodenia lanata</i>	---	1-	---	1-	1-	1-1-1-1-	---
<i>Leptorhynchus squamatus</i>	2-1-	111-1-	121-	1-	12-	2-	2-
<i>Orchidaceae</i> spp.	---	---	---	1-	1-	1-	---
<i>Bursaria spinosa</i>	1-	1-1-1-1-1-	1-	1-	1-	11-	1-1-1-
<i>Holcus lanatus</i>	---	---	---	---	12-	---	---
<i>Gahnia radula</i>	2-122-	333232232-	2331-33322-22333222333333-	1-2-	321322-	2-1-2211-	2-3333331122322-
<i>Olearia ramulosa</i>	---	1-	---	---	---	---	---
<i>Allocasuarina verticillata</i>	1-11-1-1-1-	1-111-111-111-	11-11-1-1211-11-21-11-	1-1-1111123-	1-1-11-1-1-11-	111-11111111-	1-1-111111-1-
<i>Stylidium graminifolium</i>	---	2-	121-	11-2-1-1-11-	1-1-	2-1-	1-2-11-1-11-
<i>Acacia dealbata</i>	22-	2-	2-2222-22-	1-11-	2-	1-121-1-	1-1-1-1111-
<i>Dillwynia cinerascens</i>	2-	1-11-1-1-2-	1-	1-	1-	1-1-1-1-	1-1-1-2-1-1-
<i>Pimelea humilis</i>	1-12-1-11112-	21122111221-212-	1222-11111-2122-211111-1111-	2-11-121-	1111-1-1121-111-211-1211-	111212111321-11112-3-	12212-21-112-
<i>Linum marginale</i>	---	---	1-	---	1-	---	---
<i>Senecio quadridentatus</i>	2-	---	---	1-	---	---	---
<i>Hibbertia riparia</i>	1-2-2-2-2-	11111111111121-	1-211-2-1-2-1-1-2211312-	1-1-12-	21222-11-111-	111121-	1112-1122121221-1-1-111-
<i>Stipa</i> spp.	22-122232212213-	33233333					
<i>Astroloma humifusum</i>	---	1-	1-1-1-11-	1-11-	12-	1-11-1-	1-12-1-
<i>Hypochoeris radicata</i>	1-1-	1-1-112-11-	1111122-1-1-1111-	11-11-1-2-	11-1-11-2-2-121-1-	11-1-11111-1-2312-11-111-	1-1-1-1-1-
<i>Leucopogon virgatus</i>	1-1-	1-2-221122211-	1-1222-1211-	22222111-	1-	12212111-11-	211-1111221-11-
<i>Ehrharta stipoides</i>	2111122212-1-	1-122-3-2-223223232322-23-212123323-	22-212-122-2-	22233212323232331-221122212-	2-2-1-1-1-21212-1-	23132-222322-21	12212-21-112-
<i>Danthonia pilosa</i>	132-12-22-1-	11312-13-111211-22-32-2123-1-12223-	12-212-1-21-	21211211-2-2331112-22-1-	11-12-211111-12-22-2212-2322-	12-1112-	1112-
<i>Oxalis perennans</i>	12-21-12-	1-11-1-1-1-11-11-	1-1-11-11-	211-1-	1-222-2-2-2-11-	1-2-	11111-
<i>Dichelachne</i> rara	222-	2-1-1211-1-	1221-11213-1-221-122-22-	12222-211-11-	2-222-211-1-2-2111-	1-212-1-2-2-2-212-22-21-2-11-22	22-21-2-11-22
<i>Brachyscome spathulata</i>	1-	1-	1-1-2-	1-1-1-	1-1-1-	1-1-1-	1-1-1-
<i>Luzula meridionalis</i>	2111-11-233-	313322231221222-	3333232323123333233333323-	2-322-12-221-	32323232223332311-223-	23322213223231311212232323-	23333233332333
<i>Dodonaea viscosa</i>	11-12-2-	12211-1-11-23-	11-1-1-1-2-2-21-1-	1-2-1111-211-	1-121-1-11-121-11-	22-12-2-12-112-131112-1-1-1-11-12-1211-2	22-21-1-12-1211-2
<i>Opercularia varia</i>	22-2-1-21-	22211-1-11-122-	111-11-11-12122-21-11-1112-	22221-	1122-2-111-	212-2121-1-1211-1112-11-	1-2211-12212-2223
<i>Dichondra repens</i>	---	---	1-	---	---	1-	---
<i>Brachyloma ciliatum</i>	---	---	1-	---	---	---	---
<i>Lomandra longifolia</i>	12-11-32-3-	1-11-	1-1-1212-1211111112-2-1-	2-21-21221212-	11-1-1-211-	11-1-1-1-1-2-21211112-21-	2211-11-
<i>Laxmannia orientalis</i>	---	---	1-1-11-1-	---	---	2-	1-1-1-
<i>Allocasuarina littoralis</i>	1-	1-	1-1211-1-1-2-	1-	1-	1-	1-1-1-1-1111
<i>Eucalyptus viminalis</i>	111-1-	1-	11-	11-1-11-1-	111-	1-1-1-1-	1-1-1-
<i>Helichrysum apiculatum</i>	3-133-3121-21-	2111-333-	2223-21122-3-	12-2-	12222-2-1-133-1-332211-	11-1332212-2-23-223222-	3-2222-
<i>Bossiaea cinerea</i>	1-1-1-	1-	---	21-	1-	---	2-
<i>Dichelachne crinita</i>	1-1-	---	1-	222-32-22-	111-1-1-	1-1-21-21-	1-1-
<i>Cassytha pubescens</i>	---	1-	1-1-1-	---	---	---	11-
<i>Wahlenbergia stricta</i>	1-3-3-	---	1-32-	31-22212-	2-1-1-	1-13-1-	1-2122-3-
<i>Poranthura microphylla</i>	1-	1-	1-1-1-	---	1-	---	1-1-2-
<i>Danthonia setacea</i>	22-21-2-1-2-	1-2-	232-131-2-2-	2-12-2-	2-2231-111-	1122-2-11-	1222-31-21-2-212-22-2-22211
<i>Thelymitra pauciflora</i>	1-1-111-112-1-	11111-21121221-1112-1-1112-	1-2-	21211-1-1-	1121-212-	111-11-21222211-2-2221-212-211-22221-1	2-2-223222
<i>Arthropodium milleflorum</i>	213-11-	33-1-2-12-1222322-	31-1-3-13-2121-12-	3223-32233-	22-2-1-2-212-	2122-13222221-13122232323-	2-2-2-223222
<i>Dianella revoluta</i>	1-22-1-1-22-	122-2-2222-	212-22-21-222-1121-1-	2-21-221-211-	332322-1132312-31-312-21-	222221-122-22-22211-2-1-1-1-23-222232131222	1-1-1-23-222232131222
<i>Cynoglossum suaveolens</i>	---	---	---	1-	---	---	---
<i>Eriostemon verrucosus</i>	---	---	12-2-	---	---	---	21-1-1-
<i>Aira</i> spp.	4-44-2-2-	3-	2133443343-32334-4333-	234-1-2-	424-4-44234444244444-23-	4443444434434-	2443433434334333-3
<i>Microtis unifolia</i>	2-	2-	2-	---	3-	11-	1-
<i>Bulbine glauca</i>	3-21-3-2-	2-	11-	2-	2-2221223-	12-122-	1-222211-2-2-2122322111212-2231223221-11-
<i>Hovea linearis</i>	11-21-	2-11-	11-11-1-11-	1-1-	21-1-	221-	1-1-1-2-112-1-1111-112-
<i>Gonocarpus tetragynus</i>	2212-1222-2-	1-1-22-2-	2-1131232222-312-	11-11-	1-1-2-	22-13-22222	22-1111-222-2-21-12222123322-22-112131322321
<i>Stackhousia patersonia</i>	---	1-	1-11-11-21-	111-11-	11-	1-1-2-1-1-1-	2-122-1-1-
<i>Thysanotus patersonii</i>	2-21-2-	1-	1-1-	1-1-111-1-	1121-2122112-111221-21-	111111222121111111-	1-1-1-1-111-12
<i>Brachyscome aculeata</i>	---	---	---	---	1-1-1-	---	---
<i>Eucalyptus amygdalina</i>	1-	---	112-1-	1-11-	---	11-	21-111-
<i>Plantago varia</i>	2-12-	---	---	1-23221-	11-2-1-	3-2-	2-2331-
<i>Diuris</i> spp.	21-32-12-	12211-1-11-22-	1-1-21-	1-1222-1-12221-	12212222222-	1-2322211	12123221221312-1-1-221-3212-11222-2112
<i>Briza maxima</i>	3314344-2433	---	3324-1-	43434323444	3343-44444433-414-232-2	34434444433344434343323	433233444334333
<i>Pterostylis concinna</i>	---	---	---	11-2-12-	2-	12-2-	2-323-2-1-
<i>Podolepis jaceoides</i>	---	2-1-1-	2-	1-122-1-	2-	2211212-	1121333-2-
<i>Helichrysum scorpioides</i>	1-1-22-	---	---	12-2-1-	2-	2-	1-1-1-
<i>Veltheia paradoxa</i>	2-	---	---	2321-	3-	2-32-3-	1-2-1-2-223
<i>Lepidosperma concavum</i>	3-21-1-	---	---	2-2-11-2-1-	3-2-	3-12-31113-2-23-1-21-	---
<i>Sonchus oleraceus</i>	1-1-	---	---	---	1-	---	---
<i>Silene gallica</i>	223-	3-	2-	1-	---	23-	11-
<i>Caladenia</i> spp.	1-	---	---	1-2-	1-111-1-	1-11-	1-11-11111-
<i>Poa sieberiana</i>	1-	31-2-	1-12-2-	1-23-	1221212-12-	1-1-1-	1231-2-1222122-2-323122132-
<i>Comesperma volubile</i>	---	---	---	1-	---	1-	---
<i>Craspedia glauca</i>	1-	---	1-1-2-	1-1-	1-2-	11-	12-1-2-2111-
<i>Festuca</i> spp.	---	3-	---	1-	---	1-	322-
<i>Eucalyptus</i> spp.	1-	---	---	---	---	1-	---
<i>Viola hederacea</i>	2-	---	---	---	---	21-	---
<i>Acaena echinata</i>	---	---	---	---	---	11-	---
<i>Scleranthus biflorus</i>	---	---	---	---	---	1-	---
<i>Acianthus exsertus</i>	2-	---	---	---	1-	---	3-
<i>Frasophyllum</i> spp.	---	---	---	---	---	---	---
<i>Epacris impressa</i>	---	1-	---	---	---	---	1-
<i>Fumaria</i> spp.	2-	---	---	---	---	---	---
<i>Cotoneaster</i> spp.	1-	---	---	---	---	---	---
<i>Pterostylis</i> spp.	1-	---	---	---	---	---	---
<i>Briza minor</i>	---	2-	---	---	---	---	---
<i>Allocasuarina littoralis</i>	3-15-1-4-	1-116-111-365131-	11-1-1231-12-22-15-3-	4-4-1564238-	1-1-3-33-1-1-12-3154-311111111-	1-1-633111-3-	1-4-3-1-1324
<i>Allocasuarina verticillata</i>	2-12-3-	112111-1-11-22-	11-1-1-1-1-11-11-	1-2-11114-2311-	111-1-11-121-11-	11-51-1-11-133-151131-	1-1-11-1111-1
<i>Dodonaea viscosa</i>	21-12-3-	5-	---	216-2-	6-56-	3-	15-2-
<i>Eucalyptus amygdalina</i>	622-5-	1-	11-	62-	45-1-51-5-	312-	2-4-5-1345-423-
<i>Eucalyptus viminalis</i>	---	---	---	---	---	---	1-1-4-3-

**Appendix 3** Summary of survivorship until December 1992 and total counts of seedlings and ramets for all mapped species at Bellerive.

Species	Survivorship % (Total seedling count)					
	1991			1992		
	M	H	C	M	H	C
<i>Allocasuarina</i> spp.	0	0	0	0	100 (1)	50 (2)
<i>Arthropodium milleflorum</i>	50 (2)	100 (1)	33 (21)	64 (11)	50 (4)	43 (23)
<i>Bossiaea cinerea</i>	0 (1)	0 (1)	0 (1)	0	0	0
<i>Bossiaea prostrata</i>	0 (3)	0 (1)	0	0	0	0
<i>Brachyscome aculeata</i>	0	0	100 (1)	0	0	0
<i>Brachyscome spathulata</i>	0 (5)	0 (1)	40 (5)	50 (10)	0	100 (6)
<i>Bulbine glauca</i>	50 (2)	25 (4)	65 (17)	0	0	0 (1)
<i>Caladenia</i> spp.	100 (6)	0	75 (8)	- (3)	-	- (2)
<i>Carex breviculmis</i>	100 (1)	0	50 (2)	0 (2)	100 (2)	14 (7)
<i>Carpobrotus rossii</i>	0 (2)	0	0	0 (1)	0	0
* <i>Centaurium erythraea</i>	0	0	0	0	0	0 (5)
* <i>Cerastium glomeratum</i>	0	0	0 (3)	0 (1)	0	14 (7)
<i>Corybas</i> spp. <sup>1</sup>	20 (5)	67 (3)	100 (1)	- (3)	-	- (1)
<i>Craspedia glauca</i>	0 (5)	0 (1)	0	0	0	0
<i>Crassula sieberana</i> <sup>3</sup>	- (55)	- (9)	- (33)	0 (124)	0 (16)	0 (15)
<i>Dianella revoluta</i>	100 (7)	0	0	0	0	0
<i>Dicotyledonae</i> spp. <sup>2</sup>	0 (125)	0 (31)	0 (108)	10 (21)	0 (5)	7 (27)
<i>Diuris</i> spp. <sup>1</sup>	93 (14)	100 (2)	85 (27)	- (3)	-	- (8)
<i>Dodonaea viscosa</i>	22 (9)	0 (3)	22 (9)	0 (2)	0	67 (6)
<i>Einadia nutans</i>	0	0	0	0	0	0
<i>Eucalyptus</i> spp.	0 (6)	0 (5)	0 (10)	0 (9)	0 (2)	0 (9)
* <i>Geum</i> spp.	0	0	0	28 (18)	10 (10)	41 (17)
<i>Gonocarpus tetragynus</i>	0	0	0 (3)	0 (1)	0	0
<i>Helichrysum apiculatum</i>	0 (25)	0 (5)	0 (13)	23 (30)	17 (6)	23 (13)
<i>Helichrysum scorpioides</i>	100 (1)	0	0	100 (2)	0	0
<i>Hibbertia riparia</i>	0	0	0	50 (2)	0	0
<i>Hypericum gramineum</i>	0 (2)	0	0 (1)	0	0	0 (1)
* <i>Hypochoeris radicata</i>	0	0	0 (1)	0 (1)	0	100 (6)
<i>Isolepis</i> spp.	0	0	0	100 (1)	0	0
<i>Kennedia prostrata</i>	0 (1)	0	0	0	0	0 (1)
<i>Lepidosperma concavum</i>	0	0	0	0	0	100 (1)
<i>Leptorhynchus squamatus</i>	0 (8)	0 (1)	17 (6)	50 (4)	0	0 (4)
<i>Liliaceae</i> spp.	0 (1)	0	0 (6)	0 (9)	0 (3)	7 (14)
<i>Linum marginale</i>	0 (2)	0	0 (1)	0	0	0
<i>Lomandra longifolia</i>	0	0	0	0	0	0
<i>Luzula meridionalis</i>	0 (1)	100 (1)	50 (8)	75 (12)	100 (1)	24 (17)
<i>Monocotyledonae</i> spp. <sup>2</sup>	0 (13)	0	0 (13)	0 (5)	0	33 (3)
<i>Opercularia varia</i>	0	0	0	0 (1)	0	0
<i>Oxalis perennans</i>	40 (5)	0 (2)	0 (6)	33 (3)	0	33 (3)
<i>Pimelea humilis</i>	0	0	0	0 (1)	0	0
<i>Plantago varia</i>	40 (5)	0	0 (6)	100 (1)	50 (2)	0
<i>Podolepis jaceoides</i>	0 (1)	0	33 (3)	0	0	0
<i>Pterostylis</i> spp. <sup>1</sup>	80 (5)	100 (1)	77 (47)	- (2)	- (1)	- (22)
* <i>Rumex acetosella</i>	50 (4)	0	0 (6)	0	0	0
<i>Schoenus apogon</i>	67 (3)	0	0	63 (8)	0	75 (4)
<i>Scleranthus biflorus</i>	0 (12)	0 (1)	0 (1)	3 (29)	0	0 (2)
<i>Senecio</i> spp.	0 (5)	0 (2)	0	0 (16)	0 (1)	9 (11)
* <i>Silene gallica</i>	0 (2)	0 (1)	0 (2)	100 (2)	0	0 (3)
* <i>Sonchus oleraceus</i>	0	0	0	0 (1)	0	0

(cont.)

## Appendix 3 (cont.)

Species	Survivorship % (Total seedling count)					
	1991			1992		
	M	H	C	M	H	C
<i>Stackhousia monogyna</i>	38 (8)	0 (1)	23 (31)	74 (23)	75 (4)	62 (39)
<i>Thelymitra pauciflora</i> <sup>1</sup>	75 (4)	0	80 (5)	- (1)	-	- (1)
<i>Thysanotus patersonii</i>	57 (7)	50 (2)	57 (14)	50 (4)	0	45 (11)
<i>Velleia paradoxa</i>	100 (1)	0 (4)	23 (13)	88 (8)	100 (1)	72 (18)
<i>Wahlenbergia stricta</i>	0 (24)	0 (13)	11 (9)	8 (85)	6 (18)	6 (50)

Survivorship is until December 1992, excluding new germinants recorded at that time.

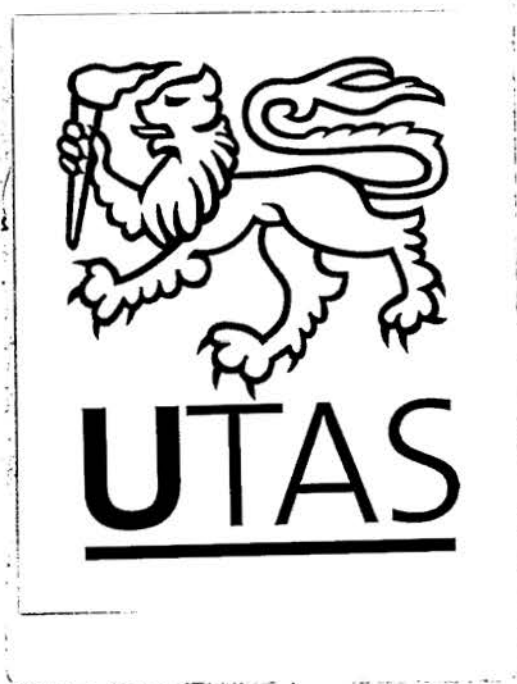
M=mounds; H=holes; C=controls.

<sup>1</sup> ramets and seedlings. Survivorship is for 1991 only, indicating individuals which reappeared in 1992.

<sup>2</sup> unidentified seedlings.

<sup>3</sup> annual species.

\* exotic species.



# Appendix 4 Complete list of vascular plant species mentioned in this thesis.

Nomenclature follows Kirkpatrick *et al.* (1991) for native taxa and Buchanan *et al.* (1989) for exotic taxa. \* denotes exotic species.

<i>Acacia dealbata</i>	Fabaceae
<i>Acacia genistifolia</i>	Fabaceae
<i>Acacia mearnsii</i>	Fabaceae
<i>Acaena echinata</i>	Rosaceae
<i>Acaena novae-zelandiae</i>	Rosaceae
<i>Acianthus exsertus</i>	Orchidaceae
<i>Acianthus</i> spp.	Orchidaceae
<i>Acrotriche serrulata</i>	Epacridaceae
<i>Agrostis aemula</i>	Poaceae
* <i>Agrostis capillaris</i>	Poaceae
<i>Agrostis venusta</i>	Poaceae
* <i>Aira caryophyllea</i>	Poaceae
* <i>Aira elegantissima</i>	Poaceae
<i>Allocasuarina littoralis</i>	Casuarinaceae
<i>Allocasuarina verticillata</i>	Casuarinaceae
<i>Arthropodium milleflorum</i> # with affinities to <i>A. milleflorum</i> )	Liliaceae (possibly an undescribed species)
<i>Astroloma humifusum</i>	Epacridaceae
<i>Bertya rosmarinifolia</i>	Euphorbiaceae
<i>Billardiera procumbens</i>	Pittosporaceae
<i>Bossiaea cinerea</i>	Fabaceae
<i>Bossiaea prostrata</i>	Fabaceae
<i>Brachyloma ciliatum</i>	Epacridaceae
<i>Brachyscome aculeata</i>	Asteraceae
<i>Brachyscome spathulata</i>	Asteraceae
* <i>Briza maxima</i>	Poaceae
* <i>Briza minor</i>	Poaceae
* <i>Bromus diandrus</i>	Poaceae
* <i>Bromus hordeaceus</i>	Poaceae
<i>Brunonia australis</i>	Brunoniaceae
<i>Bulbine glauca</i>	Liliaceae
<i>Bursaria spinosa</i>	Pittosporaceae
<i>Caladenia catenata</i>	Orchidaceae
<i>Caladenia caudata</i>	Orchidaceae
<i>Caladenia clavigera</i>	Orchidaceae
<i>Caladenia dilatata</i>	Orchidaceae
<i>Callistemon pallidus</i>	Myrtaceae
<i>Carex breviculmis</i>	Cyperaceae
<i>Carpobrotus rossii</i>	Aizoaceae
<i>Cassytha pubescens</i>	Lauraceae
* <i>Centaurium erythraea</i>	Gentianaceae
<i>Centrolepis strigosa</i>	Centrolepidaceae

* <i>Cerastium glomeratum</i>	Caryophyllaceae
<i>Chamaescilla corymbosa</i>	Liliaceae
<i>Cheilanthes austrotenuifolia</i>	Sinopteridaceae
* <i>Chenopodium album</i>	Chenopodiaceae
* <i>Chrysanthemoides monilifera</i>	Asteraceae
* <i>Cirsium vulgare</i>	Asteraceae
<i>Comesperma volubile</i>	Polygalaceae
<i>Corybas incurvus</i>	Orchidaceae
* <i>Cotoneaster</i> spp.	Rosaceae
<i>Cotula australis</i>	Asteraceae
<i>Craspedia glauca</i>	Asteraceae
<i>Crassula sieberana</i>	Crassulaceae
* <i>Cupressus</i> spp.	Cupressaceae
<i>Cymbonotus lawsonianus</i>	Asteraceae
<i>Cynoglossum suaveolens</i>	Boraginaceae
* <i>Cynosurus echinatus</i>	Poaceae
* <i>Dactylis glomerata</i>	Poaceae
<i>Danthonia caespitosa</i>	Poaceae
<i>Danthonia pilosa</i>	Poaceae
<i>Danthonia setacea</i>	Poaceae
<i>Daviesia ulicifolia</i>	Fabaceae
<i>Deyeuxia quadriseta</i>	Poaceae
<i>Dianella revoluta</i>	Liliaceae
<i>Dichelachne crinita</i>	Poaceae
<i>Dichelachne inaequiglumis</i>	Poaceae
<i>Dichelachne rara</i>	Poaceae
<i>Dichondra repens</i>	Convolvulaceae
<i>Dillwynia cinerascens</i>	Fabaceae
<i>Diplarrena moraea</i>	Iridaceae
<i>Diuris maculata</i>	Orchidaceae
<i>Diuris sulphurea</i>	Orchidaceae
<i>Dodonaea filiformis</i>	Sapindaceae
<i>Dodonaea viscosa</i>	Sapindaceae
<i>Drosera peltata</i>	Droseraceae
<i>Ehrharta distichophylla</i>	Poaceae
<i>Ehrharta stipoides</i>	Poaceae
<i>Einadia nutans</i>	Chenopodiaceae
<i>Elymus scabrus</i>	Poaceae
<i>Epacris impressa</i>	Epacridaceae
<i>Epilobium billardierianum</i>	Onagraceae
* <i>Epilobium ciliatum</i>	Onagraceae
* <i>Erica</i> spp.	Ericaceae
<i>Eriostemon verrucosus</i>	Rutaceae
<i>Eucalyptus amygdalina</i>	Myrtaceae
<i>Eucalyptus cordata</i>	Myrtaceae
<i>Eucalyptus globulus</i>	Myrtaceae
<i>Eucalyptus pauciflora</i>	Myrtaceae



<i>Eucalyptus pulchella</i>	Myrtaceae
<i>Eucalyptus risdonii</i>	Myrtaceae
<i>Eucalyptus rodwayi</i>	Myrtaceae
<i>Eucalyptus viminalis</i>	Myrtaceae
<i>Euphrasia scabra</i>	Scrophulariaceae
<i>Exocarpos cupressiformis</i>	Santalaceae
<i>Exocarpos strictus</i>	Santalaceae
<i>Festuca</i> spp.	Poaceae
* <i>Fumaria</i> spp.	Fumariaceae
<i>Gahnia radula</i>	Cyperaceae
<i>Gahnia rodwayi</i>	Cyperaceae
<i>Galium</i> spp.	Rubiaceae
<i>Galium australe</i>	Rubiaceae
<i>Geranium solanderi</i>	Geraniaceae
<i>Glycine latrobeana</i>	Fabaceae
<i>Gnaphalium collinum</i>	Asteraceae
<i>Gonocarpus tetragynus</i>	Haloragaceae
<i>Goodenia lanata</i>	Goodeniaceae
<i>Goodenia ovata</i>	Goodeniaceae
<i>Helichrysum apiculatum</i>	Asteraceae
<i>Helichrysum costatifructum</i>	Asteraceae
<i>Helichrysum dendroideum</i>	Asteraceae
<i>Helichrysum obcordatum</i>	Asteraceae
<i>Helichrysum scorpioides</i>	Asteraceae
<i>Hibbertia hirsuta</i>	Dilleniaceae
<i>Hibbertia riparia</i>	Dilleniaceae
* <i>Holcus lanatus</i>	Poaceae
* <i>Hordeum</i> spp.	Poaceae
<i>Hovea linearis</i>	Fabaceae
<i>Hydrocotyle callicarpa</i>	Apiaceae
<i>Hydrocotyle hirta</i>	Apiaceae
<i>Hypericum gramineum</i>	Clusiaceae
* <i>Hypochoeris glabra</i>	Asteraceae
* <i>Hypochoeris radicata</i>	Asteraceae
<i>Indigofera australis</i>	Fabaceae
<i>Isolepis marginata</i>	Cyperaceae
<i>Juncus</i> spp.	Juncaceae
* <i>Juncus articulatus</i>	Juncaceae
<i>Juncus bufonius</i>	Juncaceae
<i>Kennedia prostrata</i>	Fabaceae
<i>Lagenifera stipitata</i>	Asteraceae
<i>Lasiopetalum micranthum</i>	Sterculiaceae
<i>Laxmannia orientalis</i>	Liliaceae
<i>Lepidium hyssopifolium</i>	Brassicaceae
<i>Lepidium pseudotasmanicum</i>	Brassicaceae
<i>Lepidosperma concavum</i>	Cyperaceae
<i>Lepidosperma inops</i>	Cyperaceae

<i>Lepidosperma laterale</i>	Cyperaceae
<i>Lepidosperma lineare</i>	Cyperaceae
<i>Leptorhynchos squamatus</i>	Asteraceae
<i>Leptospermum scoparium</i>	Myrtaceae
<i>Leucopogon virgatus</i>	Epacridaceae
<i>Linum marginale</i>	Linaceae
<i>Lissanthe strigosa</i>	Epacridaceae
* <i>Lolium</i> spp.	Poaceae
<i>Lomandra longifolia</i>	Xanthorrhoeaceae
<i>Luzula meridionalis</i>	Juncaceae
<i>Microtis unifolia</i>	Orchidaceae
* <i>Moenchia erecta</i>	Caryophyllaceae
<i>Odixia achlaena</i>	Asteraceae
<i>Odixia angusta</i>	Asteraceae
<i>Olearia ericoides</i>	Asteraceae
<i>Olearia hookeri</i>	Asteraceae
<i>Olearia myrsinoides</i>	Asteraceae
<i>Olearia ramulosa</i>	Asteraceae
<i>Opercularia varia</i>	Rubiaceae
<i>Oxalis perennans</i>	Oxalidaceae
* <i>Parentucellia viscosa</i>	Scrophulariaceae
<i>Pelargonium inodorum</i>	Geraniaceae
<i>Picris</i> spp.	Asteraceae
<i>Pimelea humilis</i>	Thymelaeaceae
* <i>Pinus</i> spp.	Pinaceae
* <i>Plantago coronopus</i>	Plantaginaceae
* <i>Plantago lanceolata</i>	Plantaginaceae
<i>Plantago varia</i>	Plantaginaceae
<i>Poa hookeri</i>	Poaceae
<i>Poa rodwayi</i>	Poaceae
<i>Poa sieberiana</i>	Poaceae
<i>Poa tenera</i>	Poaceae
<i>Podolepis jaceoides</i>	Asteraceae
<i>Pomaderris pilifera</i>	Rhamnaceae
* <i>Populus</i> spp.	Salicaceae
<i>Poranthera microphylla</i>	Euphorbiaceae
<i>Prasophyllum</i> spp.	Orchidaceae
<i>Pteridium esculentum</i>	Dennstaedtiaceae
<i>Pterostylis alata</i>	Orchidaceae
<i>Pterostylis concinna</i>	Orchidaceae
<i>Pultenaea daphnoides</i>	Fabaceae
<i>Pultenaea humilis</i>	Fabaceae
<i>Pultenaea pedunculata</i>	Fabaceae
<i>Ranunculus</i> spp.	Ranunculaceae
<i>Ranunculus lappaceus</i>	Ranunculaceae
* <i>Rumex acetosella</i>	Polygalaceae
<i>Schoenus apogon</i>	Cyperaceae

<i>Scleranthus biflorus</i>	Caryophyllaceae
<i>Sebaea ovata</i>	Gentianaceae
<i>Senecio glomeratus</i>	Asteraceae
<i>Senecio hispidulus</i>	Asteraceae
<i>Senecio quadridentatus</i>	Asteraceae
* <i>Senecio vulgaris</i>	Asteraceae
* <i>Silene gallica</i>	Caryophyllaceae
<i>Solanum nigrum</i>	Solanaceae
<i>Solenogyne</i> spp.	Asteraceae
* <i>Sonchus oleraceus</i>	Asteraceae
<i>Stackhousia gunnii</i>	Stackhousiaceae
<i>Stackhousia monogyna</i>	Stackhousiaceae
* <i>Stellaria media</i>	Caryophyllaceae
<i>Stenanthemum pimeleoides</i>	Rhamnaceae
<i>Stipa aphylla</i>	Poaceae
<i>Stipa mollis</i>	Poaceae
<i>Stipa pubinodis</i>	Poaceae
<i>Stipa rudis</i>	Poaceae
<i>Stipa semibarbata</i>	Poaceae
<i>Stylidium graminifolium</i>	Stylidiaceae
<i>Taraxacum aristum</i>	Asteraceae
* <i>Taraxacum officinale</i>	Asteraceae
<i>Tetralthea labillardieri</i>	Tremandraceae
<i>Thelymitra epipactoides</i>	Orchidaceae
<i>Thelymitra pauciflora</i>	Orchidaceae
<i>Themeda triandra</i>	Poaceae
<i>Thysanotus patersonii</i>	Liliaceae
* <i>Trifolium</i> spp.	Fabaceae
* <i>Trifolium subterraneum</i>	Fabaceae
* <i>Ulex europaeus</i>	Fabaceae
<i>Velleia paradoxa</i>	Goodeniaceae
<i>Veronica calycina</i>	Scrophulariaceae
<i>Viola hederacea</i>	Violaceae
<i>Vittadinia cuneata</i>	Asteraceae
<i>Vittadinia muelleri</i>	Asteraceae
* <i>Vulpia bromoides</i>	Poaceae
* <i>Vulpia myuros</i>	Poaceae
<i>Wahlenbergia gracilentia</i>	Campanulaceae
<i>Wahlenbergia gracilis</i>	Campanulaceae
<i>Wahlenbergia gymnoclada</i>	Campanulaceae
<i>Wahlenbergia multicaulis</i>	Campanulaceae
<i>Wahlenbergia stricta</i>	Campanulaceae

## Appendix 5 Management implications for rare species.

### *Brunonia australis*

*Brunonia australis* germinates in autumn and winter. The seeds are large and are capable of germinating successfully through litter. The species does not appear to be dependent on mechanical soil disturbance for regeneration, nor is it likely to depend on other disturbance mechanisms such as fire.

### *Lasiopetalum micranthum*

*Lasiopetalum micranthum* is a species which is largely dependent on some kind of disturbance to stimulate regeneration; both fire and mechanical soil disturbance are capable of providing this stimulus. Given the low frequency of natural digging observed in the habitat of *L. micranthum*, fire is probably the more important agent of disturbance. However, it is not known how representative of the longer term these digging rates are, nor whether digging is more intensive in occasional years. There is some evidence that sporadic intense digging does occur on dolerite. For example, the study site at Hospital Creek was selected because of the many diggings visible at the start of the project, but the subsequent digging rate was very low. Similar 'once off' patches of scratching by bandicoots were observed at Bellerive on dolerite. Occasional but intense digging activity may be important for the regeneration of *L. micranthum*.

Although *L. micranthum* is a hard-seeded species with an apparent preference for hot fires (on the basis of oven trials, Chapter 6), cooler burning appears to be adequate to stimulate some regeneration (Chapter 6). Therefore, a burning regime which provides an occasional intense fire may be preferable, but cooler fires will possibly suffice. Protection from intense sheep grazing is another prerequisite for the survival of this species, because it is palatable and grazing heavily depletes seed production.

*Lepidium hyssopifolium* and *L. pseudotasmanicum*

Experimental soil disturbances stimulated the germination and establishment of both *Lepidium hyssopifolium* and *L. pseudotasmanicum*. The responses were so strong, that it seems very likely that natural soil disturbances created by bettongs and bandicoots should favour the establishment of *L. hyssopifolium* at Annandale, at least in some years. The combination of a long-lived soil seed bank and the bringing of seed to the surface by animal digging, could be an asset in enabling *L. hyssopifolium* to await a suitable year for establishment.

The management of the road verge population of *Lepidium hyssopifolium* at Bagdad presents considerable problems. It is relatively easy to stimulate germination of this species, by applying simple mechanical disturbance, but the exotic species which regenerate vegetatively must be controlled. A somewhat drastic but perhaps necessary approach may be to scrape away the top 5 cm of soil to remove seed and roots of exotic species, plant advanced seedlings of local native trees (e.g. *Acacia mearnsii*, *Eucalyptus viminalis*), broadcast *L. hyssopifolium* seed in June and August around tree seedlings (some seed of *L. hyssopifolium* should still be present in the soil) and mow regularly (if necessary) until seedlings of *L. hyssopifolium* have bolted. Selective herbicide application may be needed to continue to keep exotic grasses and forbs at bay, until the density of the tree canopies is sufficient to maintain reasonably bare areas underneath.

*Odixia achlaena*

In the natural situation, *Odixia achlaena* only germinates in response to fire (Chapter 5), and the stimulus appears to be a change in some factor(s) in the soil which is induced by heating (Chapter 6). Given the higher germination with a longer period of soil heating, germination may be more prolific after a moderately intense fire compared with a cool fire, although more work is needed to confirm this. Mechanical soil disturbance created by mammals does not provide a stimulus, nor does it present microsite conditions which are more favourable for the survival of seedlings of this species. In fact survival

of seedlings on holes is poorer than on undug areas, presumably because of some adverse condition associated with deep litter accumulation.

The life history of *O. achlaena* makes it a species with a very fragile reliance on an appropriate disturbance regime. Plants appear to be short-lived (perhaps less than 15-20 years) and adults are killed outright by fire. The permanent store of seed in the soil is apparently not large, at least not compared with northern hemisphere examples (e.g. Roberts, 1981). Therefore the species could easily be eliminated from a site where it is now prolific, if the site was burnt by two fires in quick succession (the juvenile period is at least 4 years), or was unburnt for a long period. It is therefore not surprising that *O. achlaena* occurs in intermittent, dense patches within its very limited geographic range.

Gill & Nicholls (1989) suggest that, as a rule of thumb, the appropriate burning interval for fire-sensitive species should be at least twice the juvenile period. When the juvenile period of *O. achlaena* is known, this rule of thumb can be applied as an initial management guideline, pending more detailed knowledge of its response to that burning regime.

### *Velleia paradoxa*

*Velleia paradoxa* germinates readily in each year from autumn until late winter and the density of germinants appears to be higher on bandicoot diggings compared with areas with more litter cover. A relatively high proportion of seedlings survive, at least in the short-term, as may be expected because of the large size of the seeds. The short-term survival of seedlings is neither better nor worse on diggings compared with undisturbed ground. I suggest that the main requirement for the regeneration of this species is the availability of bare ground and that this may be provided by animal disturbance or fire.

*Velleia paradoxa* lacks a permanent store of seed in the soil and would therefore be particularly vulnerable to depletion if grazed repeatedly during the period of seed production.

*Vittadinia muelleri*

*Vittadinia muelleri* germinated prolifically on the bare areas created in a simulated animal digging experiment. This species grows mainly on dolerite soils, where mechanical soil disturbance by mammals is not frequent (Chapters 2 & 4), but may occur sporadically in intense patches. *Vittadinia muelleri* may benefit from other processes that create bare soil e.g. fire or grazing. It is probable that at least one of these disturbance mechanisms is necessary to maintain populations of this species, unless bare ground is feature of the particular habitat (e.g. on rock plates).

*Other rare species*

No germination of *Olearia hookeri* or *O. ericoides* was observed in the field during this study, either on or off mammal diggings. Like *Odixia achlaena*, these Asteraceae shrubs probably depend on fire to provide the stimulus for germination—*O. hookeri* is known to regenerate prolifically after fire. Given the extremely bare soil surface in the habitat of *O. hookeri*, it is difficult to conceive how digging mounds could provide any resource to benefit *O. hookeri* seedlings. Litter accumulation in holes would probably be as detrimental to *O. hookeri* seedlings as it is for those of *O. achlaena* (Chapter 5).

No germination of *Gahnia rodwayi* was observed at Chimney Pot Hill, either on or off diggings, although it had colonised bare soil on road batters at the same site. Attempts were made to germinate this species in the laboratory, with a variety of heat treatments, but these were unsuccessful. The germination requirements of *G. rodwayi* are still not known.

No germinants of *Glycine latrobeana* were observed at Powranna. *Glycine latrobeana* is a hard-seeded species and, based on work on the closely related *G. clandestina* (Auld & O'Connell, 1991), probably requires fire to break seed dormancy. High levels of predation on pods were observed at this site and may have been responsible for limiting seed production.



*General comments*

In places such as the Waverley Flora Park at Bellerive, where mammal digging is abundant and possibly plays a role in the regeneration of a number of plant species, it is desirable to maintain populations of the digging mammals as part of the overall strategy to maintain the full diversity of native plant species (as well as protecting the animals in their own right of course). Unfortunately, this is a small bush remnant with intense pressures on the populations of bandicoots; three were found dead after mauling by dogs during this study and another was observed being hotly pursued by a large German shepherd. Thus, while any management of a nature reserve of this size will be intensive and costly, the maintenance of populations of bandicoots may well prove more difficult than the maintenance of the populations of rare (and common) plant species. The mechanical soil disturbance can easily be simulated, but the bandicoots may well require protection from exotic predators and possibly re-introductions to maintain gene flow.

The imposition of artificial mechanical soil disturbance may be an option in efforts to manage populations of rare plant species, even as a substitute for other vegetation influences such as fire and grazing, where these cannot be imposed for what ever reasons. It is necessary to keep in mind that mechanical soil disturbance may also encourage the proliferation of exotic species. For this very reason, there is certainly a widely held belief amongst managers of grassy vegetation in south-eastern Australia that all mechanical soil disturbance is bad. This may well be the case in some situations, but mechanical soil disturbance which simulates two key conditions provided by mammal digging: a low nutrient soil surface with a smaller seed bank of exotics, could be of overall benefit to some native species.

The Tasmanian bettong is now extinct on the Australian mainland, but would have no doubt caused the same levels of soil disturbance as in Tasmania within its former geographical range. There are many important grassland and grassy woodland areas in Victoria which occur on nutrient poor soils, which are the soils most intensively dug by bettongs and bandicoots in Tasmania (Taylor, 1992a; Chapters 2 & 4). The absence of appropriate digging from these ecosystems may be an important factor, not only for the

germination and establishment of understorey species, but possibly for the trees as well (Taylor, 1991). The loss of soil disturbance which was formerly caused by indigenous Australians may be an important ecological consideration on more productive soils, given the intense plant competition in these areas.

Some rare species in Tasmania occur mostly in bush remnants which no longer sustain populations of digging mammals. For these populations, mechanical soil disturbance by mammals is no longer an option. Land managers in Tasmania and Victoria may have to consider substituting analogous soil disturbance to maintain the diversity of species in some grasslands and grassy woodlands, where soil disturbance is no longer present. The management options for small remnants of grassy vegetation need to be flexible, experimental and open to change, because we still know very little about the regeneration and disturbance requirements of most native species.