FACTORS LIMITING THE RECRUITMENT OF *EUCALYPTUS SALMONOPHLOIA* F. MUELL. (SALMON GUM)

This thesis is presented for the degree of
Doctor of Philosophy of Murdoch University

1994

Submitted by

Colin John Yates

B. Sc. (University of Western Australia)
B. Sc. Hons (Australian National University)

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary educational institution.

C. J. Yates

Colin John Yates

ABSTRACT

Woodlands dominated by *Eucalyptus salmonophloia* F. Muell. occur throughout the fragmented landscape of the Western Australian wheatbelt. In most of these remnant woodlands there is no regeneration of *E. salmonophloia* and this has become a concern for the conservation of biodiversity in the region. The research reported in this thesis contributes to solving this problem firstly by describing aspects of *E. salmonophloia's* life history, and secondly by documenting the conditions under which recruitment has occurred in unfragmented populations to the east of the Western Australian wheatbelt.

Pattern of flowering, seed production, seed viability, pattern of seed fall, post dispersal seed predation, soil seed reserves and factors affecting germination and establishment were investigated. These studies revealed that *E. salmonophloia* has a suite of life history characteristics that are common to *Eucalyptus* spp. which recruit seedlings following fire. In particular during inter-fire periods these include a canopy stored seed reserve; a light seed rain from this reserve; high rates of seed predation by ants following dispersal; the absence of a soil seed reserve; and a low probability of seedling establishment should a seed escape predation and germinate.

Given the life history characteristics, the study examined the response of unfragmented *E. salmonophloia* woodlands to the east of the wheatbelt, to disturbance caused by fires and also floods, windstorms and drought. Woodlands known to have experienced disturbances of these types in the last 50 years were found to have cohorts of similar sized *E. salmonophloia* saplings, this contrasted with undisturbed woodlands. Sites disturbed either by fire, flood or wind storm during 1991/92 displayed adult tree mortality and extensive seedling establishment; although rates of establishment and survival varied between sites. No regeneration was observed at equivalent undisturbed sites. These results indicate that not only fire but several other types of large scale disturbance facilitate seedling recruitment in *E. salmonophloia*. Increases in resource availability in the post-disturbance environment were measured and the processes responsible discussed. It is postulated that increased resource availability is, at least in part, responsible for enhanced seedling recruitment.

This study suggests that large scale natural disturbances of several types are important drivers of the dynamics of *E. salmonophloia* woodlands. The known lack of recruitment in remnant woodlands is likely to be due to changes in the disturbance regime and/or changes in the ability of *E. salmonophloia* to regenerate successfully following disturbance. The effects of fragmentation and surrounding agricultural land use on these processes are discussed. The implications of these findings for management of remnant woodlands are considered and areas for further research are suggested.

ACKNOWLEDGMENTS

I would like to thank my supervisors Richard Hobbs and Richard Bell for their encouragement, guidance, moral support, and constructive criticism throughout this project. Additionally, thanks is extended to Ross Taplin for statistical advice; Steve Hopper for comments on manuscripts; Anne Brandenberg, Phil Ladd, Robert Lambeck, Patrick Piggott and Geoff Stoneman for fruitful discussions; Don Couper for assistance with locating sites in the wheatbelt and provision of rainfall data; the Riley family and the Western Australian Department of Lands Administration for access to remnant woodlands in the Kellerberrin area; Ian Kealley, Andrew Chapman, Phil Grey, Bill Brennan and the Western Australian Department of Conservation and Land Management for assistance with location and access to sites in the goldfields and Peak Charles; Lyn Atkins for general technical support; Shona Kennealley, Caroline McKenzie, Matthew Tchan and Craig Wilson for help with field work; and Alison Yates for assistance with the construction of seed traps.

The support and continued encouragement of my family is gratefully acknowledged; and last but not least, thanks to Sue Yates for her support and sense of humour throughout this thesis.

PUBLICATIONS

The publications listed below form the basis for parts of this thesis:

Yates, C.J., Hobbs, R.J., and Bell, R.W. (1994). Landscape scale disturbances and regeneration in semi-arid woodlands of southwestern Australia. *Pacific Conservation Biology* **1**, 214-221.

Yates, C.J., Hobbs, R.J., and Bell, R.W. (1994). Factors limiting the recruitment of *Eucalyptus salmonophloia* in remnant woodlands. I. Pattern of flowering, seed production and seed fall. *Australian Journal of Botany* **42**, 531-542.

Yates, C.J., Taplin, R., Hobbs, R.J., Bell, R.W. (1995). Factors limiting the recruitment of *Eucalyptus salmonophloia* in remnant woodlands. II. Post dispersal seed predation and soil seed reserves. *Australian Journal of Botany* **In press 43 (2)**.

TABLE OF CONTENTS

CHAPTER 2: PATTERN OF FLOWERING, SEED PRODUCTION AND SEED FALL

CHAPTER 3: POST-DISPERSAL SEED PREDATION AND SOIL SEED RESERVES

CHAPTER 4: RECRUITMENT OF *E. SALMONOPHLOIA* SEEDLINGS FOLLOWING LANDSCAPE-SCALE DISTURBANCES IN UNFRAGMENTED WOODLANDS

CHAPTER 5: CONDITIONS NECESSARY FOR SEED GERMINATION IN *E. SALMONOPHLOIA*

CHAPTER 6: CHANGES IN RESOURCE AVAILABILITY FOLLOWING LANDSCAPE SCALE DISTURBANCES AND THEIR POTENTIAL IMPACT ON THE ESTABLISHMENT OF *E. SALMONOPHLOIA* SEEDLINGS

CHAPTER 7: THE EFFECTS OF WATER AND NUTRIENT AVAILABILITY ON THE EARLY GROWTH OF *E. SALMONOPHLOIA* SEEDLINGS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The fragmentation of natural ecosystems by human action is one of the major threats to biodiversity worldwide. The fragmentation process reduces the area of native ecosystems and leaves isolated remnants of native vegetation which are subject to species loss, invasions by non-native species and changes in population and ecosystem processes (Schafer 1990; Saunders *et al.* 1991; Bierregaard *et al.* 1992; Hobbs 1993).

The widespread and rapid clearance of mediterranean ecosystems in Australia for cereal growing and its detrimental effect on biodiversity has received increasing attention over the last ten years (Saunders *et al.* 1987; Hobbs 1992; Saunders *et al.* 1993; Sivertsen 1994). This thesis concerns itself with an aspect of this problem in the wheatbelt of Western Australia. This region has a Dry Mediterranean climate characterized by hot dry summers and cool wet winters (Details in Chapter 2).

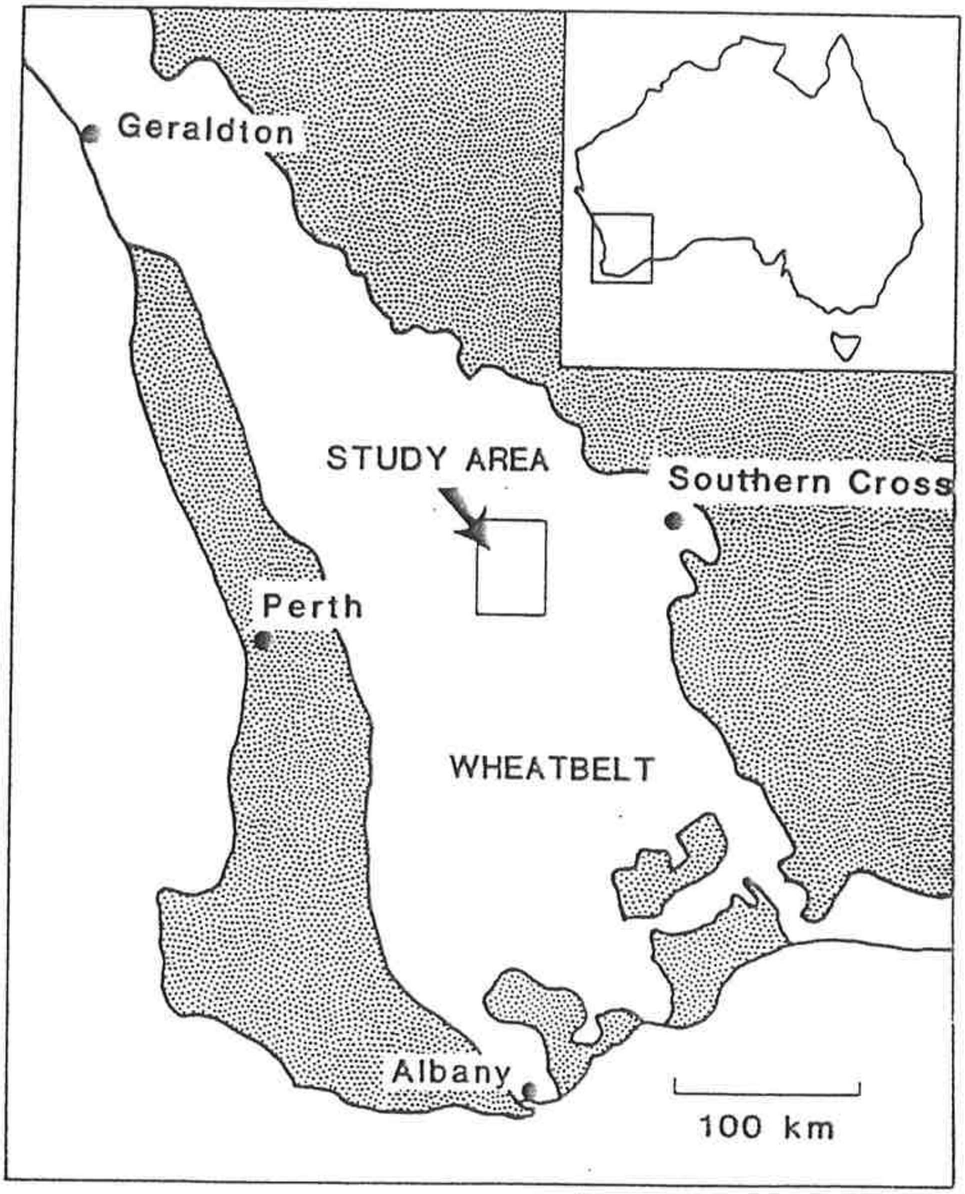
The landscape in this region is gently undulating and generally of low relief, except where occasional granite outcrops protrude. The soils are closely related to the landforms and have developed through the differential erosion of an ancient laterised land surface; as a consequence they generally have low concentrations of essential plant nutrients. Native plant species in the region have evolved a wide array of mechanisms allowing them to grow on depauperate soils in a climate with seasonal summer drought and high temperatures and comprise of a complex mosaic of vegetation associations, their distribution determined by rainfall, soils and landforms (Lamont 1984; Pate and Dell 1984; Pate *et al.* 1984; Beard 1990; Groves and Hobbs 1992). Generally, Kwongan scrub heath grows on sandy lateritic upland soils; mallee *Eucalyptus* woodlands on the duplex soils of upper valley slopes; *Eucalyptus* woodlands on the sandy loams, loams, and heavy loams found on mid to lower slopes and valley floors; and finally halophytes on saline soils in valley floors and salt lakes. The unweathered granite outcrops are generally surrounded by *Eucalyptus* woodlands growing on grey sandy soils (Beard 1990).

Since European settlement 93% of the native vegetation in this region has been cleared, resulting in the transformation of natural ecosystems to predominantly agricultural, producing an entirely new landscape mosaic of agricultural land, salt pans and native vegetation remnants (Saunders *et al.* 1993). What now exists is a highly fragmented landscape with many small remnants of native vegetation (Hobbs 1992). For example, in a 1680 km^2 area of the central wheatbelt Arnold and Weeldenberg (1991) mapped 459 patches of remnant vegetation, 270 of these were less than 10 ha and 353 less than 20 ha; overall the remnants ranged in size from 1 ha to 1030 ha.

It is in this assemblage of remnants that the regions remaining biodiversity exists (Saunders *et al.* 1993). Clearly, this situation presents many problems for nature conservation. The reduction and isolation of habitat, species extinctions and the introduction of feral animals and exotic weeds have resulted in new biotic assemblages and changes to population and ecosystem processes (Hobbs *et al.* 1992; Hobbs 1993; Saunders *et al.* 1993; Scougall *et al.* 1993). As a consequence many remnants of native vegetation are unlikely to persist in the long term without efforts to ameliorate these changes (Main 1987; Hobbs and Hopkins 1990; Hobbs 1993; Lambeck and Saunders 1993; Saunders *et al.* 1993).

In response to this problem the national research organisation, CSIRO Division of Wildlife and Ecology, commenced a study on the ecological dynamics of remnant vegetation in the Western Australian wheatbelt. This was undertaken with a view to developing management strategies that would contribute to the conservation of the region's biodiversity (Saunders *et al.* 1993). Most of the research is being undertaken in a 1680 km^2 region of the central wheatbelt north of the town Kellerberrin (Saunders *et al.* 1993) (Figure 1.1). The subject of this thesis contributes to that programme.

Figure 1.1: The extent of the Western Australian Wheatbelt and location of the CSIRO remnant vegetation study area.

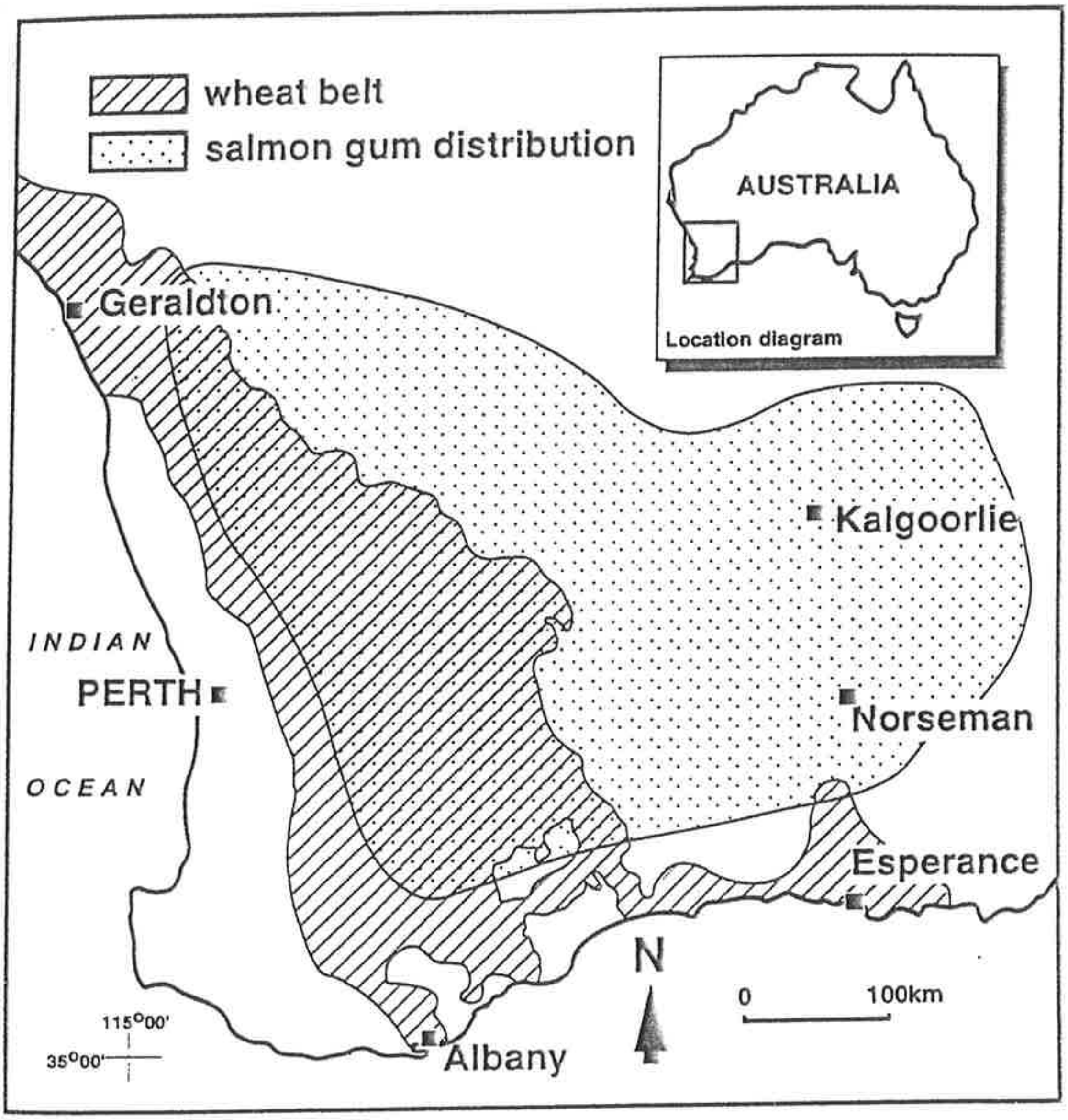


Prior to European settlement and the subsequent clearing, woodlands dominated by *Eucalyptus salmonophloia* F. Muell. (salmon gum) or a mixture of *E. salmonophloia* and other *Eucalyptus* spp. occurred extensively throughout the Western Australian wheatbelt and extended into the adjacent goldfields region (Figure 1.2). These woodlands were preferentially cleared for agriculture because they grew on the heavier more fertile soils and were considered indicators of good farmland (Burvill 1979). Beard and Sprenger (1984) have estimated that in the wheatbelt 20% of the *E. salmonophloia* woodlands remain. In some areas this may constitute only 0.4% of the landscape (Arnold and Weeldenberg 1991). As a consequence, *E. salmonophloia* woodlands are relatively under represented in the remaining vegetation and occur in isolated remnants or on road verges. Many of these are degraded, and in most cases there is little or no regeneration of *E. salmonophloia* . Norton *et al.* (1994) observed in the central wheatbelt that in 57% of salmon gum woodland remnants there were no trees with a diameter at breast height (DBH) of less than 10 cm and in 28% of remnants there were no trees with a DBH less than 20 cm.

Whilst it is difficult to speculate on the size class structure of *E. salmonophloia* prior to fragmentation, observations of unfragmented populations to the east of the wheatbelt indicate that trees are unevenly distributed amongst size classes and cohorts of similar sized saplings (< 10 cm DBH) occur in patches amongst older trees (Yates *et al.* 1994).

These observations of size class distributions suggest that the processes which underlie recruitment in *E. salmonophloia* may have been upset by the impacts of agricultural development. The absence of juvenile trees in many remnants of salmon gum woodland has therefore become a concern for the conservation of biodiversity in the wheatbelt. Clearly, without recruitment remnant woodlands will disappear as mature trees die. This has important implications for wildlife management as *E. salmonophloia* produces the majority of habitat hollows in the region (Saunders 1979; Saunders *et al.* 1982; Saunders and Ingram 1987; Abensperg-Traun and Smith 1993).

Figure 1.2: The distribution of *E. salmonophloia* woodlands.



For recruitment to occur trees have to flower, the flowers have to be pollinated, and set and disperse viable seed; the seed then has to escape predation so that it can be incorporated into a soil seed bank where it must persist until the right conditions stimulate germination; the young plant then has to survive and grow (Harper 1977). The conservation of any plant species requires an understanding of the processes which regulate the movement of individuals through these life cycle stages (Harper 1977; Auld 1990). Events which are rare may be particularly important in this respect. For example *E. salmonophloia* is widely distributed across a region with a seemingly reliable mediterranean climate. However, there are events which can cause considerable deviations from this picture. These include tornadoes and severe storms, associated with thunderstorms and intense cold fronts (Clarke 1962; Minor *et al.* 1980); heavy rain associated with thunderstorms and decaying tropical cyclones (Pierrehumbert 1973; Lourenz 1981); drought, when annual rainfall is well below average (Fitzpatrick 1970; Southern 1979); and lastly, fires which occur following certain sequences of the above events. Main (1987) suggested that the above events, although rare, may be amongst the most important processes driving the dynamics of native ecosystems in the wheatbelt. Indeed this has been shown to be the case for many ecosystems elsewhere. The literature on the physical disturbance of ecosystems by episodic events is vast and has been reviewed by multiple authors in Pickett and White (1985) and more recently by Attiwill (1994). In many plant species disturbance provides the opportunity for seedling recruitment (Pickett and White 1985; Attiwill 1994).

Currently, little is known about the processes that underly seedling recruitment in mediterranean climate *Eucalyptus* woodland species including *E. salmonophloia* . As a consequence there are no scientific guidelines for managing the remaining wheatbelt populations.

The research reported in this thesis aims to understand the processes which underly seedling recruitment in *E. salmonophloia* and determine which of these processes has been disrupted and therefore responsible for the lack of seedling recruitment in the remnant woodlands.

This document is structured such that Chapter 2 investigates the pattern of flowering, seed production and seed dispersal in *E. salmonophloia* to determine whether the availability of viable seed is limiting recruitment in remnant woodlands. Following dispersal, seed has to escape predation so that it may be incorporated into a soil seed bank. Chapter 3 looks at the fate of *E. salmonophloia* seed once it has been dispersed and investigates whether seed eating ants are responsible for the absence of recruitment in remnant woodlands. As discussed earlier, uncommon natural events may drive native ecosystem dynamics throughout *E. salmonophloia's* distribution. Chapter 4 investigates the effects of large scale natural disturbances on *E. salmonophloia* populations in unfragmented woodlands to the east of the wheatbelt to determine the role of such events. Chapters 5, 6 and 7 examine the conditions which influence the germination and establishment of *E. salmonophloia*. Finally in Chapter 8 the findings of the research are synthesized and discussed.

CHAPTER 2

PATTERN OF FLOWERING, SEED PRODUCTION AND SEED FALL

2.1 INTRODUCTION

As discussed in Chapter 1, there appears to be little or no recruitment of *E. salmonophloia* seedlings in remnant woodlands throughout the Western Australian wheatbelt. It was suggested that the effects of habitat fragmentation and impacts of surrounding agricultural land use may have affected the population and ecosystem processes which sustain these woodlands. The disruption of reproductive processes and the resultant lack of viable seeds may be important in this respect. This chapter aims to determine if this is the case for *E. salmonophloia* by examining, flowering, seed production, seed viability and seed dispersal in remnant woodlands.

2.2 METHODS AND MATERIALS

2.2.1 STUDY SITES

The study was undertaken within a 1680 km^2 area north of Kellerberrin in the central Western Australian wheatbelt approximately 200 km east of Perth (approximately 117^o 45' E, 31^o 23'S) (Figure 1.1). This area has been the focus of research into the ecological dynamics of remnant vegetation and its associated fauna (Saunders *et al.* 1993). The region has a Dry Warm Mediterranean climate (Beard 1990) typical of the wheatbelt with a mean annual rainfall of 334 mm which falls predominantly in the winter months between May and September (Western Australian Bureau of Meteorology Records). Summer rainfall associated with thunderstorms and decaying tropical cyclones occurs but is unpredictable.

The annual rainfall variability is considered to be low to moderate and the mean number of rainfall days is 75 (Southern 1979; Western Australian Bureau of Meteorology Records). Mean maximum temperature ranges from approximately 34°C in January to 16°C in July (Western Australian Bureau of Meteorology Records). Evaporation exceeds rainfall in all months and by 2000 mm over a whole year (McFarlane *et al.* 1992). The study area lies approximately in the middle of *E. salmonophloia's* distribution. Taking into consideration that rainfall is higher on the western edge of the species distribution (approximately 450 mm) and lower on the eastern edge (between 200 and 250 mm) (Chippendale 1973), the Kellerberrin study area's climate is representative of *E. salmonophloia's* entire distribution.

Salmon gum woodlands occupied 16% of the Kellerberrin study area prior to clearing (based on estimates from soil types) but now comprise only 0.4% of the total area (Arnold and Weeldenburg 1991). Salmon gum woodlands are found predominantly on the broad alluvial valley floors on calcareous red earths but also occur to a lesser extent on different soil types elsewhere in the landscape (McArthur 1991, 1992). Norton *et al.* (1994) found only 14 fragments and 14 roadside corridors of salmon gum woodland in the study area. The choice of sites was therefore limited. Moreover the shape, size, extent of degradation, proximity to other vegetation and position in the landscape of these remnants was highly variable and therefore replication of sites with similar characteristics impossible. As a consequence, four remnants with diverse characteristics were chosen to encompass the variation present (Table 2.1). Remnants containing *E. salmonophloia* woodland were chosen in different positions of the landscape. These included woodlands on valley floors with red duplex soils and woodlands on an upper slope and adjacent to a granite outcrop on yellow duplex soils (Northcote 1971; McAurthur 1992). The remnants contained other vegetation associations adjacent to *E. salmonophloia* woodland and varied in size from 20-150 ha. The area of *E. salmonophloia* woodland in each remnant varied from 2.4-47 ha (Table 2.1).

At each site, in areas with similar tree densities, six 50 m transects spaced 5 m apart were laid out and on each transect 11 points spaced 5 m apart were marked to create a 50 m x

Table 2.1: Characteristics of the four study sites. Values for % litter cover are arithmetic means of 20 replicate observations and values for % shrub and herb cover are arithmetic means of four replicate observations.

	Sites			
	Moore's East	Gents Rd	Minniberri	Huandanning
Area of remnant (ha)	150	20	113	40
Area of *E. salmonophloia* woodland within remnant (ha)	2.4	12.9	47	12
Landscape position	Upper slope	Valley floor	Valley floor	Upper slope below granite outcrop
Soil type	Yellow duplex	Red duplex	Red duplex	Yellow duplex
Grazing history	Rarely grazed	Heavily grazed	Rarely grazed	Rarely grazed
% litter cover	61	35	61	62
% shrub and herb cover	55	10	58	45
Rainfall (mm) 1991/1992	385	313	308	331
Rainfall (mm) 1992/1993	389	299	316	346

25 m grid with 66 locations. In each grid, the stem diameter at breast height was measured for each *E. salmonophloia* individual and placed in a size class 0-10 cm, 11-20 cm, 21-40 cm, 41-80 cm and >80 cm. *E. salmonophloia* was the only tree species present in the grids and densities of between 72 -104 stems ha^{-1} were recorded. Trees at each site were mainly confined to the 21-40 cm size class and 41-80 ha size class. There were no trees in the 0-10 cm size class (Table 2.2).

As an indication of the species associated with *E. salmonophloia*, the vascular plant species were identified in the 25 m x 50 m grids at each site (Table 2.3 a, b, c, d). Species authors are listed by Green (1985) and Marchant *et al.* (1987). Non-native annual species were present at each site.

At four random locations on each grid, the percentage cover of shrubs and herbs were assessed in 5 m by 5 m quadrats and a mean cover value calculated (Table 2.1). Similarly, at 20 random locations on each grid, the percentage cover of litter was assessed in 50 cm x 50 cm quadrats and a mean cover value calculated (Table 2.1).

Three of the remnants, Moore's East, Minniberri Reserve and Huandanning Water Reserve, are apparently healthy woodlands with an intact understorey and have a history of little or no grazing by livestock (Table 2.1, Table 2.3 a, c, d). In contrast the fourth remnant, Gents Rd, is frequently grazed by sheep, and as a consequence has a depleted understorey of unpalatable shrubs, large areas of exposed soil and reduced litter cover, and is badly degraded (Table 2.1, Table 2.3 b).

Rainfall at each site was recorded in storage rain gauges which were emptied at 2 month intervals coinciding with surveys of flowering (see below). Rainfall at each site over the study period was just below or above the long term average for Kellerberrin (Table 2.1).

Table 2.2: The frequency of *E. salmonophloia* individuals in stem diameter classes (DBH cm) at the four study sites in 1250 m^2 sampling grids.

	Sites			
Size class (DBH)	Moore's East	Gents Rd	Minniberri	Huandanning
0-10 cm	0	0	0	0
11-20 cm	0	0	1	1
21-40 cm	5	5	8	8
41-80 cm	5	4	4	1
>80 cm	1	0	0	1

Table 2.3 a: The vascular plant species present in the 25 m x 50 m grid at Moore's East. Species preceded by * are non-native.

Trees	Shrubs	Herbaceous	Annuals
Eucalyptus salmonophloia	*Acacia acuarea*	*Amphipogon caricinus*	*Actinoble uliginosum*
	Acacia erinacia	*Borya sphaerocephala*	*Arctotheca calendula
	Alyxia buxifolia	*Danthonia caespitosa*	*Blennospora drummondii*
	Dodonaea bursariifolia	*Dianella revoluta*	*Brassica tournefortii
	Enchylaena lanata	*Lepidosperma sp.*	*Bromus diandrus
	Olearia revoluta	*Lomandra effusa*	*Bromus rubens
	Olearia muelleri	*Loxocarya sp.*	*Calandrinia eramaea*
	Rhagodia preissii	*Neurachne alopecuroidea*	*Calandrinia polyandra*
		Stipa elegantissima	*Calotis hispidula*
		Stipa hemipogon	*Crassula colorata*
			Dichopogon sp.
			*Ehrarta longiflora
			Erodium cygnorum
			Goodenia beardiana
			*Hypochaeris glabra
			Lawrencia lindleyi
			*Lolium perenne
			*Mesembryanthemum crystallinum
			Millotia tenuifolia
			*Osteospermum clandestinum
			*Pentaschistis airoides
			Podolepis capillaris
			Podotheca angustifolia
			Podotheca gnaphalioides
			Rhodanthe pygmaea
			Schoenia cassiniana
			Senecio glossanthus
			*Sonchus oleraceus
			Trachymene cyanopetala
			Triglochin calcitrapa
			Ursinia anthemoides
			Waitzia acuminata

Table 2.3 b: The vascular plant species present in the 25 m x 50 m grid at Gents Rd. Species preceded by * are non-native.

Trees	Shrubs	Herbaceous	Annuals
Eucalyptus salmonophloia	*Acacia acuaria*	*Stipa elegantissima*	*Actinobole uliginosum*
	Acacia erinacea		**Arctotheca calendula*
	Enchylaena lanata		**Brassica tournefortii*
	Exocarpus aphyllus		**Bromus rubens*
	Scaevola spinescens		*Calandrinia eramaea*
			Calandrinia polyandra
			Calotis hispidula
			Crassula colorata
			**Hordeum leporinum*
			**Hypochaeris glabra*
			**Mesembryanthemum crystallinum*
			**Mesembryanthemum nodiflorum*
			**Oxalis pes - caprae*
			**Pentaschistis airoides*
			Ptilotus sp.
			**Rhodanthe spicata*
			**Spergularia salina*
			**Sisymbrium orientale*
			**Trifolium sp.*
			**Triticum aestivum*
			**Vulpia myuros*

Table 2.3 c: The vascular plant species present in the 25 m x 50 m grid at Minniberri. Species preceded by * are non-native.

Trees	Shrubs	Herbaceous	Annuals
Eucalyptus salmonophloia	Acacia acuaria	Carpobrotus modestus	*Arctotheca calendula
	Acacia chrysella	Danthonia caespitosa	Asteridea athrixioides
	Acacia colletioides	Dianella revoluta	*Brassica tournefortii
	Acacia hemiteles	Stipa elegantissima	*Bromus sp.
	Acacia merrallii	Stipa scabra	Calandrinia eramaea
	Alyxia buxifolia		*Centaurea melitensis
	Atriplex sp.		Cephalipterum drummondii
	Cassia nemophylla		Dauchus glochidiatus
	Enchylaena lanata		Erodium cygnorum
	Eremophila decipiens		Goodenia convexa
	Eremophila desertii		*Hordeum leporinum
	Eriochiton sclerolaenoides		*Hypochaeris glabra
	Exocarpus aphyllus		*Lolium perenne
	Lycium sp.		*Lupinis cosentinii
	Maireana trichoptera		*Mesembryanthemum crystallinum
	Maireana sp.		*Osteospermum clandestinum
	Maireana sp.		*Plantago sp.
	Olearia muelleri		Ptilotus holosericeus
	Pimelia microcephala		Ptilotus polystachyus
	Rhagodia drummondii		Ptilotus spathulatus
	Rhagodia preissii		Rhodanthe spicata
	Santalum acuminatum		Senecio glossanthus
	Scaevola spinescens		*Sonchus oleraceus
	Sclerolaena diacantha		Streptoglossa liatroides
	Templetonia sulcata		*Trifolium sp.
			*Triticum aestivum
			Waitzia nitida
			Waitzia acuminata
			Zygophyllum fruticulosum
			Zygophyllum glaucum
			Zygophyllum ovatum

Table 2.3 d: The vascular plant species present in the 25 m x 50 m grid at Huandanning. Species preceded by * are non-native.

Trees	Shrubs	Herbaceous	Annuals
Eucalyptus salmonophloia	*Acacia acuaria*	*Danthonia caespitosa*	*Actinobole uliginosum*
	Acacia erinacea	*Lomandra effusa*	**Arctotheca calendula*
	Acacia hemiteles	*Stipa elegantissima*	**Brassica tournefortii*
	Atriplex sp.		**Bromus diandrus*
	Enchylaena lanata		**Bromus rubens*
	Eremophila decipiens		*Calandrinia eramaea*
	Eremophila ionantha		*Calandrinia polyandra*
	Hakea preissii		*Calandrinia granulifera*
	Rhagodia drummondii		*Calotis hispidula*
	Rhagodia preissii		*Cotula bipinnata*
	Templetonia sulcata		*Crassula colorata*
			Eremophyllum tenellum
			**Hypochaeris glabra*
			Lepidium rotundum
			**Medicago truncatula*
			**Mesembryanthemum crystallinum*
			Parietaria cardiostegia
			Pentaschistis airoides
			Podolepis capillaris
			Podotheca gnaphalioides
			Rhodanthe citrina
			Ursinia anthemoides
			Senecio glossanthus
			**Sonchus oleraceus*
			Trachymene ornata
			**Vulpia myuros*
			Waitzia acuminata

2.2.2 PATTERN OF FLOWERING AND SEED PRODUCTION

All trees (Table 2.2) within the 50 m x 25 m experimental grids were surveyed with binoculars every 2 months from August 1991 until October 1993 and observations made on the presence or absence of flowers.

In August 1991, ten sampling traps were located on the experimental grid at each site; five beneath tree canopies and five in gaps between tree canopies. Each trap consisted of a 44 cm diameter (0.15 m^2 opening) x 30 cm deep canvas cone attached to a steel ring suspended 1 m above the ground on three metal posts, and secured at the bottom to prevent the contents from being dislodged. Ants and other invertebrates were excluded from the traps by a "tangletrap" barrier at the base of each post. Canopy cover over seed traps was assessed using a converse spherical densiometer and data were analysed using a two-way analysis of variance to determine if differences existed between sites and trap positions.

The contents of sampling traps were collected every 2 months until October 1993 and opercula, flowers, immature and sterile fruits sorted. *E. salmonophloia* belongs to the subgenus *Symphyomyrtus* and therefore its floral buds have two opercula. Observations of young *E. salmonophloia* floral buds indicated that the outer operculum, like in many other *Symphyomyrtus* spp., is shed early in the buds development (Brooker and Kleinig 1990), and because of its very small size was not detected in traps. By contrast the inner operculum remains on the bud until flowering and is easily identified. Flowering abundance and periodicity were measured by counting the number of these inner opercula; at flowering one operculum falls from every flower (Ashton 1975a). Fruit set was estimated by subtracting the total number of aborted flowers, sterile fruit and immature fruit from the total number of opercula (Ashton 1975a). This figure was multiplied by the mean number of seeds per fruit (see section 2.2.3) to estimate seed production.

2.2.3 CANOPY SEED STORES

At both Minniberri and Huandanning, two trees were chosen to estimate canopy seed stores. Selection was restricted to trees with canopies that could be reached with 9 m pole pruners. Salmon gum's canopy architecture is modular, and similar sized clumps of branches and leaves are easily recognised. On each tree the number of these modules was counted. Four of these were cut from different locations, determined from the cardinal points on the compass, around each tree and the number of fruit on each counted. From each of these a sub sample of 25 fruit was randomly selected and the number of seeds in each counted. From these data canopy seed stores for each tree were estimated.

2.2.4 PATTERN OF SEED FALL

In most eucalypts, including *E. salmonophloia*, the proportion of seeds set is low relative to ovule number (Brooker and Kleinig 1990). Fertile *E. salmonophloia* seeds were, however, easily distinguished from infertile ovular structures and aborted embryos. Fertile seeds were sorted from the contents of sampling traps every 2 months and counted to assess temporal patterns of seed fall.

Total seed fall data were pooled across sites for traps both beneath canopies and in gaps and analysed with an unpaired two tailed t - test (on log transformed data) to determine if differences in seed fall existed between the two locations.

2.2.5 SEED VIABILITY

Germination tests were undertaken on seed collected from sampling traps. All of the seeds collected were placed on paper germination pads in 9 cm petri dishes moistened with 25 mL of water. Petri dishes were placed on trays and enclosed in a plastic bag to reduce water loss, and then placed in a controlled temperature room at 25^{o}C with constant light (500 lx). Dishes were checked once a week for 4 weeks and germinants counted and removed. Seeds were counted as germinated when the radicle had emerged.

2.3 **RESULTS**

2.3.1 CANOPY COVER

At all sites, canopy cover was significantly higher surrounding traps beneath canopies than traps in gaps (F=1.6, d.f.=1, 32, p <0.001). There were, however, no significant differences in canopy cover surrounding sampling traps among the four study sites (F=1.6, d.f.=3, 32, p >0.05). Similarly the interaction between site and trap position was not significant (F=1.3, d.f.=3, 32, p > 0.05).

2.3.2 PATTERN OF FLOWERING AND SEED PRODUCTION

Trees were observed flowering from April to December 1992 at all four sites and in April and October 1993 at Gents Rd (Figure 2.1). Individual trees flowered only once during this period. At each site there was a peak in the number of individuals flowering synchronously. This occurred in August 1992 at Minniberri, October 1992 at Gents Rd, and December 1992 at Huandanning and Moore's East (Figure 2.1).

Thirty six percent of trees at Moore's East, 33% of trees at Gents Rd, 15% of trees at Minniberri and 9% of trees at Huandanning did not flower. Of these, single trees at Minniberri, Huandanning and Moore's East, and two trees at Gents Rd had no flower buds or fruits. In other cases flowering did not occur despite the trees being reproductive with floral buds and fruit from previous years.

Generally the number of opercula found in sampling traps showed a similar pattern to the number of trees flowering at each site (Figure 2.2). An exception to this occurred from April to June 1992 when one tree at Huandanning flowered heavily resulting in a large number of opercula being found in several traps. Flowering was heavier and there were more opercula

Figure 2.1: The % of trees in the study grids which were observed flowering at 2 month intervals during August 1991 to October 1993.

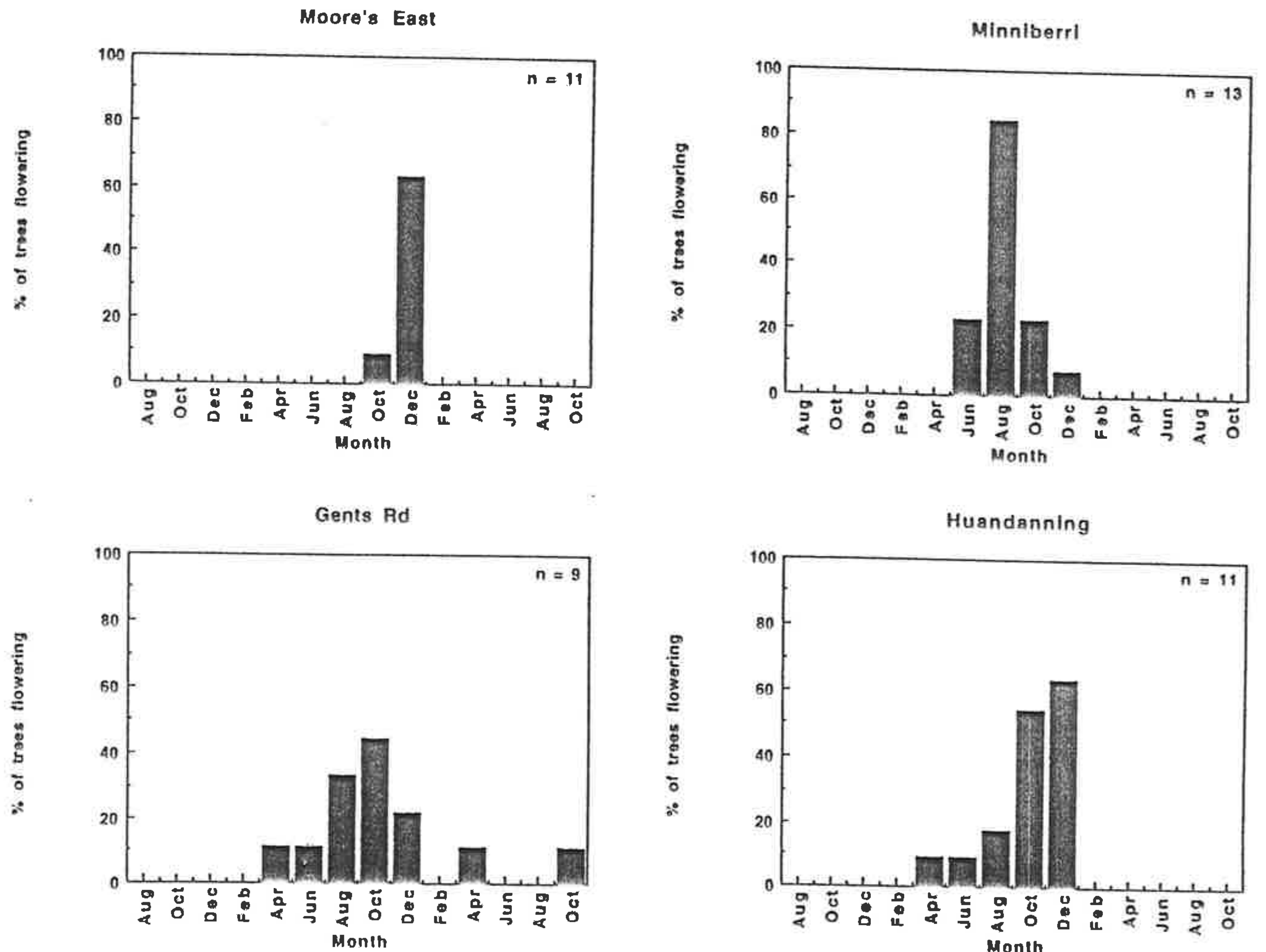
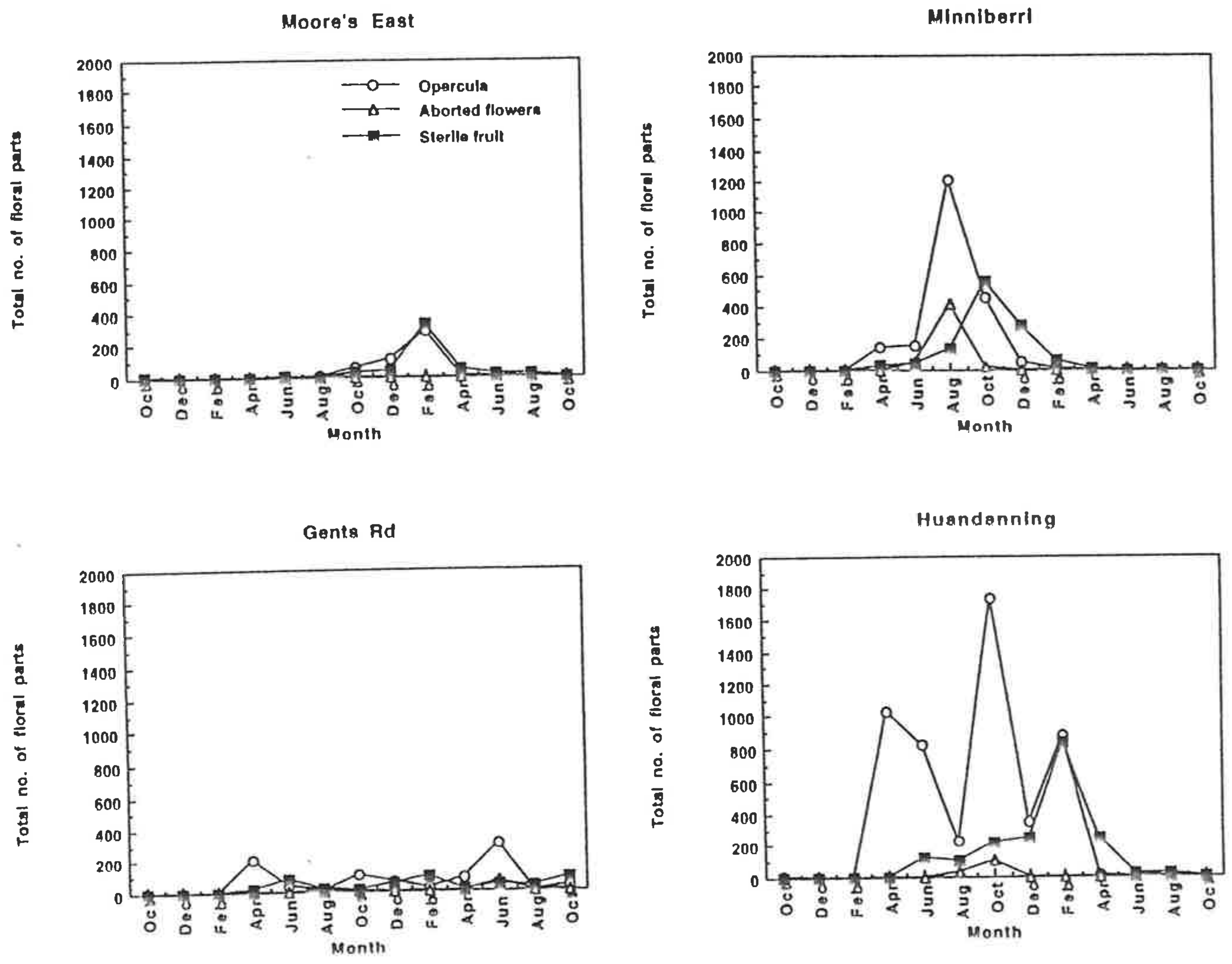


Figure 2.2: The total number of opercula, aborted flowers and sterile fruit falling in 2 month periods from August 1991 until October 1993 into ten sampling traps (total area = 1.5 m^2) at each of the four study sites.



at Huandanning and Minniberri than at Gents Rd and Moore's East despite equivalent canopy cover over the traps (Table 2.4).

The proportion of flowers which set fruit and estimates of seed production varied greatly between sites (Table 2.5). At Moore's East only 1% of flowers set fruit whilst at Huandanning 61% of flowers set fruit.

2.3.3 CANOPY SEED STORES

Two crops of fruit were found in the canopies of sampled trees and observed in the canopies of other trees at each site. Estimates of canopy seed stores ranged from approximately 60 000 to 420 000 seeds per tree (Table 2.6).

2.3.4 PATTERN OF SEED FALL

By contrast with flowering which exhibited strong peaks in seasonal activity, seed fall occurred throughout the year but was generally lowest in the winter months (Figure 2.3). Exceptions occurred at Huandanning and Gents Rd. At Huandanning maximum seed fall (200 seeds m^{-2}) occurred in the first summer following flowering and corresponded with a large number of decapitated and dissected fruit in the sampling traps. Galahs (*Cacatua roseicapilla*) and twenty - eight parrots (*Barnardius zonarius*) were frequently seen in the canopy feeding on fruits; evidently the fruit is cracked open and the seed eaten, but in some cases seeds escape predation and fall to the ground. Fruits damaged by predators were also recorded but to a lesser extent at other sites throughout the study period. Seeds were also found in sampling traps with mature open fruit; however, in many cases seeds were recorded in sampling traps without predated or mature fruits. At Gents Rd no seeds were found in sampling traps on four occasions.

Seed fall beneath canopies was double that in gaps and significantly different (t =1.982, d.f.=38, p <0.05). The mean total number of seeds falling into traps beneath canopies over

Table 2.4: Mean % canopy cover surrounding sampling traps beneath canopies and in gaps at the four sites. Values are arithmetic means (S.E.) of five measurements.

	Site			
Trap position	Moore's East	Gents Rd	Minniberri	Huandanning
Beneath canopy	87 (6)	78 (7)	88 (4)	90 (6)
In gap	52 (5)	38 (7)	32 (6)	40 (6)

Table 2.5: The total number of opercula, aborted flowers and sterile fruit found in ten sampling traps (total area = 1.5m^2), and estimates of fruit set, flowering success and seed set at the four sites from August 1991-October 1993. Seed production = No. of fruit set x mean number of seeds per fruit.

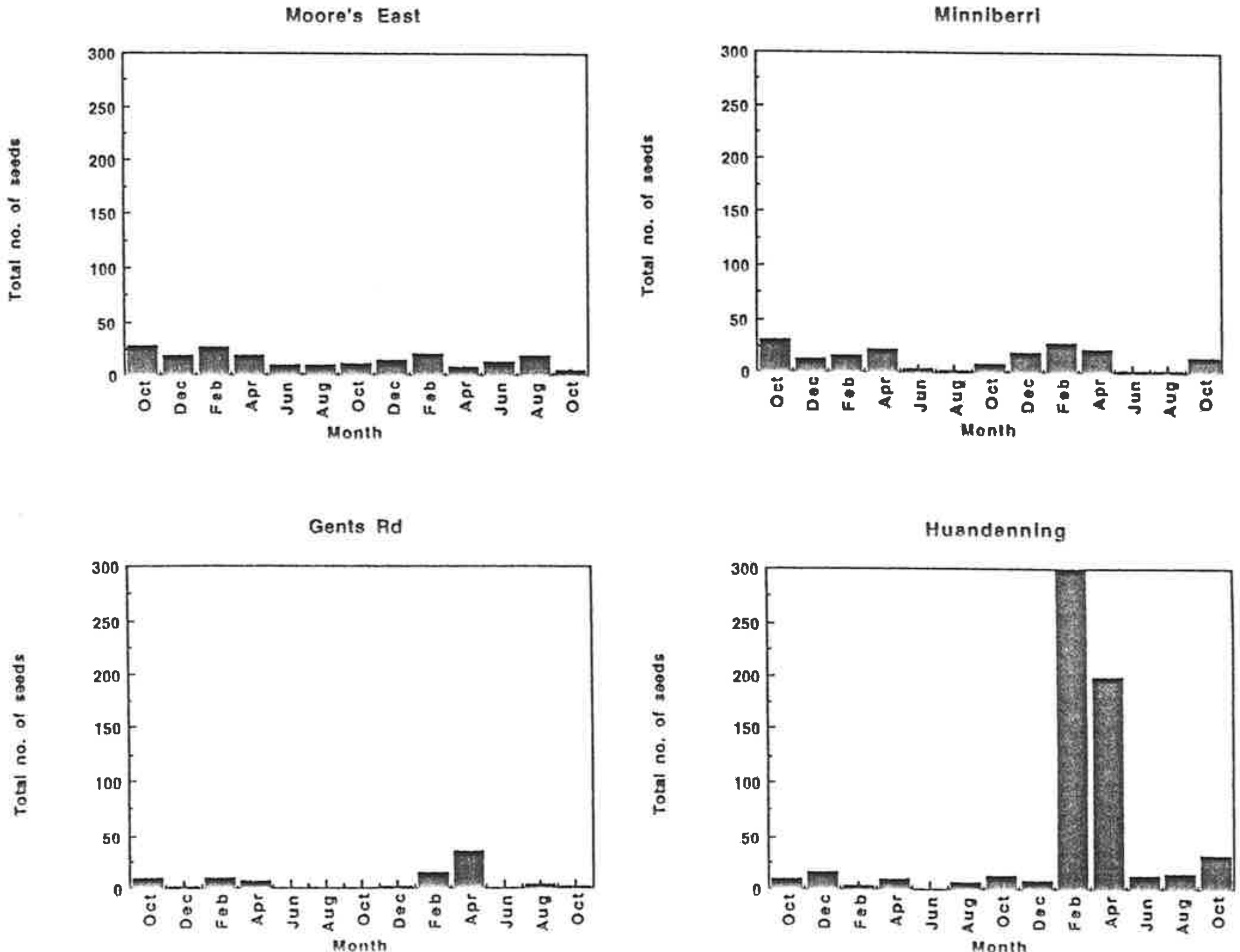
	Sites			
	Moore's East	Gents Rd	Minniberri	Huandanning
No. of opercula	490	862	2033	5048
No. of aborted flowers	2	68	485	135
No. of sterile fruit	484	447	1102	1811
No. of fruit set	4	347	446	3102
% of flowers which set fruit	1	40	22	61
Estimated seed production[A]	8	742	954	6638

[A] Calculated using mean of 2.14 seed per fruit (see Table 2.6).

Table 2.6: Estimates of canopy seed stores on two trees at Minniberri and Huandanning. Canopy seed store = no. of modules x mean no. of fruit per module x mean no. of seeds per fruit. Values are means (S.E.) of four observations on number of fruit per module and 25 observations on number of seeds per fruit.

Site	No. modules	Mean no. fruit per module (S.E.)	Mean no. seed per fruit (S.E.)	Estimate of canopy seed store
Tree 1 Minniberri	199	729 (286)	2.89 (0.20)	419 250
Tree 2 Minniberri	115	286 (39)	1.83 (0.15)	60 190
Tree 3 Huandanning	168	1061 (309)	2.36 (0.18)	420 660
Tree 4 Huandanning	151	620 (264)	1.49 (1.05)	139 490

Figure 2.3: The total number of fertile seeds falling in 2 month periods from August 1991 to October 1993 into ten sampling traps (total area = 1.5 m^2) at each of the four study sites.



the 2 year study period was 233 seeds m^{-2} and into gaps 120 seeds m^{-2}. The viability of seeds found in sampling traps at each site was high and ranged from 67% to 100% (Table 2.7).

2.4 DISCUSSION

E. salmonophloia flowered at each site during the 2 year study period, but no tree flowered more than once and 23% of trees did not flower at all. The reasons for some trees not flowering are unclear but at Minniberri and Huandanning some trees appeared to be suppressed by larger individuals and had not reached reproductive maturity. At Moore's East and Gents Rd, trees appeared to be recovering from crown damage possibly caused by wind, phytophagous insect outbreaks and galahs and consequently consisted largely of epicormic regrowth that had not reached reproductive maturity. In other cases (Moore's East, Gents Rd and Minniberri) trees were reproductive and had floral buds but did not flower. Ashton (1975a) found in *Eucalyptus regnans* that during poor flowering years some trees flowered but others did not and attributed this to individuals having their own cycle of bud production. Good flowering years occurred when there was a coincidence of phases between individuals. Observations of *E. salmonophloia* canopies during this study revealed that phytophagous insects stripped young leaves and inflorescence buds in some trees but not in others. Losses of buds in some trees to insect predation and not in others may also result in flowering not being synchronous between individuals in a population.

The intensity and success of flowering was highly variable between the four sites. Trees at Huandanning had the heaviest flowering and set the most seed. Flowering at Minniberri was much heavier than at Gents Rd. However, fruit set at Minniberri was considerably less than at Gents Rd and as a consequence there was little difference in seed production between the two sites. At Moore's East, only 1% of flowers set fruit. The reasons for this variation are unknown, but clearly the relationship between flowering intensity and seed production in these remnants is not a simple one. The amount of seed produced following flowering is dependent on resource availability, pollinator abundance and pollen quality. Rainfall during

Table 2.7: % germination of the seed in sampling traps at the four sites. All seeds recovered at each sampling date were tested. The number of seeds tested on each occasion can be found in Figure 2.3.

	Seed germination (%)											
Site	'91 Dec	'92 Feb	Apr	Jun	Aug	Oct	Dec	'93 Feb	Apr	Jun	Aug	Oct
Moore's East	100	85	83	78	90	91	78	95	71	92	89	100
Gents Rd	100	89	83	*	*	*	100	78	100	*	100	100
Minniberri	85	94	86	67	100	100	89	70	95	100	100	83
Huandanning	94	67	70	*	100	77	86	95	95	100	86	95

* No seeds found in sampling traps

the 2 year study period was just below or above the average at each of the study sites. Site characteristics such as remnant area, population size, frequency of grazing and level of degradation may affect the above factors. Unfortunately, the pattern of clearing in salmon gum woodlands makes replication of remnants with the same characteristics impossible, and it is therefore difficult to draw firm conclusions from the data about the impact of certain site characters on seed production. Other studies have concluded that habitat fragmentation can affect the processes which underlie seed production in plant populations. Plants in small fragmented populations may receive fewer visitations from pollinators than plants in unfragmented populations and as a consequence set less seed (Jennersten 1988). Similarly, as population size declines, pollen quality may be reduced because pollen transfer occurs more frequently between closely related neighbours (Lamont *et al.* 1993). These factors can lead to a disproportionate decrease in seed production with declining population size (Lamont *et al.* 1993). As a consequence the viabilities of populations may decrease with a decline in their size (the Allee effect) (Allee 1949; Lamont *et al.* 1993). Thus in the present study, the very low seed set observed at Moore's East may be due to reduced population size since it was by far the smallest remnant of *E. salmonophloia* woodland.

However, it should be noted that massive variation in flowering intensity and success has also been observed for eucalypts in unfragmented populations (Ashton 1975a). Caution therefore needs to be exercised in ascribing poor seed production from a single flowering event to the effects of fragmentation . Interestingly, in this study fruit set at Gents Rd, a small remnant badly degraded by sheep grazing, was much higher than at Minniberri, one of the largest and apparently least degraded sites in the region.

Although great variation in seed production can occur, the estimated seed set at Huandanning (4400 seeds m^{-2}) shows the potential of *E. salmonophloia* to form a substantial seed store, and estimates of canopy seed reserves confirm this finding. Canopy seed reserves are a characteristic of many tall open forest eucalypts (Grose 1957,1960; Christensen 1971; Ashton 1975a; Cremer *et al.* 1978; Ashton 1981; O'Dowd and Gill 1984) and mallee eucalypts (Wellington and Noble 1985a; Davies and Myerscough 1991). The length of time that seeds can be stored on the plant is variable. Christensen (1971) found that in *Eucalyptus diversicolor* seeds fell mainly in the first two summers after maturation. In *E. regnans* most seeds fell within 3 years of maturity and rarely did fruits remain alive on a tree beyond 4 years although 6-7 year-old fruits were observed (Ashton 1975a). Grose (1957, 1960) found that *Eucalyptus delegatensis* shed most of its seed in the third and fourth years after maturation. The length of time that seed can be stored on the plant in *E. salmonophloia* is unknown; however, observations of two distinct crops of unopened fruits in the canopy suggest that seeds from two consecutive flowering seasons were present. Individual trees flowered only once during the study which spanned three potential flowering seasons. The oldest of the two fruit crops in the canopies must therefore have arisen from a flowering event which occurred before the beginning of this study, indicating that seed can be stored on the plant for at least 2 years. *E. salmonophloia* may therefore be classed as being serotinous (Lamont *et al*. 1991b)

In *E. salmonophloia,* seeds are gradually released from the canopy seed reserve in three ways; firstly when branches subtending the fruit die and capsules dry out; secondly when unopened fruit are blown from the canopy and dry out on the ground; and thirdly when cockatoos and parrots feed on seeds and some escape predation and fall to the ground freely or in dissected fruit. Not surprisingly, seed fall was heaviest beneath canopies but seeds were also dispersed into gaps. Seed fall was at its lowest during the winter sampling but generally seeds were found in sampling traps throughout the year even at Gents Rd where seed fall was lowest overall. Moreover, with one exception, there was no period of extremely heavy seed fall. The single exception was at Huandanning and was apparently caused by birds feeding in the canopies during the summer of 1993 following a heavy flowering event.

This chapter has demonstrated that, in a diverse range of remnant salmon gum woodlands, viable *E. salmonophloia* seeds are being produced and dispersed. Whether these populations are producing enough seeds to persist is unknown and depends on the fate of seeds following dispersal. It is possible that the amount of seed produced in these remnants has declined due to the Allee affect. However, several studies of plant population dynamics suggest that the relationship between seed production and population viability is not linear (Bradstock 1991; Lamont *et al.* 1991a). Obviously in populations where seed production is zero, extinction will occur unless the plants can reproduce vegetatively. However, in populations where plants are producing viable seeds, the absolute number of seeds required to maintain the population is hard to determine. This is particularly evident in species which rely on the co-occurrence of infrequent unrelated events for recruitment. In these species, population numbers are not limited by seed reserves but by factors which control germination and establishment (Bradstock 1991; Lamont *et al.* 1991a); in some cases population size was reported to be more sensitive to these factors than a 50% reduction in seed production (Bradstock 1991).

In conclusion it therefore seems unlikely that the availability of viable seed is responsible for the lack of *E. salmonophloia* recruitment in the remnant woodlands studied. Clearly the other processes which underly recruitment need to be examined. Subsequent chapters will therefore consider the fate of seed following dispersal and the factors affecting germination and establishment of seedlings.

CHAPTER 3

POST-DISPERSAL SEED PREDATION AND SOIL SEED RESERVES

3.1 INTRODUCTION

Chapter 2 demonstrated that in the remnant woodlands studied, *E. salmonophloia* trees were producing viable seeds which were stored in woody fruit held in the canopy for periods of up to several years. Seeds were dispersed onto the soil surface when branches subtending the fruit died and capsules dried; when unopened capsules were blown from the canopy and subsequently dried on the ground; and finally when seeds escaped predation and fell to the ground freely or in dissected fruit whilst cockatoos and parrots were feeding.

In a wide variety of grasslands, heathlands, woodlands and forests throughout the world seeds are an important resource for granivores including rodents, birds, ants, lygaeid bugs and carabid beetles (Crawley 1992). The behaviour of post dispersal seed predators affects the establishment of a soil seed reserve and therefore may affect seedling recruitment (O'Dowd and Gill 1984; Andersen 1987; Andersen 1989; Crawley 1992; Samson *et al.* 1992). In Australian eucalypt communities, ants are the most important predators of eucalypt seed following dispersal. Studies have reported ants removing seed of *Eucalyptus* spp. in mallee woodlands (Andersen 1982; Wellington and Noble 1985a), woodlands (Andersen and Ashton 1985; Clayton-Greene and Ashton 1990), open forest (Majer 1980; O'Dowd and Gill 1984; Abbott and van Huerck 1985) and tall open forest (Ashton 1979).

This chapter aims to determine whether firstly, seed harvesting ants are active in remnant *E. salmonophloia* woodlands; secondly whether *E. salmonophloia* forms a soil seed reserve; and thirdly the length of time that *E. salmonophloia* seeds remain viable in the soil.

3.2 **METHODS AND MATERIALS**

3.2.1 STUDY SITES

The study was undertaken in the four remnant *E. salmonophloia* woodlands where surveys of flowering, seed production and seed dynamics were conducted (Chapter 2). These have been described in detail in Chapter 2.

3.2.2 SEED REMOVAL

Rates of seed removal were assessed by recording the loss of seeds from artificial baits (Majer 1980; Andersen and Ashton 1985). Each bait consisted of a modified 5 cm plastic petri dish glued to a 10 cm x 10 cm plywood board and contained ten *E. salmonophloia* seeds. The dishes had lids and three 5 mm entrances spaced equidistantly in their sides which allowed access to ants but excluded vertebrates.

A preliminary survey of seed removal was undertaken in February 1992 to establish the most effective exposure time for the purpose of this study. Two seed baits were placed at each of ten randomly chosen locations on experimental grids (Chapter 2) at the four sites. Ants had access to one of the seed baits but were excluded from the other by a 'Tanglefoot' barrier placed around the petri dish on the plywood board. The exclusion treatment acted as a control to quantify the removal of seeds by wind and rain. Strong winds occur frequently in the area and remnant salmon gum woodlands are very open and exposed. Baits were exposed for 4 days and the number of seeds removed from each recorded every 24 hours.

Following the preliminary survey a longer term study was undertaken at the four study sites. Baits were placed on the experimental grids at 2 month intervals from April 1992 to February 1993. On each occasion two seed baits, as described above, were placed at ten randomly chosen locations on the grids such that no location was duplicated in time. The number of seeds removed from each bait were recorded after 24 hours; preliminary studies indicated that estimates of seed removal by ants became less reliable with longer exposure (see Section 3.3.1).

The effect of site, time of year and the interaction of these two factors on seed removal from baits was tested with a generalised linear model using the statistical programme GLIM. This analysis offers advantages over traditional regression analysis or analysis of variance as it allows selection of the appropriate statistical distribution (e.g. binary, binomial, Poisson) (McCullagh and Nelder 1989). The statistical model used was the binomial logit link model (or logistic regression) which takes the form

$$\log(p/1-p) = \text{linear function of environmental variables}$$

where p is the probability of seeds being removed from baits for that combination of environmental variables (site, time of year). The analyses estimate the probability of seeds being removed within each cell of a factor table, and also for various additive linear combinations of the environmental variables. Each environmental variable and its interactions account for a proportion of the deviance or total variability within the data, and using a chi-square test the significance of the proportion of deviance that a variable accounts for can be tested against the null hypotheses concerning the removal of seeds.

Ant activity at seed baits was observed throughout the study. On two occasions, July 1992 and February 1993, baits were monitored at Minniberri and Gents Rd at 3 hour intervals over a 24 hour period. Ants observed removing seed were collected for identification and assigned genus names with a species code number that relates to the Durrakoppin ant collection deposited at the School of Environmental Biology, Curtin University, Western Australia. Ant names are synonymous with those collected by van Schagen (1986), Lobry de Bruyn (1990) and Scougall *et al.* (1993).

3.2.3 SOIL SEED RESERVES

The ability of *E. salmonophloia* to form a soil seed reserve was assessed by means of a seed burial-retrieval experiment.

In February (summer), April (autumn), August (winter) and October (spring) 1992, 16 lots of 50 *E. salmonophloia* seeds were buried to a depth of 1 cm in a 3 cm diameter area at randomly selected locations on the experimental grid at Minniberri.

Four lots of seeds were retrieved either immediately, 2 months, 6 months or 12 months after burial by taking a 9 cm diameter by 1.5 cm deep soil core. The presence of seeds in the soil was assessed by spreading soil samples to a depth of no more than 10 mm on filter paper covering 30 g of vermiculite (approx. 50 mm deep) watered to saturation, in 15 cm diameter plastic containers. These were sealed in plastic bags to prevent moisture loss and placed in a controlled temperature room for four weeks at the optimal temperature for germination of *E. salmonophloia*, 25^{o}C (Chapter 5). Emerged seedlings were counted and removed weekly.

E. salmonophloia seed germinates readily under conditions of optimal temperature and moisture (Chapter 5); the seed used in the experiment was 96% viable. Preliminary studies using the above technique, where the number of seeds in the soil sample was known, found that 65% of seeds had emerged after 28 days; thereafter the rate of seedling emergence plateaued and by 84 days 75% of seeds had been detected.

Identical soil cores were collected adjacent to seed burial sites and treated in the same manner to assess natural soil seed densities.

Two monthly rainfall totals at Minniberri Reserve were measured in storage gauges when soil samples were collected and surveys of flowering, seed production (Chapter 2) and post dispersal seed predation were being undertaken.

The effect of season and duration of burial on the persistence of seed in the soil was determined using a two way ANOVA. Assumptions of homogeneity of variance were checked with residual plots and no transformations were required.

Germination data was pooled across treatments and regressed against cumulative rainfall for the period that seeds were buried.

3.3 **RESULTS**

3.3.1 SEED REMOVAL - PRELIMINARY SURVEY

The percentage of seeds removed from baits increased with increasing exposure, but the reliability of estimates declined (Table 3.1). The ratio of seed removal between baits to which ants had access and control baits declined with increasing exposure from 14.5 after 1 day to 4.8 after 4 days, indicating that the probability of seed being removed by agents other than ants increased with longer exposure. Seeds were seen to be blown from baits on several occasions.

3.3.2 SEED REMOVAL - LONGER TERM SURVEY

The ant exclusion treatment was highly effective. Twenty one percent of the *E. salmonophloia* seeds were removed after 24 hours from baits to which ants had access. In contrast 0.25% of seeds were removed from the baits where ants were excluded.

Four species of ants were seen removing seeds from baits. Three species, *Pheiodole sp D 9*, *Monomorium sp D 8* and *Monomorium sp D132*, were consistently seen removing seed

Table 3.1: Mean percentage seed removal from ten seed baits each containing ten *E. salmonophloia* seeds over four days at the four study sites.

	% seed removal from baits							
	One day exposure		Two days exposure		Three days exposure		Four days exposure	
Site	Access	No access	Access	No access	Access	No access	Access	No access
Moore's East	29	1	42	4	52	12	60	12
Gents Rd	55	7	58	12	59	14	60	14
Minniberri	21	0	23	1	28	1	50	1
Huandanning	11	0	21	13	31	14	31	15

from baits during the day. The fourth species, *Meranophus sp D132,* was seen removing seeds on two occasions at night. All species appeared to be recruit foragers and *Pheiodole sp D 9* and *Monomorium sp D132* were very efficient; in some instances all of the seeds were removed from baits within ten minutes of being located on the experimental grid. Thus it was anticipated that the number of seeds removed from a dish at any site by time of year combination would not follow a Binomial distribution. This is due to the fact that once a bait has been discovered by ants it is likely that all seeds will be removed, and so removal of seeds in the same dish is unlikely to be independent. Figure 3.1 shows the distribution for the number of seeds removed from the baits over all 24 (= 4x6) site by month combinations. The logistic regression model for the number of seeds removed from a dish using site, time of year, and their interaction, resulted in a deviance of 1798 with 216 degrees of freedom. The extremely high significance of this result suggests that the Binomial distribution is not appropriate for the number of seeds removed from a dish, and thus agrees with observations of the foraging behaviour of the ants.

The data was therefore analysed by considering the number of dishes at each of the 24 site by month combinations where ant activity was detected. Ant activity at a dish was initially interpreted as at least one seed being removed from the dish (see below). The resulting analysis with logistic regression is summarised in Table 3.2. Note the significant interaction effect between site and time of year ($p < 0.005$). This suggests that the effect of time of year on seed removal rates was different at the different sites, and hence both site and month are important in explaining seed removal. The pattern of this interaction is displayed in Figure 3.2.

The above analysis considered the number of dishes where seeds were removed from baits but it was observed that this could occur by wind or rain as well as by predation. On only four occasions were seeds removed from the dishes in the ant exclusion treatment. Twice, one seed was removed (Minniberri in April and Gents Rd in December) and twice, two seeds were removed (Moore's East in December and February). The analysis was therefore repeated with ant activity interpreted as more seeds removed than at the nearby exclusion treatment,

Figure 3.1: Frequency distribution of 240 observations (four sites x six samplig periods x 10 replicates) of percentage seed removal from baits.

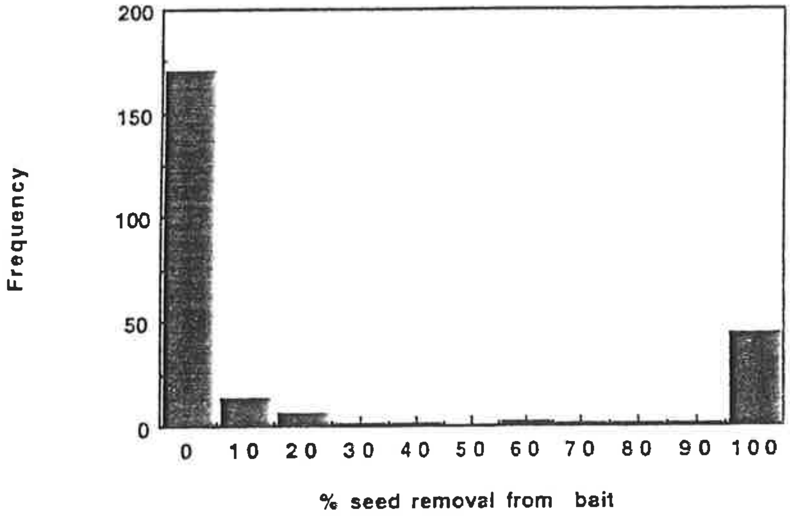


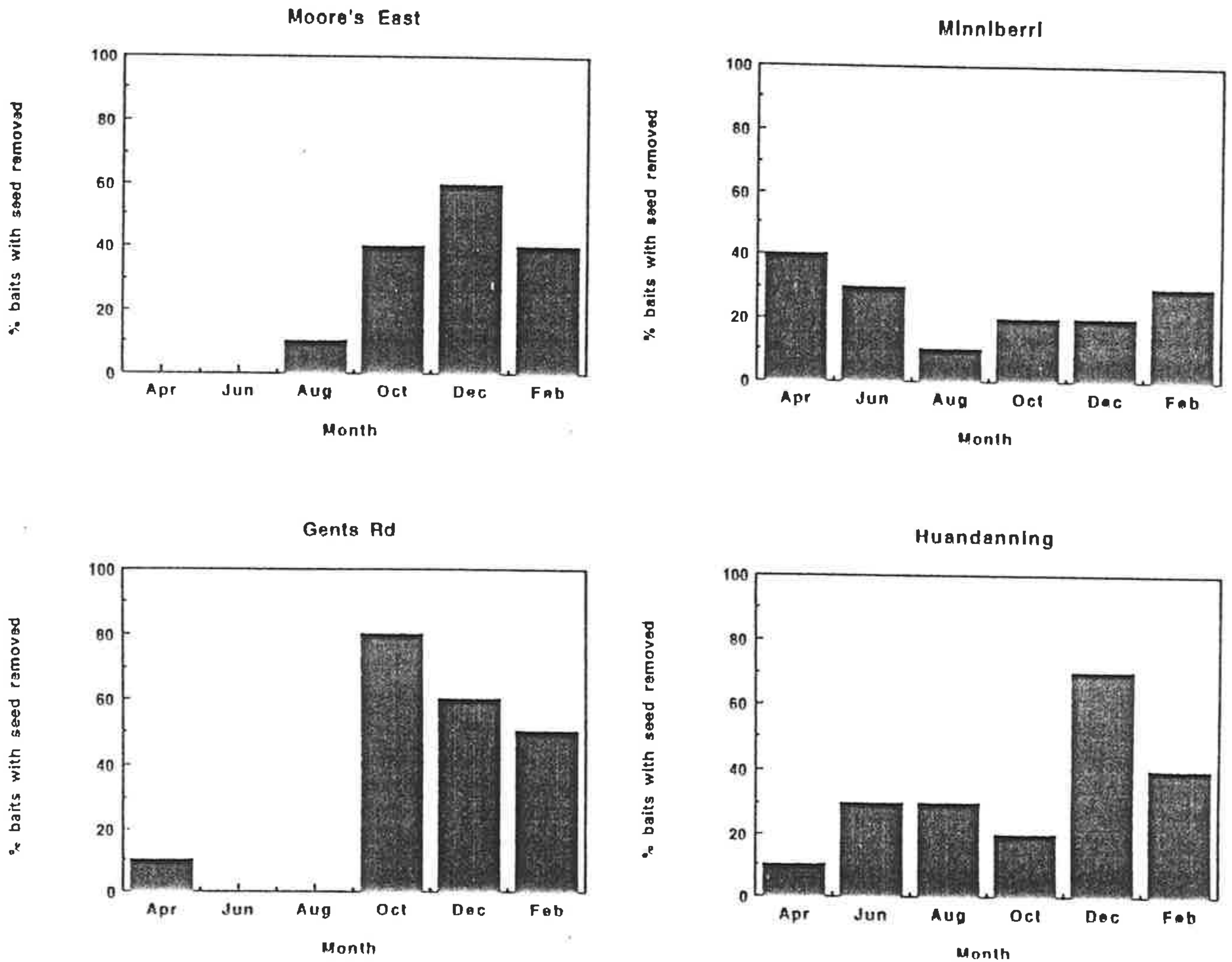
Table 3.2: Logistic GLIM analysis describing the effects of site, month and their interaction on removal of *E. salmonophloia* seeds by ants from seed baits.

Model	Deviance	d. f.	Factors	[A] Deviance change	d. f.	*P*
Site + Month + Site x Month	0	0				
Site + Month	36.76	15	- Site x Month	36.76	15	**
Site	65.974	20	- Month	29.21	5	***
Month	39.06	18	- Site	2.29	3	N.S.

[A] Change in deviance distributed as Chi squared

** $p < 0.01$, *** $p < 0.001$

Figure 3.2: Percentage of baits with seeds removed after 24 hours when baits were placed at Moore's East, Gents Rd, Minniberri and Huandanning at two monthly intervals over a 12 month period.



more than 1 seed removed, and as more than 2 seeds removed. Similar results to those in Table 3.2 were obtained in each case, although for the last two the significance of the interaction was reduced to only being significant at the 5% level.

3.3.3 SOIL SEED RESERVES

Season of burial (F=3.25, d.f.=3,48, p <0.05), duration of burial (F=35.28, d.f.=3,48, p <0.001) and their interaction (F=4.09, d.f.=9,48, p <0.001) had a significant effect on the persistence of viable seeds in the soil (Figure 3.3). However, with increasing duration of burial, seedling emergence rates declined and in all seasons very few or no seeds emerged after 12 months burial (Figure 3.3). Seeds buried in October persisted for longer than seeds buried in February, April and August (Figure 3.3). The most rapid decline in the recovery of buried seed occurred in sampling periods during winter when most rain falls in the study region (Chapter 2) (Figure 3.3). The number of seeds detected was negatively correlated with cumulative rainfall (r = 0.76, p <0.0001) (Figure 3.4). The relationship between winter rainfall and the decline in soil seed reserves is very clear for seeds which were buried in October at the end of winter. Similar numbers of these seeds were recovered in the first 6 months following burial; this period occurred over summer when very little rain fell (Figure 3.3). By contrast no seeds were detected following the winter wet season 6 months later (Figure 3.3).

No *E. salmonophloia* seeds were detected in soil samples collected adjacent to burial sites.

3.4 DISCUSSION

The study provides evidence that harvester ants remove *E. salmonophloia* seed from the soil surface. Seed removal, however, does not necessarily mean that the seeds are eaten. Many plant species, known as myrmecochores, have seeds adapted to dispersal by ants (Berg 1975; Westoby *et al.* 1991) and are common in the sclerophyll vegetation found on infertile soils in Australia. These plants have a food body (elaiosome) attached to their seeds

Figure 3.3: Mean number ~~of seeds detected~~ (emergent seedlings) after 0, 2, 6 and 12 months burial in February, April, August and October, and cumulative rainfall for corresponding periods. Vertical bars represent S. E. of four replicates (50 seeds each).

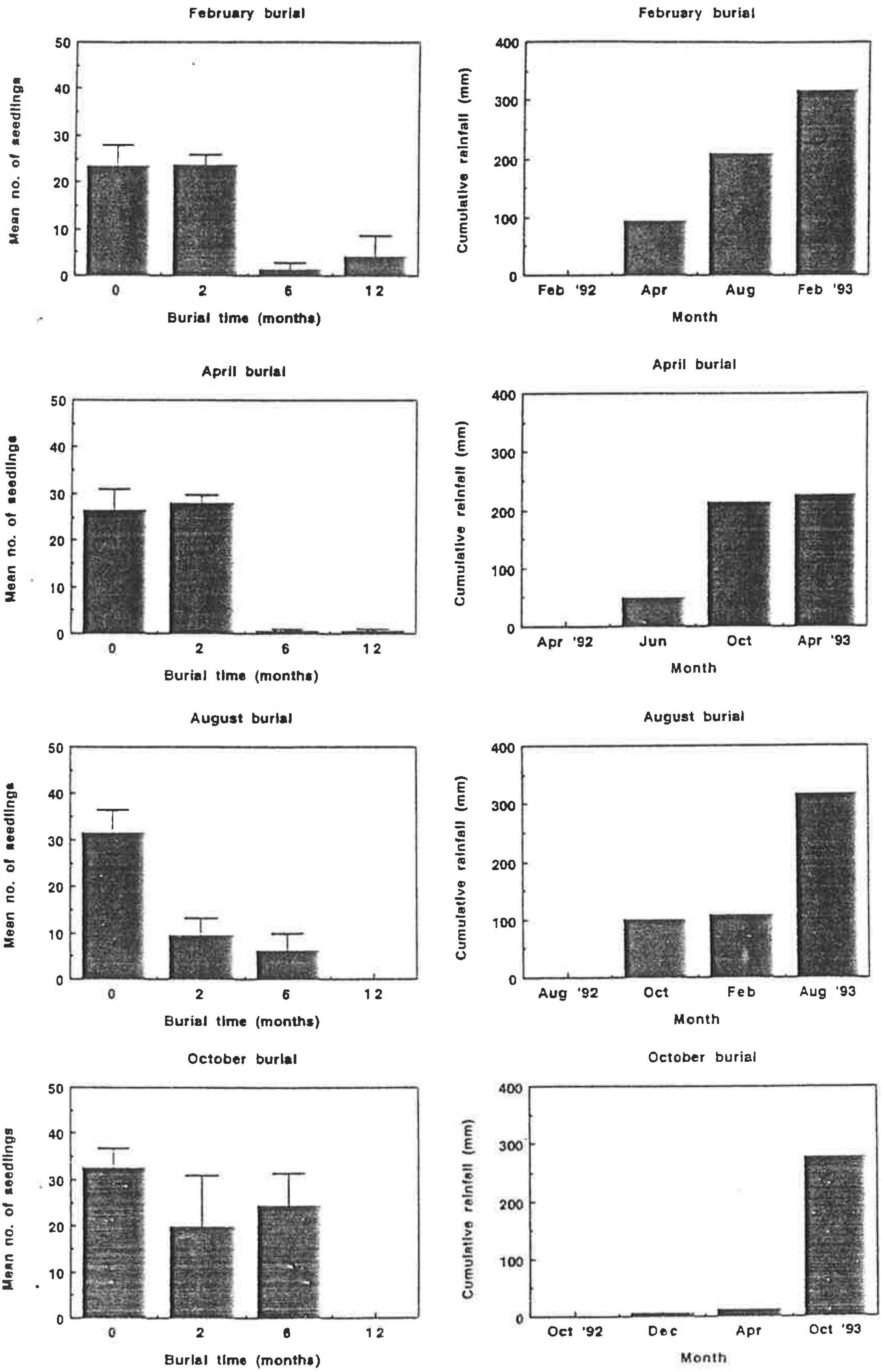
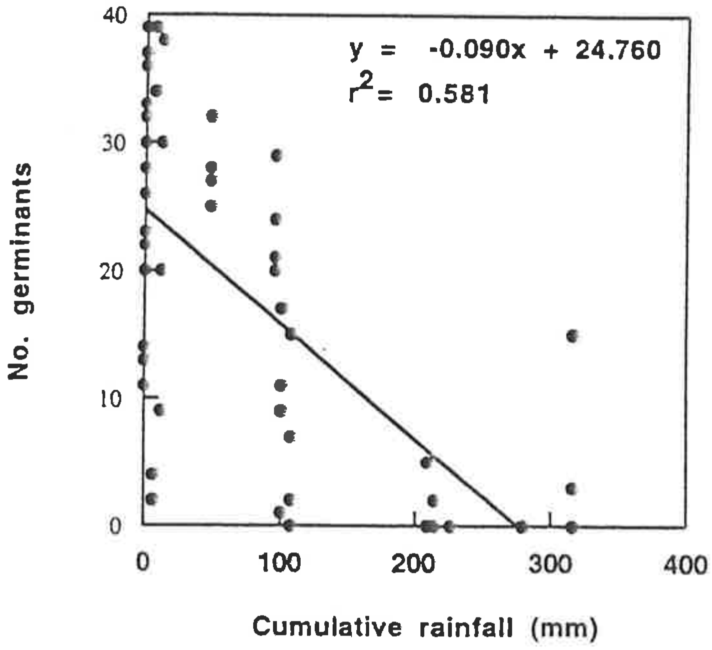


Figure 3.4: Regession plot of number of seeds detected after burial for either 0, 2, 6 and 12 months versus cumulative rainfall for the period of burial.



which entices ants to carry the seeds back to their nest where the elaiosome is eaten and the seed discarded unharmed (Berg 1975; Westoby *et al.* 1991). Myrmecochores occur in a large number of genera but have not been found in *Eucalyptus* (Berg 1975). *E. salmonophloia* does not possess an elaiosome and it is therefore unlikely that its seeds are dispersed by ants in this manner. Studies of seed harvesting in other eucalypt species have found that the seeds are eaten either *in situ* (Wellington 1989) or stored in the nest and eaten at a later date (Ashton 1979; Andersen and Yen 1985; Wellington and Noble 1985a). Some of this seed stored in granaries germinates (Andersen and Yen 1985); however, many species of harvester ants do not maintain granaries within 15 cm of the soil surface (Andersen 1982). *E. salmonophloia* has a very small seed (1 mm x 1 mm) which makes it very difficult for seeds to emerge from depth. Data presented in Chapter 5 demonstrates that the emergence of *E. salmonophloia* seedlings declines with depth of seed burial, and at a depth of 2 cm is almost zero. It therefore seems unlikely that *E. salmonophloia* seeds harvested by ants and stored in granaries below ground are a source of seed for regeneration.

These findings suggest that *E. salmonophloia* can establish a soil seed reserve only when ants do not remove 100% of the seeds which fall from the canopy. Seeds are only likely to escape predation if they are dispersed to a site where they cannot be detected by predators or where there is consistently low predator activity (Andersen and Ashton 1985). Andersen and Ashton (1985) observed that the presence of litter significantly reduced removal of *Eucalyptus baxteri* seeds; Wellington and Noble (1985a) reported considerable spatial variation in predator activity and observed sites where there was consistently lower removal of *Eucalyptus incrassata* seeds. In the present study, ants removed 20% of seeds from baits over a 24 hour period. However, seed removal was not evenly distributed across the baits and in most cases either 100% of seeds were removed or no seeds were removed. This pattern reflects the recruit foraging strategy whereby an ant locates seeds and signals its find to other workers who then assist with removal. Seeds located in this manner were removed rapidly from baits. In instances where seeds were not removed from baits, exposure times may not have been sufficiently long for ants to locate the baits or alternatively baits were located in areas where there was low predator activity. Studies of post dispersal seed predation in other *Eucalyptus* spp. where exposure times have been longer have reported 60 to 100% seed removal from baits (Ashton 1979; O'Dowd and Gill 1984; Andersen and Ashton 1985; Wellington and Noble 1985a) and this is likely to be the case with *E. salmonophloia*.

Seed storage in the canopy of *E. salmonophloia* woodland can be enormous due to heavy flowering seasons and the accumulation of fruit crops (Chapter 2). Seed fall has been reported to occur throughout the year when branches subtending the fruit die and capsules dry out; when unopened fruit are blown from the canopy and dry out on the ground; and when cockatoos and parrots feed on seeds and some escape predation and fall to the ground freely or in dissected fruit (Chapter 2). Seed fall occurred throughout the study period with up to 200 seeds per m^2 falling every 2 months (Chapter 2). Despite this no *E. salmonophloia* seeds were detected in the soil. This, together with observations of seed removal from baits, indicates that ants remove a very high proportion of *E. salmonophloia* seeds following dispersal from the canopy.

In instances where seeds do escape predation it is unlikely that they persist in the soil seed bank for long. When an artificial soil seed reserve was established, the number of seeds that were recovered declined with increasing exposure and very few seeds were detected after 12 months burial. This decline was correlated with cumulative rainfall. Observations of germinants in burial-retrieval soil samples collected in winter suggest that most seeds germinated with the onset of suitable climatic conditions in late autumn and winter (germination physiology is explored in Chapter 5). Wellington and Noble (1985a) reported similar findings in *E. incrassata*.

The results of this chapter and the previous chapter suggest that *E. salmonophloia* shares life history characteristics with eucalypts that recruit seedlings following fire (O'dowd and Gill 1984; Wellington and Noble 1985a). These include canopy seed stores (Grose 1957, 1960; Christensen 1971; Ashton 1975; Cremer *et al.* 1978; Wellington and Noble 1985a;

Davies and Myerscough 1991), heavy seed predation by ants (Ashton 1979, O'dowd and Gill 1984; Andersen and Ashton 1985; Wellington and Noble 1985a) and the absence of a persistent soil seed bank (Carol and Ashton 1965; Barbour and Lange 1967; Wellington and Noble 1985a) . It has been observed that fire induces a massive and synchronous release of all canopy stored seed (O'Dowd and Gill 1984; Andersen 1988; Burrows *et al.* 1990) which causes a temporary satiation of seed eating ants, resulting in lower rates of seed predation (O'dowd and Gill 1984; Wellington and Noble 1985a; Andersen 1988) and the establishment of a soil seed bank. However, fire also increases the abundance of safe sites for germination and establishment (O'Dowd and Gill 1984; Andersen 1987, 1989).

Andersen (1989) suggested that the impact of seed predation on recruitment of long lived perennials was related to the abundance of safe sites for germination and establishment (for Andersen's purposes seed predators do not influence the safeness of a site). It was zero when safe sites were absent; negligible when safe sites were rare; and greatest when safe sites were numerous enough for recruitment to be limited by seed supply (Andersen 1989). Andersen (1987) observed that the elimination of ants increased the number of emergent *E. baxteri* seedlings 15 fold in an unburnt woodland. However, all the seedlings subsequently died and Andersen (1987) therefore concluded that seed losses to ants had no impact on recruitment. Andersen (1989) suggested that in long lived perennials such as *E. baxteri* which recruit seedling following fires, safe sites are absent or rare in interfire periods and abundant after fires. In these species, seed predators might be important only if they prevent the establishment of a soil seed bank capable of exploiting the post fire abundance of safe sites. This is likely to occur only if seed supply is low; an event which is rare in species which maintain large canopy seed reserves.

In conclusion this chapter has demonstrated that in remnant woodlands following dispersal from the canopy, a large proportion of *E. salmonophloia* seeds are eaten by ants thereby preventing the establishment of a soil seed reserve. However, studies of other *Eucalyptus* spp. would suggest that this factor is not necessarily responsible for the lack of recruitment in remnant woodlands. These studies have shown that conditions suitable for germination and establishment only occur following disturbance by fire. In interfire periods when conditions are unsuitable for germination and establishment, the removal of seeds by predators has no impact on recruitment. The impact of seed predators on *E. salmonophloia* recruitment in remnant woodlands therefore cannot be determined without an understanding of the conditions necessary for germination and establishment; subsequent chapters will look at these factors.

CHAPTER 4

RECRUITMENT OF *E. SALMONOPHLOIA* SEEDLINGS FOLLOWING LANDSCAPE-SCALE DISTURBANCES IN UNFRAGMENTED WOODLANDS

4.1 INTRODUCTION

Little is known about the conditions necessary for the germination and establishment of *E. salmonophloia* seedlings. Studies of other *Eucalyptus* spp. with life history characteristics similar to those described for *E. salmonophloia* have documented seedling recruitment following fire, but rarely during interfire periods (Ashton 1976, 1981; O'Dowd and Gill 1984; Wellington and Noble 1985a,b; Burrows *et al.* 1990; Wellington 1989; Hopper 1993).

E. salmonophloia occurs throughout an environment where fire is not the only agent responsible for large scale disturbance of native ecosystems. Also prevalent are tornadoes and severe storms (Clarke 1962; Minor *et al.* 1980); floods brought about by heavy summer rainfall associated with thunderstorms and decaying tropical cyclones (Pierrehumbert 1973; Lourenz 1981); and droughts, when rainfall is below average (Fitzpatrick 1970; Southern 1979).

The impact of these disturbances on *Eucalyptus* population dynamics is not well documented. Dexter (1978) and Bren (1993) have described seedling regeneration of *Eucalyptus camaldulensis* following flooding in riparian communities but there are no studies describing the effects of severe storms and droughts. Studies of other plant taxa and communities have, however, documented seed regeneration following these events.

Hnatiuk and Hopkins (1980) described the effects of winter drought on Western Australian kwongan vegetation. They found that drought-affected species regenerated both vegetatively and by seed and concluded that there were many similarities in the response of the vegetation to both fire and drought. Similarly, wind related disturbances have been found to be an important component of seed regeneration in temperate deciduous forests (Runkle 1985), subtropical rainforests (Olsen and Lamb 1988) and tropical forests (Webb 1958; Brokaw 1985).

This chapter aims to determine whether fires, floods, severe storms and droughts initiate seedling recruitment in *E. salmonophloia* and thereby provide a basis for understanding the conditions necessary for germination and establishment.

4.2 **METHODS AND MATERIALS**

4.2.1 STUDY SITES

The study was undertaken at nine sites to the east of the agricultural wheatbelt where extensive unfragmented *E. salmonophloia* woodlands still exist. This area corresponds roughly to the region east of the 300 mm rainfall isohyet (Figure 4.1). Sites were chosen with known disturbance histories determined from Department of Conservation and Land Management records at Kalgoorlie. Table 4.1 describes the location, woodland type, dominant tree species and type and date of disturbance at each of the study sites.

Sites 1-4, respectively, were located in woodlands where flood, fire, drought and a severe storm had occurred in the last 50 years and apparently initiated seedling regeneration of *E. salmonophloia*. Sites 5 and 6 were located in *E. salmonophloia* woodland where there was no known history of disturbance in the last 50 years and were included for comparison with the disturbed sites. Sites 7, 8 and 9, respectively, were located in woodlands where fire, a severe storm and flooding had occurred in the last 3 years.

Figure 4.1: The extent of the Western Australian wheatbelt, distribution of *E. salmonophloia* woodlands and location of the study sites.

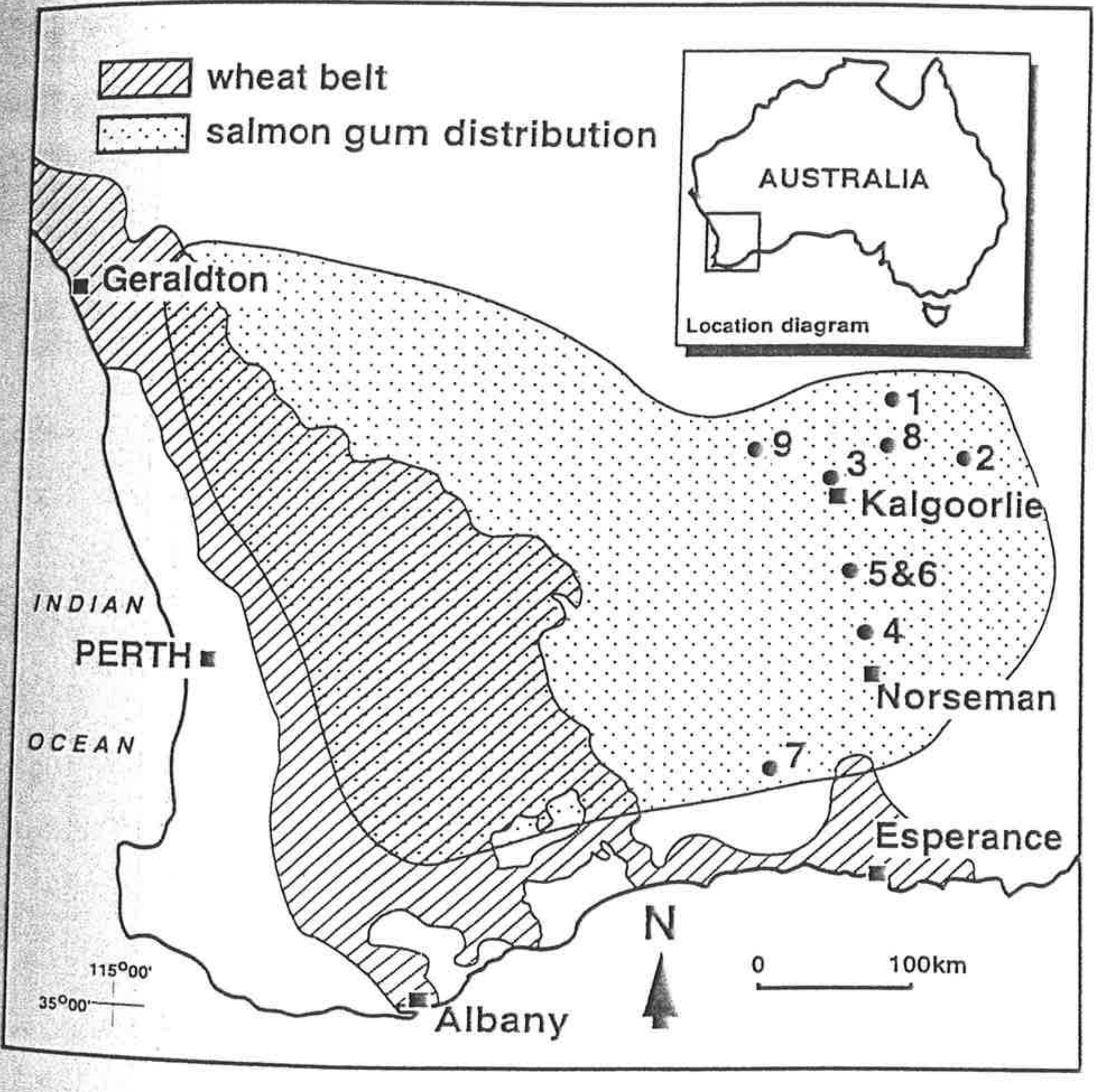


Table 4.1: Descriptions of *E.salmonophloia* study sites. Surveys of size class structure were conducted at sites 1-6 and surveys of germination and establishment of seedlings at sites 7-9.

Site	Location	Woodland type	Dominant tree species	Disturbance	Disturbance date
1	Lake Emu	Salmon gum	*Eucalyptus salmonophloia* *Eucalyptus gracilis*	Flood	1948
2	Kurnalpi	Salmon gum	*Eucalyptus salmonophloia*	Fire	Summer 1974/75
3	Kalgoorlie	Mixed eucalypt	*Eucalyptus salmonophloia* *Eucalyptus salubris* *Eucalyptus lesouefii*	Drought	1976
4	Norseman	Mixed eucalypt	*Eucalyptus salubris* *Eucalyptus salmonophloia* *Eucalyptus lesouefii* *Eucalyptus flocktoniae*	Severe storm	1976
5	Kambalda Timber Reserve	Salmon gum	*Eucalyptus salmonophloia*	Undisturbed	
6	Kambalda Timber Reserve	Salmon gum	*Eucalyptus salmonophloia*	Undisturbed	
7	Peak Charles National Park	Salmon gum	*Eucalyptus salmonophloia*	Fire	January 1991
8	Gindalbie	Salmon gum	*Eucalyptus salmonophloia*	Severe storm	March 1992
9	Canegrass Lagoon	Salmon gum	*Eucalyptus salmonophloia* *Eucalyptus gracilis*	Flood	1992

4.2.2 SIZE CLASS STRUCTURE

At sites 1-6, a 100 m x 100 m quadrat was established and the stem diameter at breast height (DBH) was measured for each *E. salmonophloia* individual and placed in a size class 0-10 cm, 11-20 cm, 21-40 cm, 41-80 cm or 81-160 cm.

4.2.3 SEEDLING EMERGENCE AND SURVIVORSHIP

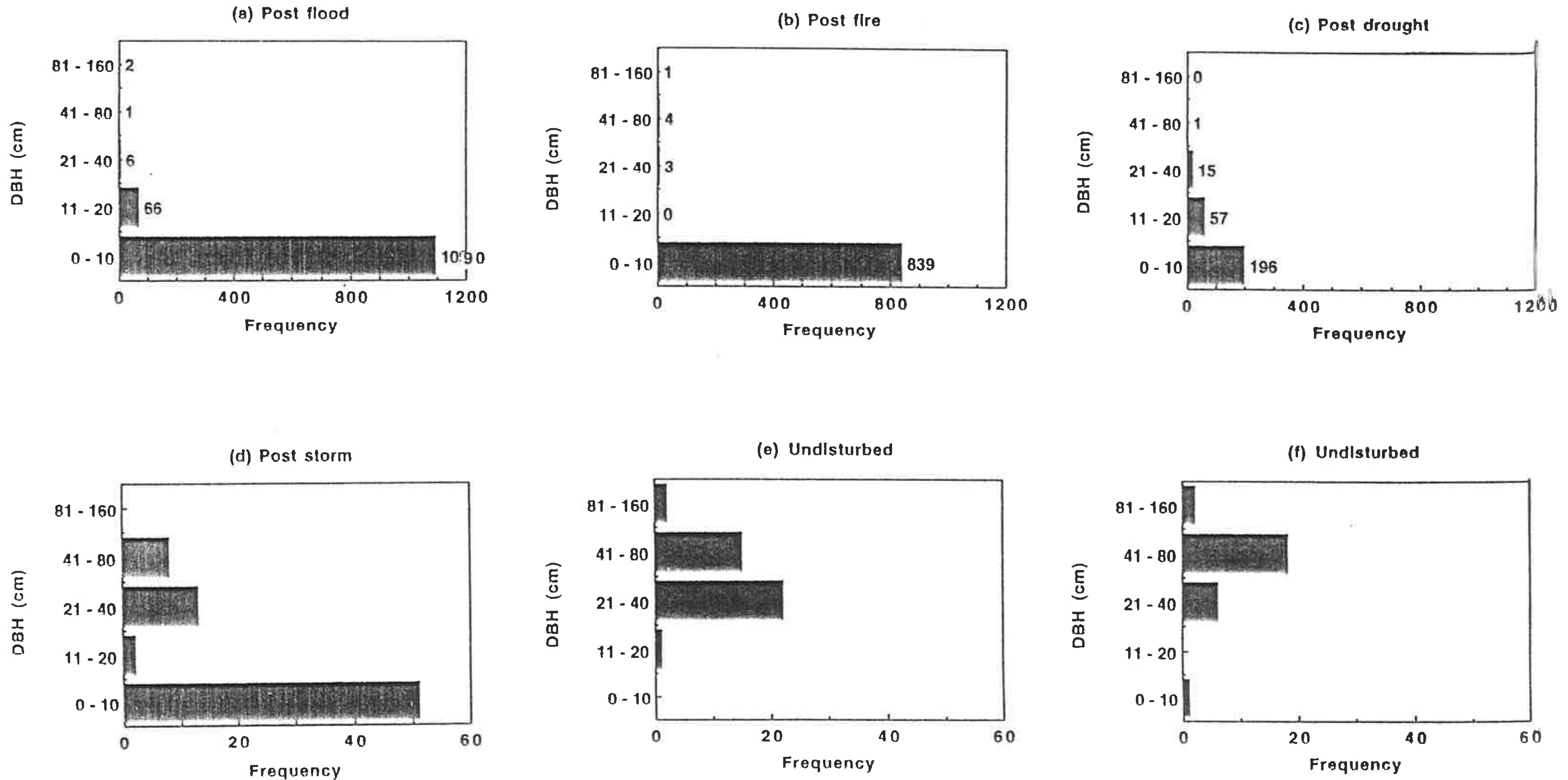
At sites 7-9, seedling emergence and survivorship were measured in transects consisting of ten, 1 m^2 contiguous quadrats. At site 7 (Peak Charles), two transects were established in September 1991 in the first spring after the fire and resurveyed in October 1992. At site 8 (Gindalbie Station), transects were established beneath each of four windthrown tree canopies in October 1992 and resurveyed in May 1993. At site 9 (Canegrass Lagoon), four transects were established in May 1993 in woodland where floodwaters had receded. At each site, equivalent numbers of control transects were established in adjacent or nearby undisturbed woodland to monitor any seedling regeneration in the absence of disturbance. At sites 7-9, observations of adult mortality following the disturbances were made.

4.3 **RESULTS**

4.3.1 SIZE CLASS STRUCTURE

Size class frequency data for *E. salmonophloia* in woodlands disturbed by flood, fire, drought and a severe storm (sites 1 - 4 respectively) showed a predominance of individuals in the 0-10 cm size class and very few individuals in the larger size classes (Figure 4 2). Many large standing and fallen dead trees, presumably killed by the disturbance, were observed at these sites. In contrast, in undisturbed woodlands (sites 5 and 6), only one individual occurred in the 0-10 cm size class with the majority of individuals in the larger size classes. No standing dead trees were observed at these sites.

Figure 4.2: The frequency of *E. salmonophloia* individuals in stem diameter at breast height classes (DBH cm) in 1 ha quadrats at (a) site 1 following a flood in 1948; (b) site 2 following a fire in 1974/75; (c) site 3 following a drought in 1976; (d) site 4 following a severe windstorm in 1976 and (e, f) site 5 and site 6 with no history of these disturbances in the last 50 years.



Relatively fewer *E. salmonophloia* were present in the 0-10 cm size class in drought and severe storm affected woodlands than at the fire and flood affected woodlands. However, differences in the composition of the tree species at each site made comparisons between sites difficult (Table 4.1). At the drought and storm affected sites *E. salmonophloia* grew with other *Eucalyptus* spp., and hence there were relatively fewer adult *E. salmonophloia* than at the fire and flood affected sites. The other *Eucalyptus* spp. (*Eucalyptus salubris* F. Muell., *Eucalyptus lesouefii* Maiden and *Eucalyptus flocktoniae* Maiden) showed similar size class distributions to *E. salmonophloia* (Table 4.2).

4.3.2 SEEDLING EMERGENCE AND SURVIVORSHIP

Large numbers of seedlings were located in sites recently burnt (Site 7), subject to windstorm (Site 8) and flooded (Site 9) (Table 4.3). Seedling densities varied with as many as 60 seedlings present per square metre. No seedlings were located in unburnt woodland near Site 7, or outside fallen canopies or in adjacent undisturbed woodland at Site 8. At Site 9, seedlings in the transects furthest from the receding waters edge were well established and larger than seedlings in transects where water had recently receded. In nearby unflooded woodland, 16 *E. salmonophloia* seedlings were located in heavy litter in four 10 m^2 control transects. Fifty two percent of the seedlings in the burned site and 99% in the storm-affected site had died during their first summer.

At sites 7 - 9, there was considerable adult mortality. The fire at Peak Charles (Site 7) was a very intense canopy fire and crown scorch was 100%. By September 1991, 9 months after the fire, few trees were sprouting epicormically. Surveys in the following spring in October 1992 revealed that only 50% of trees had survived the fire and were resprouting. At Gindalbie Station (site 8), the storm passed through only a small area of *E. salmonophloia* woodland and it was difficult to identify its exact path and therefore difficult to determine what percentage of the trees in the woodland had been affected. However, it was estimated that about 30% of the trees were uprooted. In May 1993, 14 months after the storm, only 1 tree was resprouting from its base. At Cane Grass Lagoon (site 9) surveys of adult mortality were

Table 4.2: Size class distribution of other *Eucalyptus* spp. growing with *E. salmonophloia* in woodlands disturbed by drought and a severe storm.

Site	Disturbance	Species	Size classes for diameter at breast height (cm)		
			0-10	11-20	21-40
Kalgoorlie (site 3)	Drought	*Eucalyptus salubris*	232	25	1
		Eucalyptus lesouefii	195	0	4
Norseman (site 4)	Severe storm	*Eucalyptus salubris*	1026	0	4
		Eucalyptus flocktoniae	40	0	0
		Eucalyptus lesouefii	12	0	0

Table 4.3: The number of *E. salmonophloia* seedlings in 10 m x 1 m transects established in woodlands after fire, severe windstorm, flood and in adjacent undisturbed woodlands (controls). Transects at Peak Charles and Gindalbie Station were resurveyed after the first summer following the disturbance.

Site	No. transects	Disturbance	No. seedlings	No. survivors
Peak Charles (site 7)	2	Fire	391 (Sept '91)	186 (Oct '92)
Peak Charles (control)	2	Control	0	
Gindalbie Station (site 8)	4	Severe storm	297 (Oct '92) 443 (May '93)	3 (May '93)
Gindalbie Station (control)	4	Control	0	
Canegrass Lagoon (site 9)	4	Flood	146 (May '93)	
Canegrass Lagoon (control)	4	Control	16	

difficult because much of the area was still flooded. However, in the area surrounding the quadrats there was 100 % mortality.

4.4 DISCUSSION

Germination of *E. salmonophloia* seedlings followed the recent fire at Peak Charles (site 7), severe storm at Gindalbie Station (site 8) and flood at Canegrass Lagoon (site 9). Nearby undisturbed woodlands at each location were devoid of seedlings except at Canegrass Lagoon where a small number of seedlings were in heavy litter. The presence of seedlings at the recently burnt, flooded and storm damaged sites and their absence or low numbers in nearby undisturbed woodlands indicates that these disturbances facilitated germination and early growth of seedlings.

Rates of seedling mortality were lower at Peak Charles than at Gindalbie Station in the first year after the fire and storm, respectively. Causes of seedling death were unknown, but other studies of seedling regeneration in semi-arid *Eucalyptus* mallee communities (Wellington and Noble 1985b) and other mediterranean scrub-heathland and woodlands (Cowling *et al.* 1990) following fire have shown that seedling mortality is highest in the first summer following the disturbance when prolonged dry periods with high temperatures occur. Rainfall differences in the first summer (December - February) following the disturbances may account for the observed differences in seedling survivorship at the two sites. Rainfall in the first summer following the fire at Peak Charles was 178 mm, three times the long term average, and 48% of the seedlings in the transects survived. By contrast, rainfall in the first summer following the storm at Gindalbie Station was 51 mm, 13 mm below the average and considerably less than at Peak Charles, and only 1% of seedlings in the transects survived.

The presence of a large number of uniformly sized cohorts of saplings at Sites 1-4 in the 0-10 cm size class in woodlands following flood, fire, drought and a severe storm in the previous 16-44 years, indicate that successful establishment can follow these disturbances.

Moreover, the absence or low number of saplings in the 0-10 cm size class in woodland in the Kambalda Timber Reserve where there was no evidence of these disturbances in the last 50 years indicates that seedling recruitment in their absence is rare.

The poor survivorship of seedlings at Gindalbie Station following the storm suggests that seedling recruitment following these disturbances does not always occur and may be contingent upon a succession of above average rainfall years following the disturbance. This has been shown in studies of other mediterranean climate taxa which recruit seedlings following fire (Wellington and Noble 1985a,b; Enright and Lamont 1992a). Wellington and Noble (1985a,b) showed that over a 15 year period, successful seedling recruitment of mallee *Eucalyptus* spp. occurred following 10% of fires. Enright and Lamont (1992a) have calculated that the coincidence of fire and above average rainfall years suitable for seedling establishment in some populations of *Banksia attenuata* may occur three times in the 300 year life span of an individual.

Large areas of *E. salmonophloia* woodlands around the gold mining centres of Coolgardie and Kalgoorlie are regrowth following clearfelling to supply mining timber and fuelwood (Kealley 1991). Exploitation began in 1890 and continued until 1960 (Kealley 1991). Evidently seedling recruitment occurred following this massive disturbance with seed arising from the remaining trees and canopy debris left after logging (Kealley 1991). However regeneration was not always successful and some regrowth woodlands are very sparse (Beard 1990).

In other *Eucalyptus* spp. which recruit seedlings following fire, studies of seed dynamics in interfire periods have shown that firstly, several seasons of seed are stored in woody fruits on the plant forming a substantial seed reserve; secondly, there is a constant seed rain from the canopy and thirdly that ants eat most of this seed and prevent the establishment of a soil seed bank (Ashton 1979; O'Dowd and Gill 1984; Andersen and Ashton 1985; Wellington and Noble 1985a; Andersen 1987, 1988, 1989; Davies and Myerscough 1991). Evidently fire interacts with these life history attributes to provide an environment suitable for seedling recruitment, firstly by causing a mass release of all canopy stored seeds, satiating predators, and thereby facilitating the establishment of a soil seed bank (Ashton 1979; O'Dowd and Gill 1984; Wellington and Noble 1985a; Andersen 1987, 1988). Secondly, changes in soil conditions following a fire can increase rates of germination and establishment (Wellington and Noble 1985a; Burrows *et al.* 1990); this has been attributed to addition of nutrients from ash and elimination of plant pathogens in the soil (Loneragan and Loneragan 1964; Humphreys and Lambert 1965; Renbuss *et al.* 1973; Humphreys and Craig 1981; Walker *et al.* 1986). Finally, there is an increase in seedling survivorship associated with an increase in resource availability particularly in gaps created by the death of adult plants (Wellington 1984; Wellington and Noble 1985b).

The research documented in Chapters 2 and 3 indicates that *E. salmonophloia* shares common life history attributes with *Eucalyptus* spp. that recruit seedlings following fire. The research presented in this chapter indicates that *E. salmonophloia* also recruits seedlings following fire. The above model describing the processes underlying seedling recruitment therefore seems relevant to *E. salmonophloia*. However fire is not the only form of disturbance that results in recruitment and the relevance of this model to flood, severe storm and drought initiated recruitment needs further consideration.

The synchronous mass release of canopy stored seeds following fire results from the death of the tree canopy. Flame residence times in parts of the canopy are brief enough not to damage the seeds which are insulated and protected by clustered woody capsules (Judd and Ashton 1991; Judd 1993). The death of the canopy results in the severance of water supply to capsules which subsequently dehisce and release their seed (Cremer 1965). This also appears to be the case following floods, severe storms and droughts. Like fire, these disturbances result in the death of tree canopies and therefore a subsequent synchronous and mass release of canopy stored seed.

Seed harvesting by ants prevents the establishment of a soil seed reserve in *E. salmonophloia* during inter-disturbance periods (Chapter 3). It would appear that, like fire, the synchronous mass seed fall induced by the death of adult trees following floods, severe storms and droughts, satiates predators allowing the establishment of a soil seed reserve.

The above model of seedling recruitment in *Eucalyptus* spp. following fire describes changes in soil conditions which enhance rates of germination and establishment. Whether this is the case for *E. salmonophloia* and other large scale disturbances which initiate recruitment is unknown. The conditions necessary for the germination and early growth of *E. salmonophloia* seedlings and the impact of large scale natural disturbances on these processes will be considered in the following chapters.

It should be noted that the observations of large scale disturbance events that initiated seedling recruitment are restricted to populations located towards the drier end of *E. salmonophloia's* distribution (Section 2.2.1 describes the rainfall gradient) and may possibly be of limited use in defining *E. salmonophloia's* regeneration niche. However, for several reasons this is unlikely to be the case. Historical records of *E. salmonophloia* recruitment in wheatbelt remnants following fire and anthropogenic disturbances (Norton *et al.* in press) together with observations of similar regeneration patterns in wheatbelt (wetter) and goldfields populations (drier) indicate that large scale natural disturbances are an important component of the species regeneration niche throughout its distribution.

CHAPTER 5

CONDITIONS NECESSARY FOR SEED GERMINATION IN *E. SALMONOPHLOIA*

5.1 INTRODUCTION

Chapter 4 demonstrated that seedling recruitment in *E. salmonophloia* occurs following large scale disturbances such as fire, severe storms, floods and droughts. Recruitment in periods between these disturbances is evidently very rare. This may be due to conditions being more favourable for germination and establishment of seedlings following these large scale disturbances.

The objective of this chapter is to define the conditions necessary for the germination of *E. salmonophloia* . Temperature and soil moisture availability are major factors affecting germination (Mott and Groves 1981). These factors are influenced by climate and the seeds of many plant species have evolved to maximise the likelihood of germination occurring when conditions are most suitable for seedling establishment (Mott and Groves 1981). Germination can also be affected by disturbance which may enhance the process by breaking seed dormancy or through providing a more favourable seed bed (Gill 1975; Keeley and Pizzorno 1986; Bell *et al.* 1987; Keeley and Keeley 1987; Portlock *et al.* 1990; Keeley 1991; Brown *et al.* 1993).

In this chapter the effects of temperature, soil wetting/drying cycles (soil moisture), depth of seed burial and post disturbance soil conditions on the germination of *E. salmonophloia* are described to determine if there are any particular characteristics of the post disturbance environment which enhance germination.

5.2 METHODS AND MATERIALS

5.2.1 PLANT MATERIAL

Seeds used in germination experiments were supplied by a commercial seed supplier (Vaughans Wildflower Seeds) and collected from remnant woodland on the western edge of *E. salmonophloia's* distribution.

5.2.2 THE EFFECT OF TEMPERATURE ON GERMINATION

Forty replicates of 50 seeds were placed in 9 cm closed petri dishes on paper germination pads (Whatman No. 4 filter paper on a 'Wettex' disc) moistened with 25 mL of sterilised de-ionised water. Ten petri dishes were randomly assigned to each of four temperature treatments: 15°C, 20°C, 25°C and 30°C, placed on trays and sealed in a plastic bag to reduce evaporation. Each tray was placed in a controlled environment chamber at the appropriate temperature, with continuous light (2500 lx) for 28 days. Germinants were counted and removed twice a week; seeds were counted as germinated when the radicle had emerged. After 28 days, five dishes from the 15°C and 30°C treatments were placed at 25°C and the subsequent effect on germination monitored.

Cumulative germination percentages were calculated on the basis of total seed numbers. Germination rates are expressed firstly as the initial germination speed ($1/T_{0.2\%}$) where $T_{0.2\%}$ is the time in days from sowing to germination of at least one seed in any replicate; and secondly the median germination speed ($1/T_{50\%}$) where $T_{50\%}$ is the time in days from sowing to the germination of at least 50% of viable seeds (Lush *et al.* 1984). The effect of temperature on germination capacity (% germination) was determined with a one way ANOVA. Analysis was performed on the number of germinants after 28 days. Assumptions of homogeneity of variance and normality were checked with residual plots and no transformations were required. Post hoc comparisons of treatment means were made with a

Tukey -Kramer Test (Zar 1984). The effect on germination of temperature transfer was determined with paired two tailed t-tests.

5.2.3 THE EFFECT OF WETTING / DRYING REGIMES ON GERMINATION

Forty replicates of 50 seeds were placed on paper germination pads in petri dishes (as described in 5.2.2). Ten replicates were assigned to each of the following wetting/drying regimes: 4 days wet/2 days dry; 2 days wet/2 days dry; 1 day wet/2 days dry; and a control treatment (continually moist). Twenty five mL of sterilised de-ionised water was added to petri dishes in each wetting/drying regime beginning with the 4 day wetting treatment so that each wetting period finished simultaneously. During the wetting period dishes were placed on trays sealed in plastic bags to prevent evaporative loss and placed in a control temperature room with constant light (500 lx), at 25°C, the optimal temperature for germination (see 5.3.1). At the end of the wet period the filter papers with seeds were removed from the petri dishes and air dried in the constant temperature room for 48 hours after which time filter papers and seeds had returned to their original air dry weight. The filter papers and seeds were then returned to their petri dishes and rehydrated; 25 mL of water was also added to control dishes at this time. Replicate dishes from each treatment were placed on trays and sealed with plastic bags to reduce evaporative loss and incubated at 25°C for 21 days. Dishes were checked twice a week and germinants counted and removed. Seeds were counted as germinated when the radicle had emerged.

Cumulative germination percentages and germination rates were calculated as described in section 5.2.1. The effect of wetting drying cycles on germination capacity (% germination) was determined with a one way ANOVA. Analysis was performed on the number of germinants after 21 days. Assumptions of homogeneity of variance and normality were checked with residual plots and no transformations were required.

5.2.4 THE EFFECT OF SEED BURIAL DEPTH ON SEEDLING EMERGENCE

Surface soil (upper 5 cm) was collected from Minniberri Reserve (described in Chapter 2), mixed thoroughly and placed into 50 dishes (9 cm diameter x 2.5 cm deep). Each dish was randomly assigned to one of five burial treatments: seeds on the soil surface, seeds buried 2 mm deep, 5 mm deep, 10 mm deep and 20 mm deep.

Fifty replicates of 50 seeds were randomly assigned to one of the five burial treatments (i.e. ten replicates per treatment); seeds were carefully placed on the surface or buried at the required depth. Forty mL of water was added to each dish. Replicates from each treatment were placed on trays and sealed in plastic bags to prevent the soil drying out. Trays were incubated at 25^{O}C with continuous light (500 lx) for 6 weeks. Seedlings were counted and removed after 1 week, 2 weeks, 3 weeks and 6 weeks; seedlings were counted when the cotyledons were visible.

The effect of seed burial depth on seedling emergence was determined using a one way ANOVA. Analysis was performed on the number of seedlings which had emerged after 42 days. Assumptions of homogeneity of variance and normality were checked with residual plots and no transformations were required. Post hoc comparisons of treatment means were made using the Tukey Kramer test (Zar 1984).

5.2.5 THE EFFECT OF SEEDBED CONDITIONS ON SEEDLING EMERGENCE AND ESTABLISHMENT; FIELD EXPERIMENT

A factorial experiment was conducted at Minniberri Reserve (see Chapter 2) using three seedbed treatments and two watering treatments. The seedbed treatments were: exposed soil, litter covered soil, and ashbed; the watering treatments were natural rainfall and supplemented rainfall.

The soil surface at the study site consists of patches of accumulated litter and exposed soil; this pattern is a characteristic of *E. salmonophloia* woodlands and seeds can be dispersed onto either substrate. This pattern determined the position of treatment quadrats; 30 quadrats (1 m^2) were located in the woodland; 10 quadrats were placed on patches of exposed soil and 20 quadrats on patches of litter, 10 of which were randomly selected for ashbed treatments. Quadrats were at least 2 m apart but no more than 4 m apart.

Treatments were applied to the quadrats in the following manner.

SEEDBEDS

Exposed soil - The surface 5 mm of soil was removed from the quadrat, half of this was replaced; 2 g of seed and chaff (infertile ovular structures and aborted embryos) mixture were spread evenly over the quadrat and buried with the remainder of the soil to a depth of approximately 2 mm.

Litter - Litter was removed from the quadrat and 2 g of seed and chaff mixture spread evenly over the quadrat and the litter replaced.

Ashbed - Litter and vegetation together with the surface 5 mm of soil were removed from the quadrat. The litter and vegetation fractions from each quadrat were bulked and burnt on top of the bulked soil fraction in a 30 cm deep x 70 cm diameter steel ring. Soil temperatures beneath the fire were measured with thermisters and reached 200°C. The litter burnt completely producing a fine white ash and charcoal. This was weighed into ten equal portions and combined with equal portions of the heated soil and this mixture spread evenly over the quadrat. Two grams of seed and chaff mix were sown evenly over the quadrat and buried to a depth of approximately 2 mm with a layer of ash and heated soil.

WATERING TREATMENTS

Natural rainfall - All the quadrats were exposed to natural rainfall which was recorded daily approximately 2 km from the study site.

Supplemented rainfall - Natural rainfall was supplemented with 10 L of tap water (equivalent to 10 mm of rainfall) on three occasions (30-4-1992; 19-5-1992; 20-5-1992) after seed was sown (29-4-1992), before the beginning of the wet season.

Following the application of seedbed treatments all quadrats were treated with 'Ant Killer Dust' at the recommended rate (Hortico, active constituent diazinon) to prevent harvesting of seed.

Fences, 30 cm high constructed from 70% shade cloth were erected around each quadrat to prevent treatments being blown or washed away. In addition a fence 1 m high constructed from wire mesh (2 cm diameter) was erected around plots to prevent grazing by rabbits, sheep or kangaroos.

Quadrats were inspected every 4 weeks and all newly emerged seedlings marked with toothpicks and their survival monitored. Seedlings were recorded when cotyledons were visible.

The effect of seed bed conditions and irrigation on seedling emergence was determined using a two way ANOVA. Assumptions of homogeneity of variance and normality were checked with residual plots and no transformations were required.

5.3 **RESULTS**

5.3.1 THE EFFECT OF TEMPERATURE ON GERMINATION

Germination commenced 2 - 7 days after sowing and reached a maximum 11 - 25 days after sowing (Figure 5.1). Maximum germination ranged from 49% at 15°C to 98% at 25°C.

Germination rate

The rate of initial germination ($1/T_{0.2\%}$) increased with increasing temperature and reached a plateau at 25°C (Figure 5.2a). The rate of median germination ($1/T_{50\%}$) increased with temperature to an optimum of 25°C and then declined (Figure 5.2b).

Figure 5.1: Germination capacity after 28 days on moistened paper substrates at 15°C, 20°C, 25°C and 30°C. Values are means of ten replicates of 50 seeds.

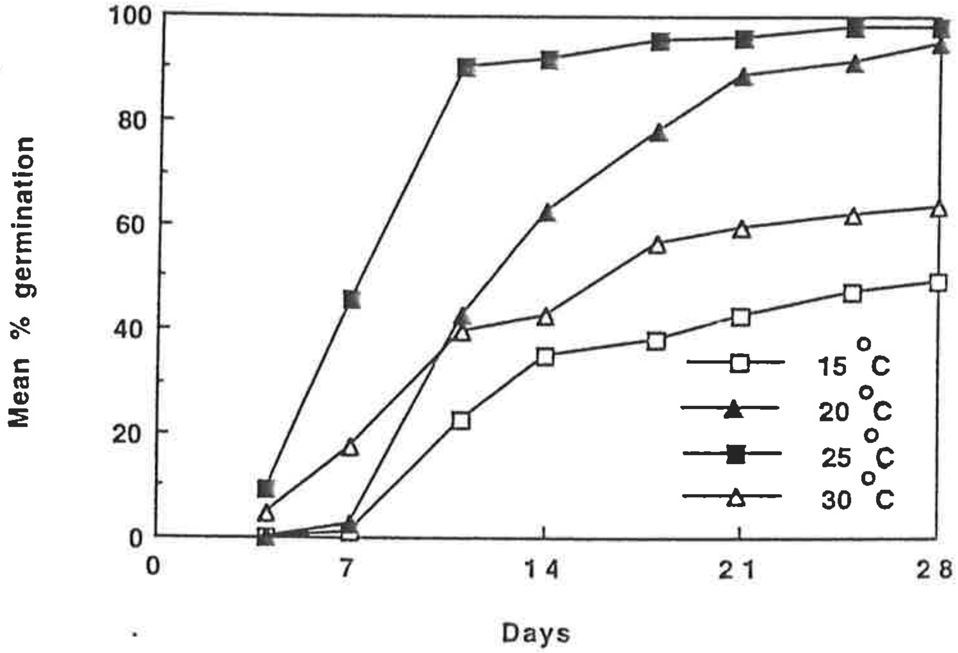
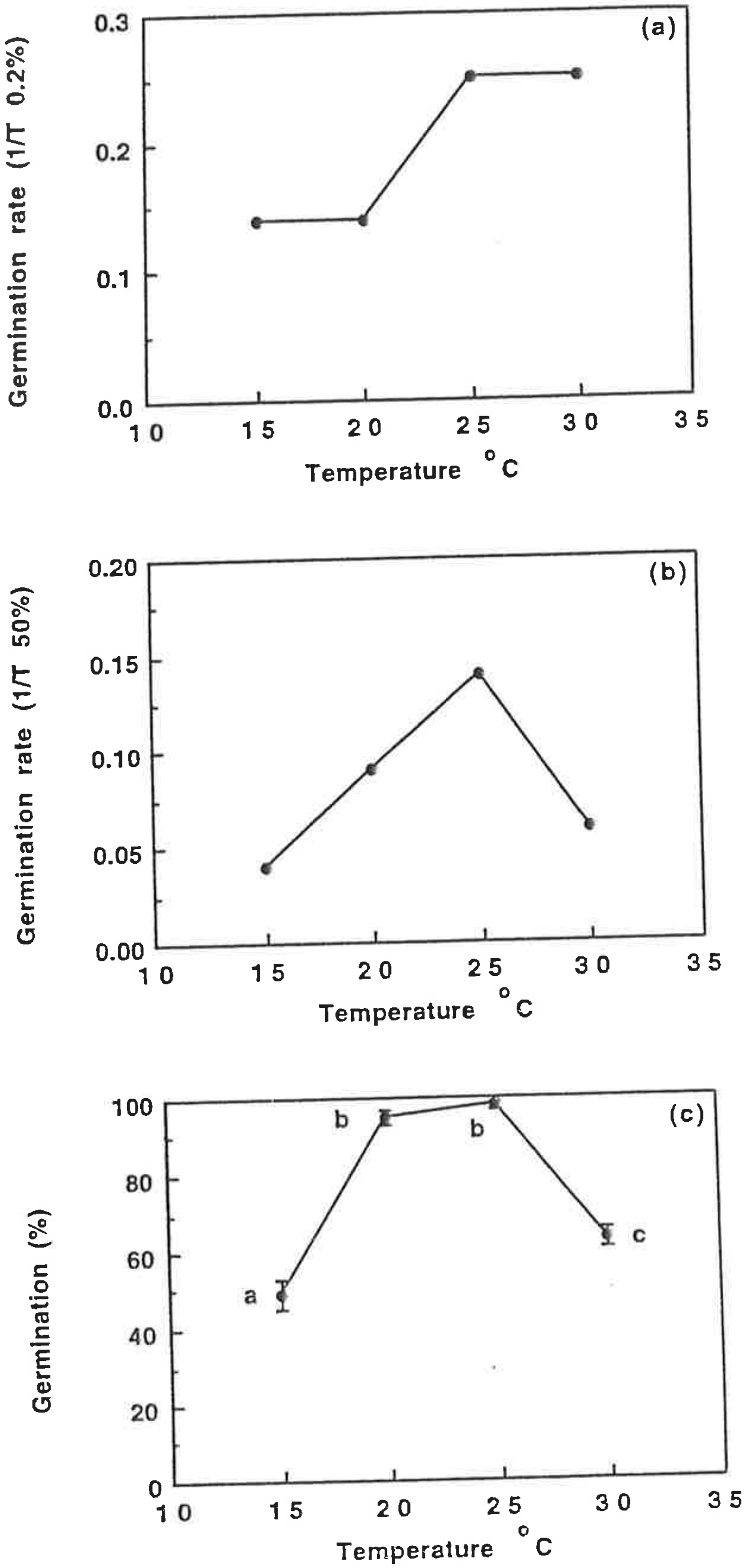


Figure 5.2: (a) initial germination rate (1/T$_{0.2\%}$), (b) median germination rate (1/T$_{50\%}$) and (c) germination capacity after 28 days at 15°C, 20°C, 25°C and 30°C. Germination capacity data was analysed with a one way ANOVA and in all cases significance was determined from Tukey- Kramer test of multiple comparisons of means. Values with the same letters are not significantly different ($p<0.05$). Vertical bars represent standard errors.



Germination capacity

Germination capacity after 28 days incubation was significantly affected by temperature (F=84.12, d.f.=3, 36, p<0.0001). Mean germination capacity, like germination rate, was highest at 25°C (98%) and significantly depressed at 15°C (49%) and 30°C (63%)(Figure 5.2c). By contrast, at 20°C germination capacity was the same as at 25°C whereas the rate of germination was depressed.

The transfer of seeds from the 15°C cabinet to the 25°C cabinet had a significant effect on germination (t=-9.04, d.f.=4, p<0.001). After 7 days at 25°C, the mean number of germinants in transferred dishes increased to 66% compared to 8% in dishes that remained in the 15°C cabinet (Figure 5.3a). Similarly, the transfer of seeds from the 30°C cabinet to the 25°C cabinet had a significant effect on germination (t=-6.16, d.f.=4, p<0.01). After 7 days the mean number of germinants in transferred dishes was 78% compared to 17% in dishes that remained in the 30°C cabinet (Figure 5.3b).

5.3.2 THE EFFECT OF WETTING / DRYING REGIMES ON GERMINATION

Germination profiles for the three wetting/drying treatments and control treatment are given in Figure 5.4. Germination rates and capacities are discussed below.

Germination rate

The rate of initial germination ($1/T_{0.2\%}$) was higher in wetting / drying treatments than in the control treatment (Figure 5.5a). The rate of median germination ($1/T_{50\%}$) was not affected by wetting / drying treatments (Figure 5.5b).

Figure 5.3: Germination response after 7 days following transfer of seeds from (a) 15°C to 25°C and (b) 30°C to 25°C. Vertical bars represent standard errors.

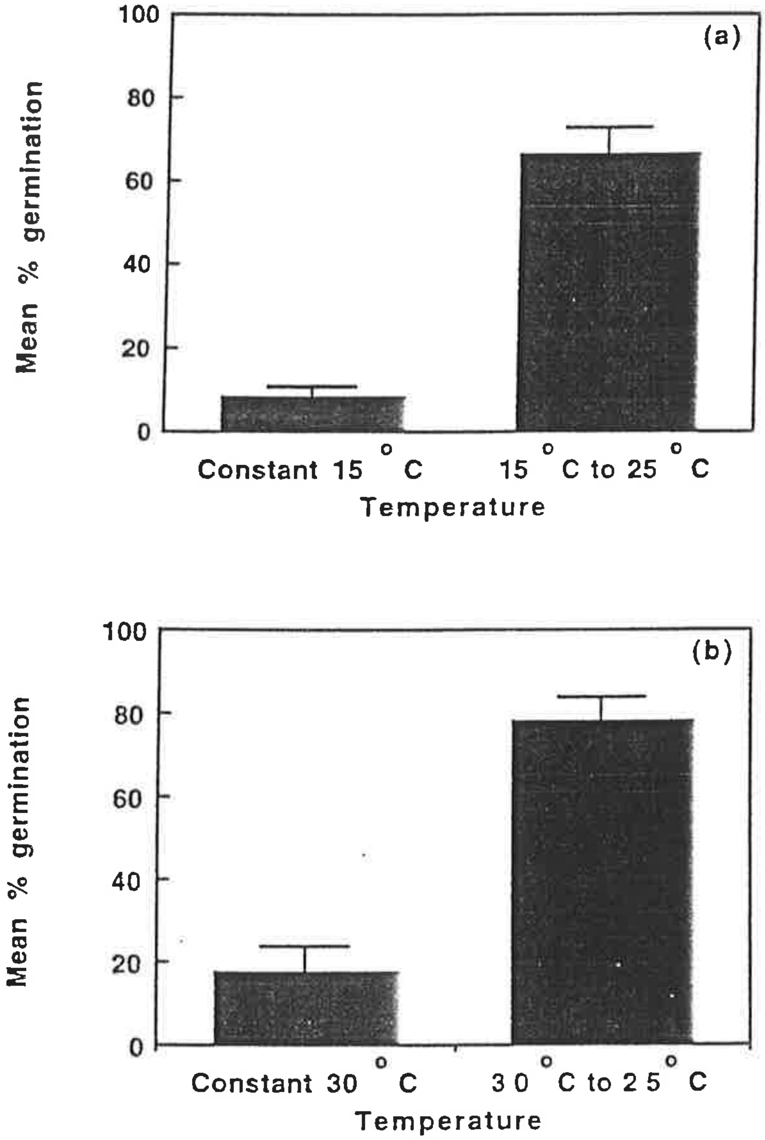


Figure 5.4: The effect of wetting and drying pre-treatments on germination capacity at 25°C. Values are means of ten replicates of 50 seeds.

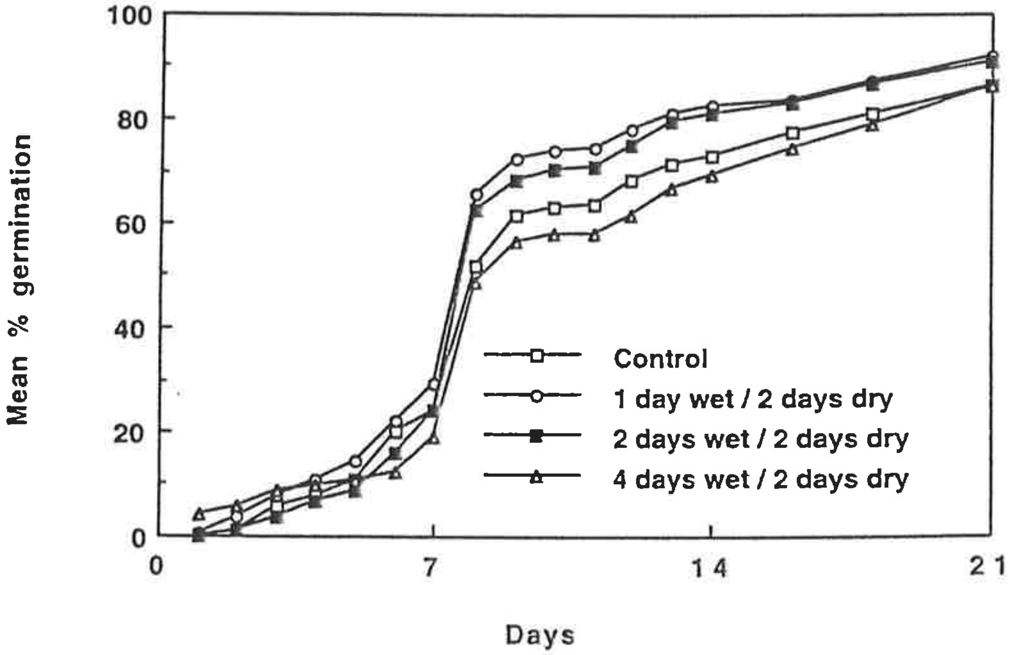
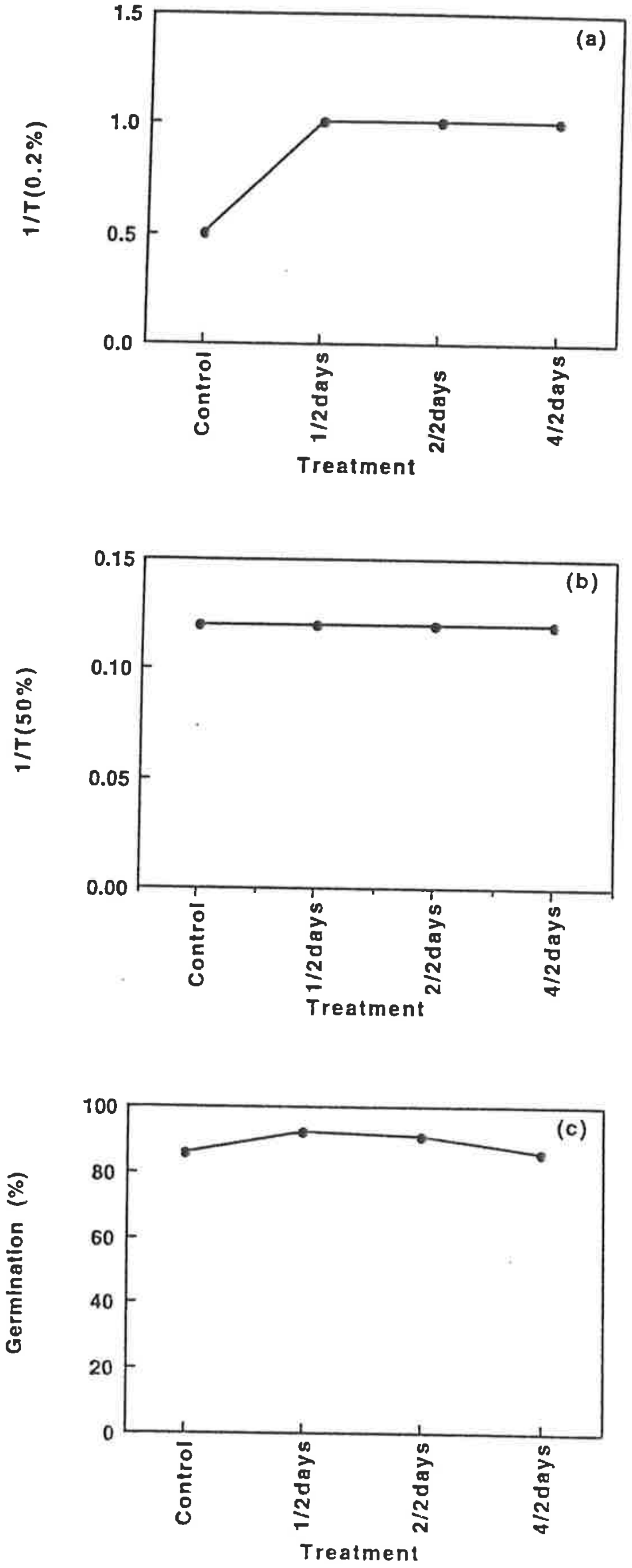


Figure 5.5: The effect of wetting drying pre-treatments on (a) initial germination rate, (b) median germination rate and (c) germination capacity after 28 days.



Germination capacity

Germination capacity was not affected by wetting drying treatments (*F* =0.89, d.f.=3, 36, *p* >0.05). After 21 days incubation, mean germination capacity was 86% in the control treatment, 92% in the 1 day wet / 2 day dry treatment, 91% in the 2 day wet / 2 day dry treatment and 86% in the 4 day wet / 2 day dry treatment (Figure 5.5c).

5.3.3 THE EFFECT OF SEED BURIAL DEPTH ON SEEDLING EMERGENCE

Seed burial at any depth depressed seedling emergence compared to unburied seed. With increasing depth of seed burial the number of emerged seedlings declined (*F* =228.64, d.f.=4, 45, *p* =0.0001). Mean % seedling emergence was 84% on the surface, 73% at 2 mm depth, 55% at 5 mm depth, 15% at 10 mm depth and 1% at 20 mm depth (Figure 5.6).

5.3.4 THE EFFECT OF SEEDBED CONDITIONS ON SEEDLING EMERGENCE AND ESTABLISHMENT; FIELD EXPERIMENT

There was a significant interaction between seedbed and watering treatments on seedling emergence (*F* =7.99, d.f.=2, 24, *p* <0.01). Mean seedling emergence on unwatered litter, exposed soil and ashbed treatments was similar to watered litter and exposed soil treatments (Figure 5.7). Seedling emergence on watered ashbeds, however, was considerably higher than all other treatments (Figure 5.7) and this accounts for the significant interaction.

The greatest number of seedlings observed was in the first census on the 27-6-92; seedlings were newly emerged and had cotyledons only. No new seedlings were observed in subsequent surveys and all seedlings had died within 3 months. The causes of death were unknown but many seedlings were wilted and desiccated. The fences erected to prevent grazing were effective as no grazed seedlings were observed.

Figure 5.6: Percentage seedling emergence after 28 days from seeds placed on the soil surface or buried at 2 mm, 5 mm, 10 mm and 20 mm. Values are means of ten replicates of 50 seeds. Values with the same letters are not significantly different ($p<0.05$). Data was analysed with one way ANOVA and in all cases significance was determined from Tukey-Kramer test of multiple comparisons of means. Vertical bars represent standard errors.

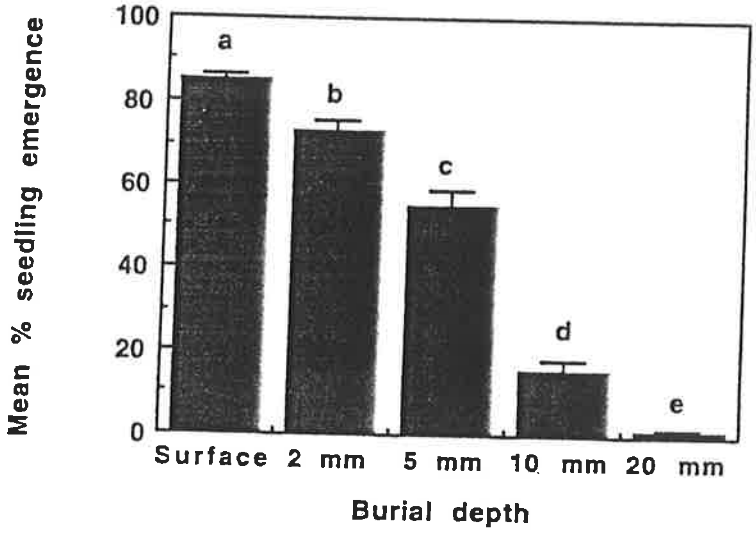
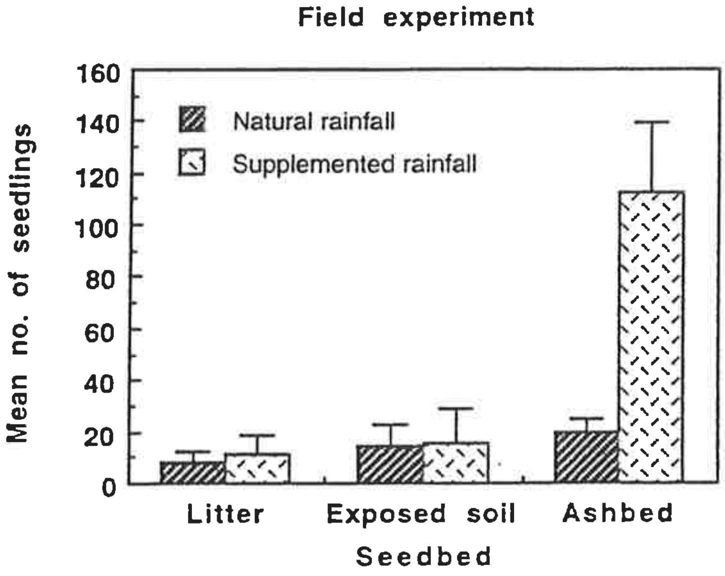


Figure 5.7: Seedling emergence in litter, exposed soil, and ashbeds under natural rainfall and supplemented rainfall at Minniberri Reserve. Values are means of five replicates. Supplemented rainfall treatments were watered prior to the beginning of the winter wet season (see Fig. 5.8). Vertical bars represent standard errors.



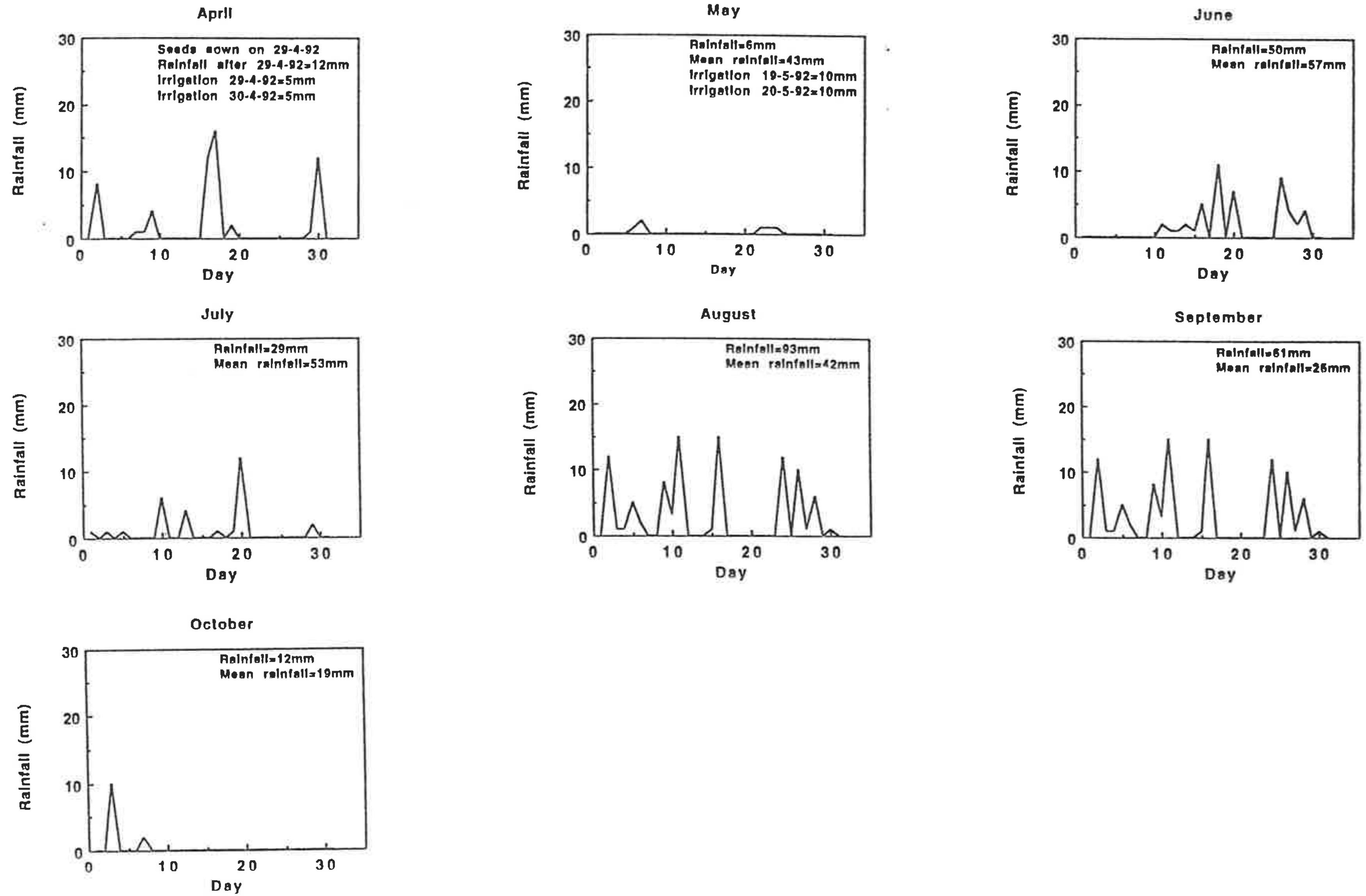
Rainfall during the experiment is shown in Figure 5.8 and was well below average in May, about average in June, well below average in July and well above average in August and September.

5.4 DISCUSSION

Germination commences with the imbibition of the seed and the establishment of metabolism in its rehydrated tissues and ends with the protrusion of the embryonic root or shoot through the seed coat (Mott and Groves 1981). This process involves a complex set of metabolic reactions which are affected by external environmental influences such as temperature and moisture availability. These factors are governed by climate, and seeds of many plant species have mechanisms which ensure that germination occurs only when conditions are likely to be suitable for seedling establishment (Mott and Groves 1981).

Seeds of many plant species, including eucalypts, germinate over a range of temperatures: within this range there is an optimal temperature, below and above which germination is delayed or depressed, but not prevented (Grose 1962; Mott and Groves 1981; Bellairs and Bell 1990). In many cases, germination is cued by temperatures which occur when conditions are most suitable for the subsequent survival of seedlings (Lodge 1981; Lodge and Whalley 1981; Cowling and Lamont 1987; Bell *et al.* 1993). In the mediterranean climate of south western Australia this often corresponds with the winter rainfall period when moisture conditions are optimal for seedling establishment (Cowling and Lamont 1987; Bell *et al.* 1993). The above strategy has evolved in some *Eucalyptus* spp. which have overlapping distributions with *E. salmonophloia* (Bell *et al.* 1993) but is not necessarily general (Bellairs and Bell 1990). Bell *et al.* (1993) observed that the optimum temperature range for germination in *Eucalyptus wandoo* was 15^{o}-20^{o}C and in *Eucalyptus oleosa* 10^{o}-20^{o}C; both ranges correspond to soil temperatures which are most likely to occur during the winter rainfall period. However, the range of temperatures optimal for germination of *Eucalyptus* spp. which have overlapping distributions with *E. salmonophloia* may not always correspond to the winter rainfall period. Bellairs and Bell (1990) observed that

Figure 5.8: Daily rainfall at a site 2 km from Minniberri Reserve and supplementary irrigation for the period of the experiment.

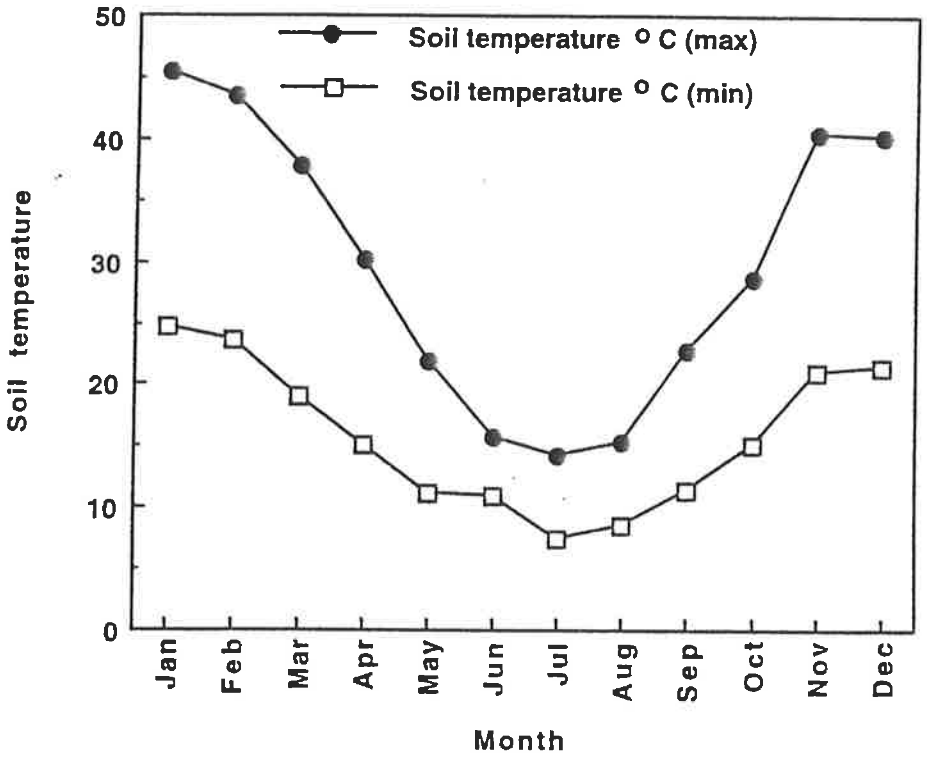


Eucalyptus tetragona had similar levels of germination in the 10°-35°C temperature range and suggested that seeds of this species would germinate at any time of the year following heavy rain.

In *E. salmonophloia,* germination rates and germination capacity displayed a distinct temperature optimum in the range of 20-25°C. Either side of the optimum, at 15°C or 30°C, germination was inhibited. However, when seeds were removed from 15°C and 30°C and placed at 25°C, levels of germination were similar to those achieved with continuous exposure to the optimum temperature. Seed dormancy induced by temperatures above and below the optimum have also been observed for other plant species from mediterranean climates in south western Australia (Bellairs and Bell 1990). Similarly Wellington (1981) observed in *E. incrassata*, a mallee species found in mediterranean climate regions of south eastern Australia, that seeds exposed to temperatures above 30°C became temporarily dormant. The above observations of *E. salmonophloia's* germination response to temperature highlight several important characteristics of the species' germination physiology. Firstly, germination is inhibited at temperatures above and below the optimum of 20-25°C; secondly, ungerminated seeds can survive in a moisture saturated environment at 15°C and 30°C for at least 28 days; and thirdly, the ungerminated seeds kept at sub- and super-optimal temperatures will germinate at a later date when exposed to optimal temperatures. Mean monthly soil temperatures (1 cm depth) recorded at Merredin approximately 40 km east of the study sites are given in Figure 5.9. These data match soil surface temperatures at Minniberri Reserve (Norton and Hobbs unpublished data) for February/March and June and therefore provide reliable estimates of all year round soil temperatures at the study sites. Using the Merredin data it can be seen that soil temperature ranges are most suitable for germination of *E. salmonophloia* in late April, May and early June (late autumn-early winter) and late August, September and October (late winter early spring).

The ability of seeds to germinate, however, is affected not only by temperature but also by moisture availability; seeds must achieve relative water contents sufficient for germination

Figure 5.9: Mean monthly soil temperatures (1 cm depth) at Merredin, 40 km from study sites.



processes to occur. Relative rates of imbibition and drying are affected by seed contact with the substrate, relative atmospheric humidity and soil matric potentials (Harper and Benton 1966; Bachelard 1985; Battaglia 1993). Battaglia (1993) found that germination of *E. delegatensis*, for example, was greatly retarded by low humidities and declining soil matric potentials. Bachelard (1985) observed similar trends in *Eucalyptus sieberi*, *Eucalyptus pilularis* and *Eucalyptus maculata*. Bachelard (1985) also observed that high atmospheric humidities could overcome the effects of lower soil water potentials. In *E. salmonophloia*, the minimum germination speed at the optimum temperature with 100% humidity and a water saturated substrate was 2 days. The median germination speed was 8 days and 100% germination occurred after 25 days. Clearly, prolonged periods of high humidity and soil moisture are needed for germination of *E. salmonophloia* to occur. The Kellerberrin area has a Dry Mediterranean climate with wet winters and hot dry summers. Rain falls mainly in the winter months between May and September when fronts associated with mid latitude depressions move across south western Australia every 1-2 weeks (Gentilli 1972). Summer rainfall does occur but is erratic and is usually associated with localised thunderstorm activity. Heavier more widespread rainfall occurs occasionally in summer when tropical cyclones which have crossed the north west coast of Western Australia degenerate into rain bearing low pressure systems and travel south east over the continent (Gentilli 1972). Soil moisture and atmospheric humidity are therefore most likely to be suitable for germination in winter when rainfall and cloud cover are highest. The results presented indicate that surface soil temperatures are most suitable for germination in early and late winter. It therefore appears that *E. salmonophloia* will germinate most successfully in early and late winter when the soil is still warm enough and soil moisture and atmospheric humidity are frequently high with the passage of rain bearing depressions and cold fronts. By contrast low rainfall and low humidity over summer generally make conditions unsuitable for germination. However, on occasions when prolonged rainfall and high humidity occur, as in the case of tropical rain bearing depressions, lower daily maxima may lower soil temperatures and allow germination to occur. Parsons' (1968) observations of germination in two mediterranean climate mallee species, *E. incrassata* and *E. oleosa* from south eastern Australia support the conclusion that germination of *E. salmonophloia* is most likely to occur at the beginning of winter. Both of these species have a 20^{o}-25^{o}C optimum temperature range for germination (Grose 1962) which is similar to *E. salmonophloia*. After sowing seed of both species in a mallee woodland, Parsons (1968) found that germination occurred throughout the period from May to July, the period of greatest soil moisture. Germination was greatest in May when temperatures were warmer (Parsons 1968).

It was established in this chapter that emergence of *E. salmonophloia* seedlings under well watered conditions was restricted to seeds which germinate in the surface 1 cm of soil. In their natural habitat, *E. salmonophloia* seeds in this fraction are subject to cycles of soil wetting and drying the length of which depend on the intensity, duration and frequency of consecutive rainfall events. In *E. sieberi* progress towards germination is made in successive wet periods and conserved during dry periods (Gibson and Bachelard 1986), a process described as stop-go germination (Lush *et al.*1984). Gibson and Bachelard (1986) suggest that stop-go germination is particularly advantageous for seeds on exposed seedbeds subject to intermittent drying. Unlike *E. sieberi*, rates of germination in *E. salmonophloia* did not increase following wetting periods; evidently *E. salmonophloia* seeds are unable to shorten the time to germination by being primed in a preceding wet period. Lush *et al.* (1984) suggest that stop-go germination is more likely to be frequent in areas with sporadic rainfall rather than mediterranean climate areas, and the results of this study support this conclusion.

In *E. salmonophloia*, wetting and drying did not affect seed viability except in instances where seeds had ruptured their seed coats during a wetting period. In these cases, seed death occurred in the subsequent drying period. Battaglia (1993) reported similar findings for *E. delegatensis*. The ability of *E. salmonophloia* seeds to withstand intermittent wetting and drying is an important feature which prevents soil seed reserves from being destroyed by light showers which occur sporadically in late spring, summer and early autumn, when conditions are least suitable for seedling establishment. This is particularly important for *E. salmonophloia* which only establishes temporary soil seed reserves following large scale disturbances (Chapter 3 and 4).

The first three experiments in this chapter examined the relationship between climate, soil temperature and soil moisture, and determined when germination of *E. salmonophloia* is most likely to occur. Germination, however, is also affected by seed bed characteristics and this may be particularly important for plant species which recruit seedlings following large scale natural disturbances. These disturbances may bring about changes in the soil which enhance germination. Studies of changes in seedbed conditions following large scale disturbances have largely focussed on fire (Humphreys and Craig 1981; Walker *et al.* 1986). Fire brings about changes in seedbed conditions in several ways; firstly through soil heating and secondly through removal of biomass and input to the soil of ash and charcoal. These processes destroy the soil-litter complex of micro-organisms inhibitory to plant growth (Renbuss *et al.* 1973) and increase the availability of nutrients; the so called ash bed effect (Humphreys and Lambert 1965). These changes may provide more suitable conditions for germination. Wellington (1981) observed in *E. incrassata* that heating or adding ash to the soil prior to sowing caused a two fold increase in germination and suggested that the destruction of the soil litter micro-organism complex may have been responsible for this. Fire may also stimulate germination in some plant species by breaking seed dormancy. This can occur in several ways; firstly soil heating can crack the seed coat in hard seeded species and allow germination to begin (Gill 1975; Bell *et al.* 1987; Portlock *et al.* 1990; Keeley 1991); secondly, exudates from charred wood can stimulate germination (Keeley and Pizzorno 1986; Keeley and Keeley 1987; Keeley 1991); and lastly, exposure to smoke can overcome seed dormancy (Brown *et al.* 1993). Clearly, in these cases fire creates a seed bed with special characteristics that enhance or stimulate germination. This does not appear to be the case in *E. salmonophloia*. Hobbs (1991) found no effect of elevated temperatures or charcoal exudates on germination of *E. salmonophloia*. Furthermore observations of substantial numbers of seedlings and saplings following not only fires but also severe windstorms, floods and drought indicates that germination can occur on a variety of seedbeds (Chapter 4) with quite different characteristics (e.g. ashbeds, litter beneath wind thrown canopies and exposed soil). These results suggest that *E. salmonophloia* has no special seedbed requirements and that germination will proceed on a variety of substrates when suitable soil temperature and moisture conditions prevail.

The results of the field germination experiment support this conclusion. Germination occurred on a variety of seedbeds at the beginning of winter when suitable moisture conditions prevailed with the passage of several rainbearing depressions and cold fronts. Similar levels of seedling emergence were recorded on exposed soil, litter and ashbed treatments under a natural rainfall regime. However, when seed beds were watered prior to the beginning of the winter wet season, significantly greater numbers of seedlings were recorded on ashbeds. The processes responsible for this interaction are difficult to determine. A possible explanation is that the irrigated ashbeds retained enough moisture for germination to proceed during a dry period in May when soil temperatures were optimal. This may have resulted in a greater number of seeds being closer to the completion of germination with the onset of winter rains in June and more suitable soil moisture conditions. In other treatments, germination may have ceased over the dry May period and not recommenced until June. By this time soil temperatures would have fallen resulting in lower rates of seedling emergence. All seedlings had died within 4 months of emergence despite average or above average rainfall in most months. Studies of other mediterranean climate *Eucalyptus* spp. and *Banksia* spp. which recruit seedlings following fires have also shown that, like *E. salmonophloia,* germination will occur in unburnt woodlands but seedlings fail to establish (Parsons 1968; Wellington and Noble 1985a,b; Cowling and Lamont 1987). Quite clearly then, changes in the soil surface environment following large scale disturbances such as fire, severe storms, floods and drought are not sufficient for establishment of *E. salmonophloia* seedlings.

This chapter has shown that germination in *E. salmonophloia* has a temperature optimum above and below which germination is retarded. Evidently seeds can remain moist at sub optimal temperatures for prolonged periods without losing viability. Furthermore *E. salmonophloia* seeds are capable of withstanding intermittent short cycles of wetting and drying. These characteristics minimise the chances of germination at times when the probability of seedling establishment is low (e.g. summer). This is particularly important because *E. salmonophloia* only establishes soil seed reserves following large scale disturbances and therefore the opportunities for recruitment may be quite rare. Evidently

E. salmonophloia has no specialised seed bed requirements and germination will occur on a variety of substrates when suitable soil temperature and moisture conditions prevail. This is most likely to occur at the beginning of the winter wet season when soil temperatures are still suitable and soil moisture and atmospheric humidity are frequently high with the passage of rain bearing depressions and cold fronts across south western Australia.

Previous chapters have shown, firstly, that *E. salmonophloia* forms a canopy seed reserve (Chapter 2); secondly, that there is a gradual attrition of seeds from successive crops in this store and that most of the seeds falling to the ground are eaten by ants (Chapter 3); and thirdly, that post dispersal seed predation together with short term seed viability leads to the absence of a persistent soil seed reserve (Chapter 3). These life history attributes are characteristics of eucalypts which recruit seedlings following fire and this has been shown to be the case in *E. salmonophloia* which also recruits seedlings following other large scale disturbances like flood, severe storms and drought (Chapter 4). Other studies have shown that fire induces a massive and synchronous release of canopy stored seed which causes a temporary satiation of seed eating ants, resulting in lower rates of seed predation and the establishment of a soil seed bank. Flooding, wind throw and drought also cause the death of tree canopies and it was suggested in Chapter 4 that these disturbances also result in massive seed fall, temporary predator satiation and establishment of a soil seed reserve.

Clearly disturbance plays a critical role in the establishment of a soil seed reserve. In this study when ants were excluded and an artificial soil seed reserve established on a variety of different seedbed types germination of *E. salmonophloia* occurred. However, no seedlings survived, indicating that the establishment of a soil seed reserve alone and suitable conditions for germination in the undisturbed woodland were not enough for recruitment. Evidently the establishment of seedlings may be contingent upon other changes which occur in woodlands following disturbances. The nature of these changes and how they effect seedling establishment will be discussed in Chapters 6 and 7.

CHAPTER 6

CHANGES IN RESOURCE AVAILABILITY FOLLOWING LANDSCAPE SCALE DISTURBANCES AND THEIR POTENTIAL IMPACT ON THE ESTABLISHMENT OF *E. SALMONOPHLOIA* SEEDLINGS

6.1 **INTRODUCTION**

Chapter 4 documented past and recent events which initiated regeneration of *E. salmonophloia* and found that seedling recruitment occurred following large scale disturbances such as fire, flood, severe storms and drought. The effect of these disturbances on germination was considered in Chapter 5. Laboratory and field studies showed, firstly, that if seeds escaped predation and were incorporated into a soil seed reserve they germinated on a variety of seed beds with the onset of suitable temperature and moisture conditions in early winter; and secondly, that seedlings which emerge in undisturbed woodland are unlikely to survive their first summer. Moreover when the soil surface conditions which follow large scale disturbances such as fire were created in an undisturbed woodland, seedlings still died in their first summer following emergence. These results suggest that soil surface conditions alone have no effect on establishment and that competitive interactions with understorey and canopy species for limiting resources such as water and nutrients may be important in this respect.

The climate throughout *E. salmonophoia's* distribution is classified as Dry Mediterranean or Semi-Arid Mediterranean. Rain falls mainly in the winter months, and summers are generally hot and dry; summer rainfall does occur but is unpredictable. In addition, class A pan evaporation exceeds rainfall in every month (McFarlane *et al.* 1992) and droughts are common (Chapter 1). In the central part of *E. salmonophloia's* distribution Farrington *et al.*

(1994) have estimated that annual transpiration in woodlands is approximately 50% of average annual rainfall. Transpiration rates and demand for water were highest in late spring and summer when rainfall was lowest (Farrington *et al.* 1994). Several years of below average rainfall together with the dry summers typical of the region can initiate considerable stress in the vegetation and may result in widespread mortality (Chapter 4; Hnatiuk and Hopkins 1980). It is therefore likely that competition for soil water in *E. salmonophloia* woodlands is high and may limit seedling establishment. Lamont (1985) has demonstrated in woodlands dominated by *E. wandoo*, a species which has an overlapping distribution with *E. salmonophloia*, that this is indeed the case. He observed that there was considerable reduction in the abundance of shrubs around most trees. The existence of this suppression zone was best explained by competition for water between the extensive lateral root system of *E. wandoo* trees and the roots of adult shrubs (Lamont 1985). At the end of summer, shrubs within and on the edge of the suppression zone had lower xylem pressure potentials and were more stressed than shrubs outside of the zone (Lamont 1985). Evidently as trees age, their extensive lateral root systems develop and come into contact with the roots of established shrubs which cannot compete effectively and eventually die (Lamont 1985). In addition, surface soil water availability in this zone during spring was less than in surrounding scrub and there was an associated reduction in germination and establishment of perennial species (Lamont 1985). Not only did competition for soil water limit perennial shrub species but conditions were also unsuitable for the recruitment of *E. wandoo* seedlings. Quite clearly then, competition for soil water is an important factor underlying vegetation dynamics in Dry Mediterranean climates and unsuitable soil water conditions in established vegetation may limit the recruitment of *E. salmonophloia* seedlings.

Many Australian soils have low concentrations of the essential plant nutrients, nitrogen and phosphorus, and natural inputs are low (Bowen 1981; Walker *et al.* 1986). *Eucalyptus* spp. found in forests and woodlands have evolved mechanisms which allow them to grow and survive on these soils. These include, firstly, efficient extraction of nutrients at low concentrations within the soil; secondly, an ability to compete effectively with other biota in the exploitation of poorly accessible or transiently available nutrients from the litter and the soil; thirdly, low absolute requirements for nutrients within the plant; and lastly, an ability to conserve and redeploy nutrients within the living plant, thereby minimising the loss of nutrients from seasonal death of plant parts and environmental stress (Pate and Dell 1984; Attiwill and Leeper1987). Nutrient cycling is therefore a conservative process within mature eucalypt forests and woodlands with a large proportion of the nutrients available for plant growth being conserved and cycled within the established vegetation. Competition for scarce nutrients is therefore likely to be intense and this could possibly affect the establishment of seedlings. *E. salmonophloia* has very small seeds (1 mm x 1 mm) and stored food reserves are therefore very low. Seedling establishment and growth are likely to rely on uptake of soil nutrients at a very early age. Limited soil nutrient availability and competition from established vegetation may therefore limit the establishment of *E. salmonophloia* seedlings in undisturbed woodlands.

Wellington and Noble (1985b) demonstrated that limitations in the availability of soil water and nutrients were critical factors limiting the establishment of *E. incrassata* seedlings in mallee vegetation. They reported that watering and fertilising seedlings in the first summer following emergence significantly reduced seedling mortality.

Large scale disturbances such as fires, severe storms, floods and droughts can destroy large areas of *E. salmonophloia* woodland and result in considerable tree death. The removal of the established vegetation may lead to increases in soil water and nutrients and thereby create a nursery environment suitable for the establishment of *E. salmonophloia* seedlings, firstly through a temporary reduction in competition for soil water and nutrients and secondly through a redistribution of these resources.

The objective of this chapter is to determine if soil water and nutrient availability increase in *E. salmonophloia* woodlands following severe storms and flooding. Changes in these resources following fire were not investigated as this is well documented for other eucalypt communities and will be discussed from the literature. Changes in resource availability following drought in *E. salmonophloia* woodlands were not investigated as no sites were available where a recent drought had initiated recruitment.

6.2 METHODS AND MATERIALS

6.2.1 STUDY SITES

The study was undertaken at two sites where a severe wind storm (Gindalbie Station) and flooding (Canegrass Lagoon) recently initiated seedling regeneration of *E. salmonophloia* (see Chapter 4). Seedling emergence and survivorship were measured in transects consisting of ten, 1 m^2 contiguous quadrats (see Chapter 4). At Gindalbie Station, one transect was established beneath each of four wind thrown tree canopies. At Canegrass Lagoon, four transects were established where floodwaters had receded. At each site, equivalent numbers of control transects were established in adjacent undisturbed woodland to monitor seedling regeneration in the absence of disturbance. Adjacent to each transect, soil samples were collected for nutrient analysis and within each transect, soil samples were collected for soil water analysis.

6.2.2 SOIL WATER

Sampling for soil water analysis was undertaken 2 weeks after the last widespread rainfall event in the region (Western Australian Bureau of Meteorology Kalgoorlie records). Five samples from the upper 5 cm of soil were collected in alternate quadrats of each transect for water content determination. Each soil sample was placed in a pre-weighed soil tin, weighed and the tin sealed for transport back to the laboratory. The soil tins and their contents were placed in an oven at 70°C and weighed regularly until there was no further decline in soil weight. Percentage soil water was calculated as follows:

$$\frac{\text{wet wt. of soil} - \text{dry wt. of soil}}{\text{dry wt. of soil}} \times 100$$

Soil water data were pooled for transects beneath wind thrown canopies and for transects in undisturbed woodland; likewise in flooded and adjacent unflooded woodland. Pooled data were analysed with an unpaired two tailed t - test to determine if differences in water contents existed between the disturbed and undisturbed sites.

6.2.3 SOIL NUTRIENT ANALYSIS

Soil samples for nutrient analysis were collected at Gindalbie Station in May 1993 approximately 1 year after the storm. The time between recession of floodwaters and collection of soil samples at Canegrass Lagoon is unknown. Department of Conservation and Land Management records in Kalgoorlie indicate that the area where transects were placed was beneath water in November 1992. Soil samples were collected in May 1993 and therefore the time between sampling and recession of floodwaters was a maximum of 6 months.

At four locations adjacent to each of the four transects beneath wind thrown canopies and in adjacent undisturbed woodland, soil in 25 cm x 25 cm square quadrats was sampled to a depth of 1.5 cm, bulked and mixed thoroughly. Two sub-samples were taken from each of the eight bulked samples and air dried for nutrient analysis.

The above sampling procedure was repeated at Canegrass Lagoon adjacent to flooded and unflooded transects, however only one sub-sample was taken from each of the eight bulked soil samples for nutrient analysis.

Soils were analysed by CSBP and Farmers Ltd. Perth. Available phosphorus and potassium were measured using the Colwell method; soils were tumbled with a 0.5 M sodium bicarbonate solution adjusted to pH 8.5 for 16 hours at 25°C using a soil/solution ratio of 1:100. The acidified extract was treated with ammonium molybdate-antimony trichloride reagent and the concentration of phosphate measured colorimetrically at 880 nm. The concentration of potassium was determined using a flame atomic absorption spectrophotometer, at 766.5 nm. The ammonium and nitrate nitrogen were measured simultaneously using a Lachet flow injection analyser. Soils were tumbled with 1 M potassium chloride for one hour at 25°C using a soil/solution ratio of 1:5. The concentration of ammonium nitrogen was measured colorimetrically at 420 nm using the indo-phenol blue reaction. The nitrate was reduced to nitrite through a copperized-cadmium column and the concentration of nitrite measured colorimetrically at 520 nm. Iron was extracted with 1 M ammonium chloride at pH 7 and assayed by atomic absorption spectroscopy. Organic carbon was determined by chromic acid digestion and measured colorimetrically at 600 nm. Soil pH was determined on an extract from a 1:5 soil/deionised water suspension which had been stirred for 1 hour at 25°C.

Soil nutrient concentration data were pooled for transects beneath wind thrown canopies and for transects in undisturbed woodland; likewise in flooded and adjacent unflooded woodland. Pooled data were analysed with an unpaired two tailed t-test to determine if differences in nutrient concentrations existed between the disturbed and undisturbed sites.

6.2.4 FOLIAR NUTRIENT ANALYSIS

Leaves were collected for nutrient analysis from wind thrown canopies and living canopies in adjacent undisturbed woodland 12 months after the storm at Gindalbie Station. Leaves were collected at ten locations around the four wind thrown trees where seedling establishment was being monitored and then bulked and mixed thoroughly. Similarly green leaves were collected at ten locations around four standing trees adjacent to control transects. Sixteen sub samples from each of the bulked samples were taken for nutrient analysis. Foliar nutrients were analysed by CSBP and Farmers Ltd. Perth. Leaf material was finely ground for all analyses. Nitrogen concentrations were measured using a Leco FP-428 Nitrogen Analyser. Ground plant material is combusted at 950°C in oxygen and the released nitrogen from the sample measured as it passes through a thermal conductivity cell. Phosphorus was measured colorimetrically with vanado-molybdate reagent. Potassium was measured by atomic absorption spectroscopy. Ground leaf material for phosphorus and potassium analysis was digested in 9:1 nitric and perchloric acid.

Nutrient concentrations from leaves in wind thrown canopies and from green leaves in living canopies were analysed with an unpaired two tailed t-test to determine if differences in nutrient concentrations existed between the disturbed and undisturbed sites.

6.3 **RESULTS**

6.3.1 SOIL WATER

Two weeks after the last rainfall event, percentage soil water beneath wind thrown canopies was significantly greater (t =5.05, d.f.=38, p <0.001) and approximately double that in adjacent undisturbed woodland (Table 6.1).

Similarly at Canegrass Lagoon, percentage soil water in transects which had been flooded was significantly greater (t =8.02, d.f.=38, p <0.001) and approximately ten times that in transects which had not been flooded (Table 6.2). The high soil water content in transects after floodwaters had receded, indicates that the perched water table in the area was still having a significant influence on surface soil water.

6.3.2 SOIL NUTRIENT CONCENTRATIONS

Twelve months after the severe storm at Gindalbie Station, soil concentrations of available phosphorus beneath wind thrown canopies were significantly greater (t =5.84, d.f.=14, p <0.0001) and approximately three times higher than in adjacent undisturbed woodland (Table 6.1). Similarly soil concentrations of potassium beneath wind thrown canopies were significantly higher (t =2.87, d.f.=14, p <0.01) than in adjacent undisturbed woodland (Table 6.1). By contrast, % organic carbon in undisturbed woodland was significantly greater (t =-3.54, d.f.=14, p <0.05) than beneath wind thrown canopies (Table 6.1). No significant differences in nitrate - nitrogen, ammonium - nitrogen, iron and pH were found for soil beneath wind thrown canopies and in undisturbed woodland (Table 6.1).

Table 6.1: Arithmetic mean values of soil nutrient concentrations (n=16) and percentage soil water (n=20) ± SE beneath wind thrown canopies in woodland damaged by a severe windstorm and in adjacent undisturbed woodland. Means followed by the same letter are not significantly different ($p < 0.05$). Data were analysed with unpaired two tailed t-tests. Soil samples were collected 12 months after the storm and their collection followed 2 weeks after the last rainfall event.

Soil attribute	Beneath wind thrown canopy	Undisturbed woodland
NO_3 (ppm)	3.38 ± 1.05 a	1.25 ± 0.16 a
NH_4 (ppm)	8.00 ± 0.78 a	7.00 ± 0.50 a
P (ppm)	12.38 ± 1.24 a	3.88 ± 0.77 b
K (ppm)	751 ± 50 a	560 ± 43. b
Fe (ppm)	517 ± 55 a	506 ± 44 a
Organic C (%)	1.29 ± 0.18 a	2.13 ± 0.15 b
pH	8.08 ± 0.28 a	7.95 ± 0.10 a
H_2O (%)	10.06 ± 0.70 a	5.16 ± 0.67 b

Table 6.2: Arithmetic mean values of soil nutrient concentrations (n=8) and percentage soil water (n=20) ± SE in flood damaged woodland and adjacent undisturbed woodland. Means followed by the same letter are not significantly different ($p < 0.05$). Data were analysed with unpaired two tailed t-tests. Soil samples were collected after flood waters had receded and their collection followed 2 weeks after the last widespread rainfall event.

Soil attribute	Flooded woodland	Undisturbed woodland
NO_3 (ppm)	13.5 ± 3.07 a	1.5 ± 0.29 b
NH_4 (ppm)	8.25 ± 0.48 a	5.75 ± 0.48 b
P (ppm)	14.25 ± 1.65 a	4.5 ± 0.29 b
K (ppm)	556 ± 47 a	263 ± 11 b
Fe (ppm)	1879 ± 144 a	268 ± 12 b
Organic C (%)	1.48 ± 0.27 a	0.50 ± 0.02 b
pH	8.38 ± 0.11 a	8.00 ± 0.01 b
H_2O (%)	26.13 ± 2.95 a	2.42 ± 0.08 b

Concentrations of all nutrients were significantly higher in soils which had been flooded than in adjacent unflooded woodland (Table 6.2). However the magnitude of the difference varied between nutrients; available phosphorus in soils which had been flooded was about three times higher than in unflooded woodland (t=5.81, d.f.=6, $p<0.001$); nitrate - nitrogen was approximately 13 times higher (t=3.89, d.f.=6, $p<0.01$); ammonium - nitrogen approximately 1.5 times higher (t=3.69, d.f.=6, $p<0.01$); potassium approximately double (t=6.02, d.f.=6, $p<0.001$); iron approximately 7 times higher (t=11.13, d.f.=6, $p<0.001$); and percentage organic carbon approximately 3 times higher (t=3.66, d.f.=6, $p<0.01$). Similarly there was an increase in soil pH (t=3.03, d.f.=6, $p<0.05$) (Table 6.2).

6.3.3 FOLIAR NUTRIENT CONCENTRATIONS

Twelve months after the severe storm at Gindalbie Station, the concentration of phosphorus in green leaves from living canopies was significantly greater (t=6.16, d.f.=30, $p<0.0001$) than leaves from wind thrown canopies (Table 6.3). Similarly concentrations of potassium in green leaves from living canopies were significantly higher (t=9.73, d.f.=30, $p<0.0001$) than those from wind thrown canopies (Table 6.3). By contrast, total nitrogen in leaves from wind thrown canopies was significantly greater (t=-6.65, d.f.=30, $p<0.001$) than in green leaves from living canopies (Table 6.3). No significant differences in nitrate - nitrogen were found (Table 6.3).

6.4 **DISCUSSION**

There is a paucity of data on changes in soil water availability following the destruction of established vegetation by fire. However, there is a general consensus that surface soil is wetter than in unburnt areas. This conclusion has been arrived at indirectly through studies of plant population dynamics in burnt and unburnt vegetation (Parsons 1968; Wellington 1984; Wellington and Noble 1985a,b; Cowling and Lamont 1987; Lamont *et al.* 1991a),

Table 6.3: Arithmetic mean values of foliar nutrient concentrations (n=16) in green leaves from living canopies and dead leaves from wind thrown canopies ± SE. Means followed by the same letter are not significantly different (*p* <0.05). Data were analysed with unpaired two tailed t-tests. Leaves were collected for nutrient analysis 12 months after the severe storm at Gindalbie Station.

Nutrient	Green leaves from living canopy	Dead leaves from windthrown canopy
N (% dry matter)	1.15 ± 0.02 a	1.45 ± 0.04 b
NO_3 (ppm)	45.8 ± 2.2 a	43.4 ± 0.7 a
P (% dry matter)	0.088 ± 0.004 a	0.061 ± 0.002 b
K (% dry matter)	0.752 ± 0.063 a	0.124 ± 0.003 b

experimental removal of vegetation (Robberecht *et al.* 1983; Stoneman *et al.* 1994) and increases in stream flow following destruction of forests by logging and fire (Kuczera 1985 cited in Attiwill and Leeper 1987).

In mediterranean climates, studies of mallee *Eucalyptus* spp.and of*Banksia* spp. which recruit seedlings following fire have shown that, like *E. salmonophloia* (see Chapter 5), germination occurred in unburnt vegetation but seedlings failed to establish (Parsons 1968; Wellington and Noble 1985a,b; Cowling and Lamont 1987). These studies reported that seedling mortality was highest in the first spring/summer following germination and this coincided with the onset of dry soil conditions caused by high temperatures and low rainfall. Wellington and Noble (1985b) showed that watering *E. incrassata* seedlings over the first summer following emergence reduced mortality and Lamont *et al.* (1991a) made similar observations in *Banksia cuneata*..

Zimmer (1940) suggested that the inability of mallee *Eucalyptus* spp. seedlings to establish in unburnt vegetation could be attributed to a deficiency of water in the surface soil caused by actively transpiring established vegetation. Furthermore, Zimmer (1940) suggested that following a fire, soil water conditions were temporarily more suitable for seedling establishment because of arrested evapotranspiration through the removal of established vegetation.

The observations of Robberecht *et al.* (1983), Stoneman *et al.* (1994), Wellington (1984) and Kuczera (1985 cited in Attiwill and Leeper 1987) confirm this hypothesis. Robberecht *et al.* (1983) demonstrated that the removal of vegetation from experimental plots caused an increase in soil water potential. Similarly Stoneman *et al.* (1994) observed that the removal of the overstorey in *Eucalyptus marginata* forest resulted in lower soil water deficits and as a consequence *E. marginata* seedlings had higher leaf water potentials and were less stressed than seedlings growing on sites with the overstorey retained. Wellington (1984) observed that the water status of *E. incrassata* seedlings and resprouting adults in recently burnt areas was more favourable than for plants in long unburnt vegetation. Measurements in *E. regnans* forests show that for the first 5 years after large scale bushfires in 1939, stream flow increased relative to that calculated from records for that forest prior to destruction (Kuczera 1985 cited in Attiwill and Leeper 1987). All these observations indicate that following removal of the established vegetation by fire, or any other large scale disturbance, there is a temporary increase in soil water.

It was found in this study that 2 weeks after the last rainfall event, percentage soil water beneath wind thrown canopies was significantly greater and approximately double that in adjacent undisturbed woodland. Reduced evapotranspiration rates are unlikely to be the only factor responsible for this difference. The soil beneath the wind thrown canopy is probably far less exposed to drying winds and solar radiation than much of the soil surface in the undisturbed woodland. As a consequence rates of evaporation from the soil surface beneath the wind thrown canopy are likely to be less than in adjacent undisturbed woodland.

Similarly at Canegrass Lagoon where there was widespread tree death after flooding, percentage soil water in transects which had been flooded was significantly greater and approximately ten times that in transects which had not been flooded. The high soil water content in transects after floodwaters had receded indicates that higher water tables following flooding in the area were still having a significant influence on surface soil water.

Another process which may affect the availability of soil water to newly establishing vegetation is a change in the distribution of rainfall brought about through the removal of established vegetation by large scale disturbances. Nulsen *et al.* (1986) observed that rainfall was intercepted by and redistributed in the canopy of mallee vegetation; stem flow was directed to the base of the trees, where it entered the soil along the soil root interface. Established vegetation therefore redistributes rainfall both within the canopy and on the soil surface so that water infiltrates deeply into the soil profile at selected points, especially around tree roots. The harvesting of limited rainfall therefore favours the established vegetation and may preclude the establishment of seedlings . Removal of the canopy by large scale disturbance would result in a more even distribution of rainfall at the soil surface.

The changes in soil water availability in *E. salmonophloia* woodlands following fire, severe storms and floods are therefore likely to be attributable to four processes; firstly reduced competition for soil water through the removal of established vegetation; secondly, following severe storms the establishment of a microclimate beneath windthrown trees which reduces evaporation from the soil surface; thirdly, following flooding higher water tables influencing surface water;and fourthly, through more even distribution of rainfall at the soil surface.

In addition to changes in soil water availability, changes in soil nutrient availability following fire in a range of ecosystems are well documented. Fire has been reported to increase the availability of nutrients for plant growth in the surface 1 to 2 cm of soil through changes brought about by soil heating and the input of nutrient rich ash (Humphreys and Craig 1981; Walker *et al.* 1986). Soil heating leads to an accumulation of NH_4 - nitrogen firstly through the chemical oxidation of organic matter and secondly, though changes in soil microbial populations and their organic nitrogen substrates (Russell *et al.* 1974; Walker *et al.* 1986; Tomkins *et al.* 1991). The amount of NH_4 - nitrogen released from chemical oxidation of organic matter increases with soil heating for temperatures up to 400^{o}C (Walker *et al.* 1986). Concentrations of inorganic minerals may also increase. Humphreys and Lambert (1965) noted an increase in available phosphorus when a sandy loam was heated to temperatures between 200^{o}C and 600^{o}C.

The quantity and composition of ash produced during a fire depends on the fuel type and degree of combustion. Ash produced from woody components is low in nutrients compared with ash from non-woody components (Walker *et al.* 1986). The concentration of nutrients are higher in fine white ash than in partially combusted material (Walker *et al.* 1986). Concentrations of nutrients in ash ranging from 0.03 to 1.77% N, 0.11 to 3.1% P, 0.24 to 19.1% K, 2.8 to 34.9% Ca, and 0.7 to 15.4% Mg have been observed (Raison 1979).

The magnitude of the change in soil nutrient budgets depends on the amount of soil heating and quantity and type of ash deposited (Walker *et al.* 1986; Tomkins *et al.* 1991).

Soil heating is affected by fire intensity, fire residence time, initial soil temperature and moisture, bulk density, pore size, soil heat capacity and thermal conductivity (Walker *et al.* 1986). Fuel type and degree of combustion determine the composition and amount of ash produced (Walker *et al.* 1986). Spatial heterogeneity in fuel types, fuel configurations, fuel moisture, wind speeds, and soil conditions therefore produces variation in the amount of soil heating and ash deposited (Hobbs and Atkins 1988; Atkins and Hobbs in press; Rice 1993). Changes in soil nutrient budgets following fires in *E. salmonophloia* woodlands are also likely to be spatially variable. These same processes would all be operative in *E. salmonophloia* woodlands leading to changes in soil nutrient availability. The other disturbance types which initiate recruitment of *E. salmonophloia* (Chapter 4) obviously do not result in soil heating or deposition of ash but the results of this study show that they also result in changes to nutrient availability. This may be related to the nature of nutrient cycling within the genus.

Conservative internal or biochemical cycling of nutrients is a feature of *Eucalyptus* spp. in forest vegetation (Ashton 1975b; Attiwill *et al.* 1978; O'Connell *et al.* 1978; O'Connell and Menage 1982) and mallee heath vegetation (Pate and Dell 1984). These studies have shown that up to 80% of phosphorus, 65% of nitrogen and 50% of potassium is withdrawn from leaves prior to senescence (Table 6.4). No data on biochemical cycling in *E. salmonophloia* exist but the widespread occurrence of the process in the genus across both soil and climatic gradients would suggest that a high proportion of nutrients are withdrawn from leaves prior to senescence. The degree to which nutrient re-translocation takes place has been reported to vary with climate and soil fertility; Ashton (1975b) and O'Connell *et al.* (1978) have suggested that biochemical cycling is less important in wet sclerophyll forests than dry sclerophyll forests since the latter grow on poorer and drier sites. *E. salmonophloia* grows throughout the semi-arid region of south-western Australia and it could therefore be expected that a relatively high degree of nutrient re-translocation occurs. O'Connell *et al.* (1978) found that in *E. marginata*, which grows in the higher rainfall zone to the west of *E. salmonophloia*, approximately 65% of nitrogen, 80% of phosphorus and 55% of potassium are withdrawn from leaves prior to senescence; similar levels of nutrient

Table 6.4: Nutrient concentrations in green and freshly senescent leaves from a variety of *Eucalyptus* spp. found in different habitats.

Species	Community	N (% dry matter)		P (% dry matter)		K (% dry matter)	
		Green leaves	Senescent leaves	Green leaves	Senescent leaves	Green leaves	Senescent leaves
E. regnans †	Wet sclerophyll	0.99	0.33	0.078	0.035	0.57	0.29
E. diversicolor ¥	Wet sclerophyll	1.00	0.49	0.052	0.018	0.78	0.26
E. obliqua ß	Wet sclerophyll	not measured	not measured	0.079	0.021	0.451	0.140
E. calophylla ∂	Dry sclerophyll	0.91	0.30	0.052	0.009	1.08	0.66
E. marginata ∂	Dry sclerophyll	0.84	0.30	0.041	0.009	0.57	0.26
		N (ug leaf $^{-1}$)		P (ug leaf $^{-1}$)		K (ug leaf $^{-1}$)	
E. todtiana ƒ	Mallee	1345	688	120	20	not measured	not measured

† Ashton, D. H. (1975b).

¥ O'Connell, A. M. and Menage, P. M. A. (1982)

ß Attiwill, P. M., Guthrie, H. B. and Leuning, R. (1978)

∂ O'Connell, A. M., Grove, T. S. and Dimmock, G. M. (1978)

ƒ Pate, J. S. and Dell, B. (1984)

retranslocation prior to leaf senescence might be expected in *E. salmonophloia*.

Disturbances which kill tree canopies may disrupt biochemical cycling and prevent the withdrawal of nutrients prior to leaf senescence. O'Connell *et al.* (1979) suggested that crown scorch by fire prevents the withdrawal of nutrients prior to senescence and that this changes the chemical composition of the post fire litter. They observed that in the first year following an intense fire leaf litter falling from scorched *E. marginata* crowns had concentrations of nitrogen and phosphorus approximately double that of leaf litter falling from crowns in unburnt forest. This, together with an increased weight of leaf litter falling from the scorched canopy, resulted in a four fold increase in the accession of nitrogen and phosphorus to the forest floor one year after the fire (O'Connell *et al.* 1979). They concluded that the relatively higher concentration of nitrogen and phosphorus in post fire litter could increase the subsequent rate of litter decomposition and therefore the cycling of nutrients.

Other disturbances, such as severe storms, may also disrupt biochemical cycling, and leaf litter following these disturbances may also have higher concentrations of nutrients. If this were the case significantly higher levels of soil nutrients might be expected to occur beneath wind thrown canopies, and this was indeed found to be the case in this study. The severe storm which passed through salmon gum woodland at Gindalbie Station uprooted and killed large adult trees up to 20 m high with trunk diameters up to 70 cm. The soil surface area covered by the wind thrown canopies was up to 100 m^2 and within this area litter fall from the dying canopy was substantially greater for at least the first 12 months after the storm than in adjacent undisturbed woodland. One year after the storm, bi-carbonate extractable phosphorus and potassium were significantly greater in soil beneath wind thrown trees than in adjacent undisturbed woodland. By contrast soil concentrations of the other major plant nutrient, nitrogen, were not different. The changes observed are attributable to accession of nutrients from the litter which developed beneath the fallen tree. Comparison of nutrient concentrations in green leaves from standing canopies with those from wind thrown canopies reflect the changes observed in the soil, as concentrations of phosphorus and potassium were significantly lower in the disturbed canopies. The lower foliar concentrations of phosphorus and potassium **in wind thrown canopies** and higher soil concentrations of these nutrients beneath wind thrown canopies indicate that fractions of these nutrients in the green leaf are soluble and readily leached following death of the tree canopy. Little difference was observed in foliar nitrogen concentrations between living and wind thrown canopies, and as might be expected, no difference in soil concentrations of these nutrients were found suggesting that nitrogen is not readily leached from leaves in wind thrown canopies.

Changes in soil nutrient concentrations were also observed in flood disturbed woodlands. The concentrations of all nutrients were significantly greater in soils which had been flooded compared to unflooded woodland. A number of processes may be responsible for this; firstly, like fire and severe storms, litter falling from tree canopies which had been killed by the flood may have higher concentrations of nutrients; secondly inputs of sediment rich in organic matter and minerals transported by floodwaters may have enriched soil nutrients; and thirdly, changes in the soil chemistry as a result of waterlogging may also be responsible. The soils on which *E. salmonophloia* woodlands occur typically have a high concentration of iron and aluminium oxides; phosphorus is strongly adsorbed by these minerals and through this process it may become unavailable for uptake by plant roots. The significantly higher concentrations of soluble iron and bicarbonate extractable phosphorus in soils which had been flooded suggests that some of the phosphorus adsorbed to iron / aluminium complexes may have been released by soil flooding (Sanchez 1976).

This chapter has demonstrated that in *E. salmonophloia* woodlands the availability of soil water and nutrients increases following fires, severe storms and floods. The effect and importance of these changes on the early growth and establishment of *E. salmonophloia* seedlings will be examined in the next chapter.

CHAPTER 7

THE EFFECTS OF WATER AND NUTRIENT AVAILABILITY ON THE EARLY GROWTH OF *E. SALMONOPHLOIA* SEEDLINGS

7.1 INTRODUCTION

Chapter 6 described increases in soil water and nutrient availability following large scale natural disturbances in *E. salmonophloia* woodlands and discussed the implications of this for seedling establishment. This chapter documents greenhouse experiments which examined the effects of different soil water and nutrient regimes on the early growth of *E. salmonophloia* seedlings.

7.2 METHODS AND MATERIALS

Soil for the study was collected from remnant *E. salmonophloia* woodland at Minniberri Reserve. This site was chosen for the study because it contains remnant woodland on the red duplex soil type on which *E. salmonophloia* most commonly occurs (Beard 1990). These soils consist of a brown loamy surface soil and a red clay subsoil (McArthur 1991). Two 20 m transects spaced 20 m apart were laid out in the woodland and at 2 m intervals along each transect the uppermost 5 cm of soil was collected from four 25 cm x 25 cm quadrats from which litter had been cleared. Soil samples were air dried and passed through a 2 mm sieve to remove root material and then bulked and mixed thoroughly. Sixty four plastic pots lined with polythene bags were each filled with 1500 g of the sieved and mixed dry soil and placed in a greenhouse at Murdoch University. Fifteen *E. salmonophloia* seeds were sown in each pot at a depth no greater than 2 mm. The undrained pots were watered to field capacity daily for 3 weeks by which time seedling germination had ceased. Seedling emergence was variable amongst pots and as a consequence the number of seedlings per pot after thinning ranged from one to five. Each pot was then randomly assigned to one of eight factorial combinations of watering and nutrient treatments such that there were eight replicates of each treatment combination. There were four watering treatments and two nutrient treatments and these were applied to soils in the following manner:

WATERING TREATMENTS

Soils were watered with deionised water to field capacity by weight every day, every second day, every fourth day and every sixth day.

NUTRIENT TREATMENTS

Fertilised pots - soils were fertilised using a combination of slow release and soluble complete fertilisers applied to the soil surface at intervals throughout the experiment; 2.5 g of slow release fertiliser 'Osmocote' (N=17%, P=4.4%, K=10%, S=4.1%, Ca=0.2%) was added to each pot at the beginning of the experiment and 30 mL of soluble fertiliser 'Thrive' (N=27%, P=5.5%, K=9%, Mg=0.15%, S=0.22%, Cu=0.005%, Zn=0.02%, B=0.005%, Mn=0.04%, Fe=0.18%, Mo=0.002%) (3 g L^{-1}) added on four occasions at 12 day intervals thereafter.

Unfertilised pots - soils were not treated with fertiliser

Pots were randomly located on a bench in the glasshouse at the beginning of the experiment in August 1993 and relocated daily to reduce any effects of bench position.

After 9 weeks of treatment application all pots were watered to field capacity and the shoots of each plant harvested. The number of plants in each pot was recorded and the fresh shoot weight and height of each measured.

Following harvest, two soil cores the depth of the pot and 2 cm in diameter were taken from each pot. Cores from each combination of water and nutrient treatment were bulked separately. Bulked samples were mixed thoroughly and two replicate samples taken from each for analysis of phosphorus, nitrate, ammonium and potassium concentrations. Soil nutrient analyses were conducted by CSBP and Farmers Ltd; analytical methods are described in section 6.2.3.

The effect on fresh shoot weight and shoot length of water and fertiliser treatments and their interaction were determined using two way analysis of co-variance. The number of plants per pot was included in the analyses as a covariate because there were unequal numbers of seedlings in each treatment combination. The data was checked for assumptions of normality and homogeneity of variance and no transformations were required. In cases where main factors had a significant effect, data were pooled and *post-hoc* comparisons were made of treatment means using a Tukey - Kramer test (Zar 1984).

The effect of fertiliser addition on soil nutrient concentrations was determined with an unpaired two tailed t-test using data pooled across watering treatments.

7.3 **RESULTS**

The number of seedlings per pot had no significant effect on shoot fresh weight (F=2.47, d.f.=1, 226, p >0.05) or shoot length (F=0.0005, d.f.=1, 226, p >0.05) and it is therefore valid to treat individual plants as the experimental unit in the analyses.

Increased frequency of watering significantly increased shoot fresh weight (F=2.92, d.f.=3, 226, p <0.05) and shoot length (F=2.96, d.f.=3, 226, p <0.05). Mean shoot fresh weight was 0.64 g for seedlings watered daily, 0.32 g for seedlings watered every second day, 0.11 g for seedlings watered every fourth day and 0.08 g for seedlings watered every sixth day (Table 7.1). Mean shoot length was 9.6 cm for seedlings watered daily, 6.1 cm for seedlings watered every second day, 3.8 cm for seedlings watered every fourth day and 3.4 cm for seedlings watered every sixth day (Table 7.1).

Unlike increased frequency of watering, additional nutrients had no significant effect on

Table 7.1: Arithmetic mean values of shoot fresh weight and shoot length for the four watering treatments; watered to field capacity daily (n=72), every second day (n=57), every fourth day (n=57), every sixth day (n=56). Means followed by the same letter are not significantly different (*p* < 0.05) as determined by a Tukey - Kramer test.

	Soils watered to field capacity			
	Every day	Every second day	Every fourth day	Every sixth day
Shoot fresh weight (g/plant)	0.64 a	0.32 b	0.11 c	0.08 d
Shoot length (cm/plant)	9.6 a	6.1 b	3.8 c	3.4 d

shoot fresh weight (*F* =0.03, d.f.=1, 226, *p* >0.05) or on shoot length (*F* =0.08, d.f.=1, 226, *p* >0.05). Mean shoot fresh weight was 0.33 g for fertilised seedlings and 0.29 g for unfertilised seedlings (Table 7.2). Mean shoot length was 5.9 cm for both fertilised seedlings and unfertilised seedlings (Table 7.2).

Similarly there was no significant interaction between watering and nutrient treatments on shoot fresh weight (*F* =0.47, d.f.=3, 226, *p* >0.05) or shoot length (*F* =0.37, d.f.=3, 226, *p* >0.05) (Figure 7.1).

The addition of fertiliser significantly increased concentrations of soil nutrients (Table 7.3). At the end of the experiment the mean nitrate concentration in fertilised pots was 405 ppm (*t* =10.60, d.f.=14, *p* <0.001) compared to 38 ppm in unfertilised pots; mean ammonium concentration in fertilised pots was 274 ppm (*t* =27.27, d.f.=14, *p* <0.001) compared to 4 ppm in unfertilised pots; the mean phosphorus concentration in fertilised pots was 63 ppm (*t* =11.99, d.f.=14, *p* <0.001) compared to 8 ppm in unfertilised pots; the mean potassium concentration in fertilised pots was 537 ppm (*t* =11.08, d.f.=14, *p* <0.001) compared to 374 ppm in unfertilised pots.

The mean values for soil nutrient concentrations in fertilised and unfertilised pots were calculated from pooled data across watering treatments. No clear trends in ammonium, bicarbonate extractable phosphorus and potassium concentrations were detected across watering treatments (Table 7.4). By contrast, in unfertilised pots, nitrate concentrations at the end of the experiment were approximately three times lower in pots watered daily compared to pots watered every second day and as much 14 times lower than pots watered every fourth day and every sixth day (Table 7.4).

7.4 **DISCUSSION**

Very few data on the factors limiting seedling establishment in *Eucalyptus* spp. from mediterranean climates exist with which to compare the results of this experiment; research

Table 7.2: Arithmetic mean values for shoot fresh weight and shoot length for fertilised (n=98) and unfertilised seedlings (n=144). Means followed by the same letter are not significantly different as determined by analysis of variance ($p < 0.05$).

	Fertilised	Unfertilised
Shoot fresh weight (g/plant)	0.33 a	0.29 a
Shoot length (cm/plant)	5.9 a	5.9 a

Figure 7.1: Arithmetic mean values ± S.E. of (a) shoot fresh weight and (b) shoot length for *E. salmonophloia* seedlings fertilised and watered to field capacity daily (n=35), every second day (n=22), every fourth day (n=21) and every sixth day (n=20) and unfertilised seedlings watered to field capacity daily (n=37), every second day (n=35), every fourth day (n=36) and every sixth day (n=36).

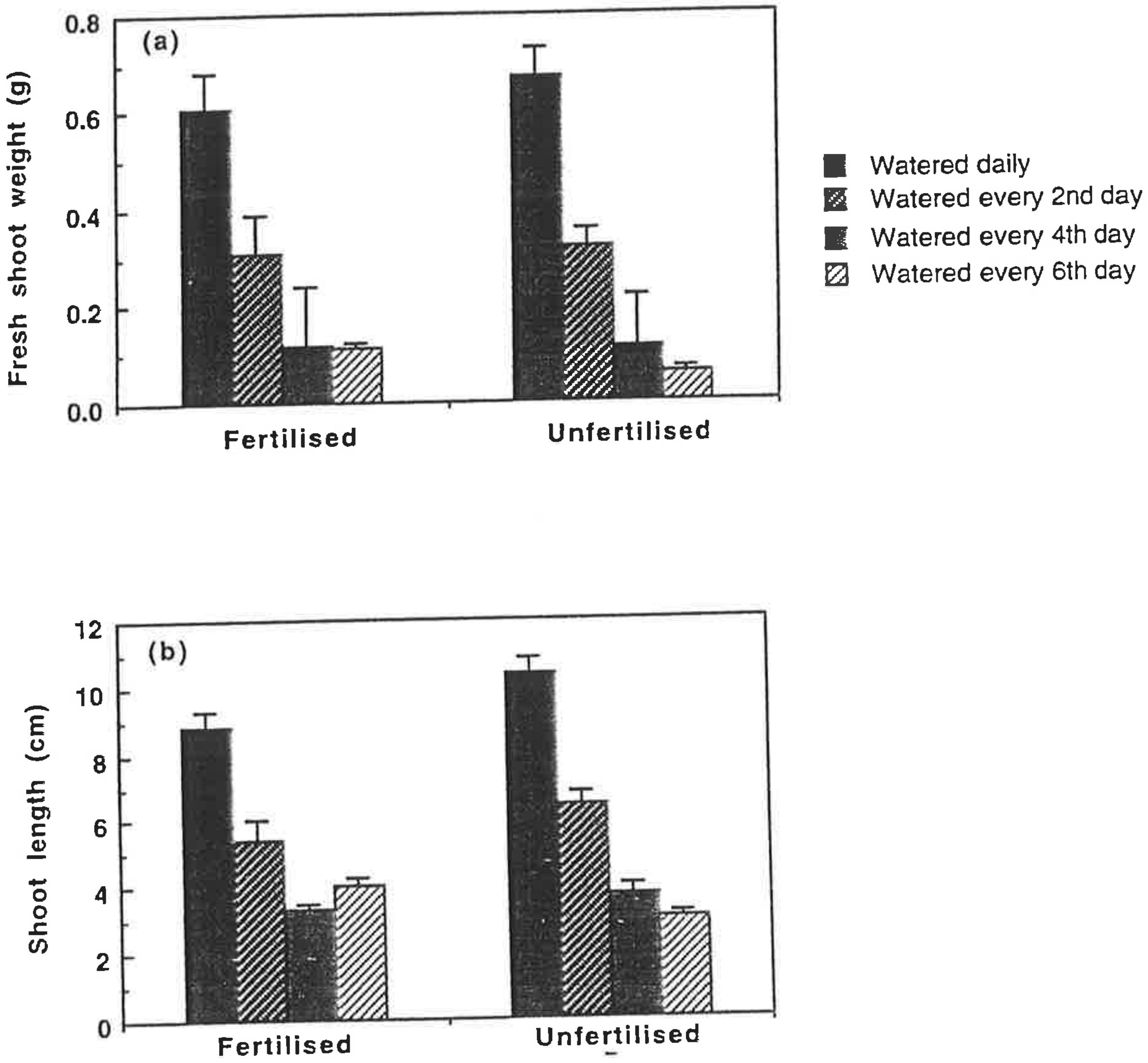


Table 7.3: Arithmetic mean values of soil nutrient concentrations in fertilised and unfertilised treatments at the end of the experiment. Values are means of eight samples (two samples per watering treatment). Means followed by the same letter are not significantly different ($p < 0.001$). Data was analysed with unpaired two tailed t-tests.

Nutrient	Fertilised pots	Unfertilised pots
NO_3^- (ppm)	405 a	38 b
NH_4^+ (ppm)	274 a	4 b
PO_4^{-3} (ppm)	63 a	8 b
K^+ (ppm)	537 a	374 b

Table 7.4: Soil concentrations of (a) nitrate - nitrogen, (b) ammonium - nitrogen (c) bicarbonate extractable phosphporus and (d) potassium for all combinations of nutrient and watering treatments. Values are means of two samples.

(a)	Pots watered to field capacity			
	Every day	Every second day	Every fourth day	Every sixth day
Fertilised	273	395	472	482
Unfertilised	5	15	63	68

(b)	Pots watered to field capacity			
	Every day	Every second day	Every fourth day	Every sixth day
Fertilised	243	268	303	283
Unfertilised	4	4	4	6

(c)	Pots watered to field capacity			
	Every day	Every second day	Every fourth day	Every sixth day
Fertilised	65	59	79	51
Unfertilised	10	7	6	8

(d)	Pots watered to field capacity			
	Every day	Every second day	Every fourth day	Every sixth day
Fertilised	527	543	551	529
Unfertilised	382	363	372	478

on seedling establishment in eucalypts has mainly focussed on forest species with commercial timber value. In most cases these species occur in more temperate climates with higher rainfall distributed evenly throughout the year; moisture availability is therefore less limiting for plant growth. In the context of this experiment these studies are of limited value. The work of Wellington and Noble (1985b) and Stoneman *et al.* (1994) are the only studies which document factors limiting the early growth and establishment of eucalypts in mediterranean climates. Both studies emphasise the central role that water availability plays in seedling establishment. Wellington and Noble (1985b) observed for *E. incrassata*, a mallee species found in dry mediterranean and semi-arid climates, that mortality of seedlings was restricted to summer when prolonged dry periods and high temperatures occurred. Moreover the factors contributing to mortality were affected by topographic position; seedling mortality was greatest at more elevated positions on sand dunes and least in dune swales. They concluded that the observed patterns of seedling mortality were caused by water availability and demonstrated this experimentally; rates of seedling mortality were reduced over the dry summer period by increasing soil water availability with irrigation.

Stoneman *et al.* (1994) documented for *E. marginata*, a mediterranean climate forest species, that seedling mortality in the first two years after emergence was highest in summer when soil water deficits developed and concluded that this was the major cause of seedling mortality.

More comprehensive studies of factors limiting seedling recruitment in mediterranean climates have been undertaken for *Banksia* spp. growing in kwongan scrub heath vegetation. Seedlings of these species emerge during cool wet winter months, mortality during this first winter is very low but increases sharply in late summer and appears to be drought induced (Cowling and Lamont 1987; Enright and Lamont 1989; Lamont *et al.* 1991a; Enright and Lamont 1992a). More specifically, Enright and Lamont (1992b) demonstrated that seedling mortality of *Banksia* spp. seedlings was highest at the time of greatest soil moisture stress (summer to early autumn) when pre-dawn xylem pressure potentials were lowest and seedlings most stressed.

Lamont *et al.* (1991a) studied differences in seedling survivorship between different microsites and topographic positions and observed in *B. cuneata* that seedlings in local depressions, particularly if shaded or amongst litter, were the last to die. In addition, seedling survival and growth were greater in moister lower lying areas than on drier ridge sites. Lamont *et al.* (1991a) concluded that these patterns of seedling growth and survival were best explained by water availability. They tested this hypothesis experimentally and found that the increase in seedling mortality associated with declining rainfall and higher temperatures could be reversed by increasing water availability using irrigation.

The above studies demonstrated, firstly, that greatest seedling mortality occurs in the first summer following germination; secondly, that rates of seedling mortality are reduced in microsites and topographic positions that are inherently moister; and thirdly, that seedling mortality can be reduced by watering over the dry summer. Clearly water availability is a major factor affecting the establishment of *Eucalyptus* spp. and *Banksia* spp. seedlings in mediterranean climates.

Water availability also appears to be an important factor limiting the establishment of *E. salmonophloia* seedlings. In this experiment the early growth of seedlings was severely inhibited by declining water availability. Increases in water availability brought about by large scale disturbances (Chapter 6) which remove established vegetation are therefore likely to favour the establishment of *E. salmonophloia* seedlings. This point is well illustrated by Stoneman *et al.* (1994). They found that mortality of *E. marginata* seedlings was lower on sites where the forest overstorey had been removed compared to sites where it had not been removed. They attributed this to differences in water availability between the two sites; soil water deficits were greater where the forest overstorey had not been removed. As a consequence seedlings beneath the overstorey had greater leaf water deficits and were more stressed than seedlings on sites where the overstorey had been removed (Stoneman *et al.* 1994).

In contrast to water availability, fresh shoot weight and shoot length were not effected by the addition of nutrients despite concentrations being considerably higher in the experimental treatment than those measured following disturbance of *E. salmonophloia* woodlands by flooding and a severe storm (Chapter 6). No data on soil nutrient concentrations in *E. salmonophloia* woodlands following fire exist but concentrations in the experiment were above the range reported by Hester and Hobbs (1992) following fire in *Eucalyptus loxophleba* woodlands which occur in the same region. Similarly concentrations were above or within the range reported for ash beds created by the burning of logging debris in eucalypt forests (Humphreys and Craig 1981).

In this experiment the application of fertiliser at intervals exposed seedlings to a range of increasing nutrient concentrations. At no stage in the experiment did seedlings in fertilised pots appear to suffer from nutrient deficiencies or toxicities. Similarly the seedlings grown on unfertilised soils showed no signs of nutrient deficiency. Evidently the early growth of *E. salmonophloia* seedlings on a brown loam is not limited by the availability of nutrients.

Other researchers have documented growth stimulation of some *Eucalyptus* spp. seedlings in response to increased availability of nutrients (Loneragan and Loneragan 1964; Barrow 1977; Groves and Keraitis 1976). Seedlings were, however, grown for longer periods in these experiments, and it is possible that nutrient availability may become more limiting for the growth of *E. salmonophloia* seedlings as their demands increase. Wellington and Noble (1985b) observed that the addition of fertiliser reduced mortality of *E. incrassata* seedlings. In contrast Stoneman *et al.* (1994) found that the addition of fertiliser had no effect on seedling survivorship. From the limited data it appears that the response of eucalypt seedlings to increased nutrients is variable.

In conclusion the results of this experiment suggest that increased nutrient availability following large scale natural disturbance (Chapter 6) has little effect on the early growth of *E. salmonophloia* seedlings on red duplex soils. However, it should be noted that soil nitrate concentrations in unfertilised pots were higher than anticipated and this may have influenced the outcome of the experiment. The mean concentration of nitrate in unfertilised soils at the end of the experiment was 38 ppm but concentrations varied from 68 ppm in pots which were watered every sixth day to 5 ppm in pots that were watered daily. This relationship was inversely proportional to seedling growth and this trend may be accounted for by the increased growth of seedlings in more frequently watered pots depleting soil nitrate supplies. Soil nitrate concentrations are therefore likely to have been similar across the range of watering treatments at the beginning of the experiment. These concentrations (approximately 68 ppm) are considerably higher than those measured for the same soil *in situ*. Kyeremeh (1994) measured a nitrate concentration of 2 ppm in a brown loam from Minniberri Reserve. The reasons for this large increase in nitrate concentration are unknown but it may be an artefact of soil preparation. Mixing, sieving and drying the soil may have resulted in increased nitrification of organic matter and ammonium. The low concentrations of nitrate in unfertilised pots watered daily (5 ppm) indicate that seedlings were close to having utilised most of the nitrate. Had plants been allowed to grow for longer seedlings in unfertilised, frequently watered treatments may have started to show signs of retarded growth and nitrogen deficiency. Caution therefore needs to be exercised when extrapolating the results of this experiment to the early growth of *E. salmonophloia* seedlings in disturbed and undisturbed woodlands.

Mean phosphorus and potassium concentrations in unfertilised soils were similar to those measured for the same soil *in situ* by Kyeremeh (1994). This, together with the fact that nutrient concentrations did not change across watering treatments, would suggest that levels of phosphorus and potassium in undisturbed woodland are adequate to sustain the early growth of seedlings and therefore elevated levels of these nutrients following large scale natural disturbance (Chapter 6) may be of little significance.

This chapter has shown that water availability is the most important factor limiting the early growth of *E. salmonophloia* seedlings. It can therefore be concluded that the probability of *E. salmonophloia* seedlings establishing in the post disturbance environment will be greater than in undisturbed woodlands due to increased soil water availability. Clearly further research into the nutrient requirements for the early growth and establishment of *E. salmonophloia* seedlings needs to be undertaken. However, it should be noted that glasshouse experiments may not be appropriate because of possible changes in soil chemistry as a result of disturbance during collection.

CHAPTER 8

GENERAL DISCUSSION

Prior to this study little was known about the processes underlying the recruitment of *E. salmonophloia* seedlings. This lack of knowledge posed a problem for conservation of remnant *E. salmonophloia* woodlands in the Western Australian wheatbelt (Chapter 1). This study contributes to solving this problem firstly by describing aspects of *E. salmonophloia's* life history, and secondly by documenting the conditions under which recruitment has occurred in unfragmented populations to the east of the Western Australian wheatbelt. This chapter will describe the findings of the study and discuss reasons for the lack of recruitment in remnant *E. salmonophloia* populations.

Large scale natural disturbances such as fires, floods, severe windstorms or tornadoes and droughts are recurring events in *E. salmonophloia* woodlands (Chapter 4). These disturbances together with seed predators, and soil water availability appear to have been major selective forces in the evolution of *E. salmonophloia's* life history. Using the classification of seed release syndromes described by Lamont *et al.* (1991b), *E. salmonophloia* is best described as serotinous. Serotinous species are characterised by delayed release of mature seeds resulting in the build up of a canopy stored seed reserve. In *E. salmonophloia*, seeds from at least two consecutive flowering seasons are stored in clusters of small woody fruit on the tree (Section 2.3.3). This can result in a large canopy stored seed reserve and estimates of up to 420 000 seeds per tree were measured in this study (Section 2.3.3; Table 2.6). The length of time that a seed is stored on the tree is unknown but is at least two years (Section 2.4). During inter-disturbance periods, seeds are released from the canopy reserve in three ways; firstly, when branches subtending the fruit die and capsules dry out; secondly, when unopened fruit are blown from the canopy and dry out; and thirdly, when cockatoos and parrots feed on seeds and some escape predation and fall to the ground freely or in dissected fruit (Section 2.3.4). Seed fall occurs throughout the year and is slightly lower in the winter months. Generally the seed rain is light (up to 25 seeds per m^2 in a two month period, this is estimated to be less than 1 % of stored seed) but pulses of heavier seed fall can occur when cockatoos and parrots are feeding on fruits and seeds (Section 2.3.4; Figure 2.3). Interestingly, despite a steady seed rain *E. salmonophloia* does not establish a soil seed reserve during inter-disturbance periods (Section 3.3.3). This is attributable to the activity of seed harvesting ants (Section 3.3.2).

The study also documented characteristics of *E. salmonophloia's* germination strategy (Chapter 5). Germination proceeds with favourable soil temperature and moisture conditions on a variety of substrates (Chapter 5). However, at temperatures above and below the optimum for germination (25°C), enforced dormancy (Harper 1957) occurs and germination is retarded (Section 5.3.1). In these situations dormancy is simply overcome when temperatures return to optimum (Section 5.3.1). Soil temperatures suitable for germination occur at the beginning of winter when soil water availability and atmospheric humidity are high with the passage of rain bearing depressions and cold fronts across south-western Australia (Section 5.4). *E. salmonophloia's* strategy ensures that germination occurs when the probability of seedling establishment is greatest. Enforced dormancy at temperatures above the optimum prevents germination from occurring in summer during rare periods when soil water availability is sufficient for germination but the probability of follow up rains and therefore seedling establishment is low. Interestingly and importantly, if seeds escape predation and are incorporated into a soil seed reserve, germination occurs in the first winter (Sections 3.3.3; 5.3.4) but seedling establishment is unlikely (Section 5.3.4).

In summary, during inter-disturbance periods, there is a light seed rain from canopy seed reserves; ants harvest this seed and prevent the establishment of a soil seed reserve; and in the unlikely event of a seed escaping predation germination will proceed with the onset of favourable conditions in early winter, but seedling establishment is highly improbable. Collectively these factors create a biological and physical resistance to seedling recruitment.

In other *Eucalyptus* spp. which display serotiny, seedling recruitment occurs following fire. This is also the case in *E. salmonophloia* but this research has demonstrated that other large scale natural disturbances also facilitate seedling recruitment (Chapter 4). Seedlings were observed in unfragmented woodlands to the east of the wheatbelt in the first winter following recent disturbance by fire, flooding and a severe windstorm, but no seedlings were found in nearby undisturbed woodland (Section 4.3.2). Further evidence of the importance of disturbance for seedling recruitment was provided by observations of uniformly sized cohorts of saplings in unfragmented woodlands which had been disturbed by flooding, fire, drought and a severe windstorm within the last fifty years (Section 4.3.1). Evidently these disturbances initiate processes which overcome the biological and physical resistance to seedling recruitment in *E. salmonophloia* woodlands. These processes have been described in the literature for fire (Sections 3.4; 4.4 and 6.4) and it appears from this research that other large scale disturbances interact with *E. salmonophloia's* life history in a similar manner.

The disturbances initiate seedling recruitment, firstly by providing seed for germination and secondly, by creating an environment more suitable for the establishment of seedlings than exists in an undisturbed woodland. Disturbances have their effect by causing the death of tree canopies which results in the synchronous mass release of canopy stored seed. This satiates predators and thereby allows the establishment of a soil seed reserve. In addition, disturbance results in increases in soil water and nutrient availability (Chapter 6). Common to all of the disturbances is the removal of established vegetation which leads to reduced competition for resources and reduced evapotranspirational demand. Other pathways, specific to each disturbance type, also contribute to increased resource availability, for example soil heating and ash deposition following fire; changes in rates of nutrient cycling and increased soil water availability in the protected environment of a wind thrown canopy; and changes to soil chemistry and soil water availability following flooding (Chapter 6). Not surprisingly, given that *E. salmonophloia* occurs in a Dry Mediterranean climate, it was demonstrated that soil water availability was the most important factor limiting the early growth of seedlings (Section 7.3). Therefore the increase in soil water availability which occurs in the post disturbance environment clearly increases the probability of seedling establishment. During inter-disturbance periods, in the unlikely event of a seed escaping predation, germination will occur but seedling establishment is highly improbable because of intense competition with established vegetation for limited soil water, particularly over dry summer months (Sections 5.3.4 and Chapter 6).

It should be noted that although large scale natural disturbance plays a key role in the recruitment of seedlings, success is also dependent upon the co-occurrence of favourable rainfall in the first summer following germination (Section 4.4). As a consequence not all disturbance events result in recruitment.

The research presented in this thesis has greatly enhanced the understanding of factors contributing to the absence of *E. salmonophloia* seedlings in remnant woodlands. Given the importance of large scale natural disturbance, declining *E. salmonophloia* populations in the wheatbelt may be attributable to either changes in the overall disturbance regime and/or changes in the ability of *E. salmonophloia* to regenerate successfully following disturbance.

Unfortunately, little is known about the disturbance regime in the wheatbelt prior to European settlement. This, together with a lack of data on the current disturbance regime, makes it difficult to determine if changed disturbance regimes are contributing to the lack of *E. salmonophloia* recruitment; one can only speculate. It is possible that fragmentation of woodlands into small isolated remnants surrounded by farmland may have affected the spread of disturbances such as fire and thereby reduced the probability of a remnant population being burnt. Indeed in urban-wildland mosaics, such as southern Californian urban and chaparral lands, processes which maintain the native vegetation have been altered by changed fire regimes brought about by fire suppression and habitat fragmentation (Pickett *et al.* 1992). It should also be considered that although the frequency of disturbance events such as severe storms and tornadoes are unlikely to have changed since European settlement, the probability of a tornado occurring in *E. salmonophloia* woodland is now lower because the area of woodland is considerably smaller. As a consequence the path of the disturbance in the fragmented wheatbelt landscape is more critical for the persistence of *E. salmonophloia* than it would have been in the unfragmented landscape. By analogy with ten pin bowling, a ball travelling down an alley is more likely to knock over a skittle when there are ten grouped together compared to a skittle standing alone.

As to the second possible explanation for the lack of recruitment in the wheatbelt, the fragmentation of *E. salmonophloia* woodlands into small isolated remnants and the surrounding agricultural land use may have had an adverse effect on the ability of *E. salmonophloia* to recruit seedlings following large scale natural disturbances. These effects could be manifested, firstly, as changes in the ability of *E. salmonophloia* to form a soil seed reserve following the disturbance and secondly, as changes in the probability of seedlings establishing.

Several factors may affect the ability of *E. salmonophloia* to form a soil seed reserve following disturbance. These include a lack of viable seed and changed seed predator population size. Reduced production of viable seed may occur as fragmentation increases and population size declines; this phenomenon is known as the Allee effect (Section 2.4). In *E. salmonophloia* a decline in seed production may reduce a population's ability to satiate predators and establish a soil seed reserve following large scale disturbance. In this study there was no clear relationship between remnant size and seed production and although the Allee effect may be operative it is unlikely that reduced seed production is affecting the ability of *E. salmonophloia* to form a soil seed reserve following disturbance. Canopy seed reserves of up to 420 000 seeds were measured in individual trees (Table 2.6) and this seems ample to form a soil seed reserve. Moreover visual estimates of canopy seed reserves in unfragmented populations were similar to those in fragmented wheatbelt populations.

Changes in the size of seed harvesting ant populations in remnant woodlands will also effect the ability of *E. salmonophloia* to form a soil seed reserve following disturbance. Obviously increases in the number of seed harvesting ants will reduce the probability of *E. salmonophloia* forming a soil seed reserve and compound any reduction in seed production. However, the converse situation may also exist where there has been a reduction in the number of seed harvesting ants. This will increase the probability of a soil seed reserve being formed and offset any reduction in seed production. Unfortunately, the effects of habitat fragmentation and degradation on the population size of seed harvesting ants has not been investigated elsewhere and was beyond the scope of this study. It is therefore unknown if changes to populations of seed harvesting ants have occurred in remnant woodlands. As a consequence the possibility of increased numbers of seed harvesting ants preventing the establishment of a soil seed reserve following disturbance cannot be dismissed; this is a problem that requires further attention.

Clearly declines in seed production and changes in the numbers of seed harvesting ants may affect *E. salmonophloia's* ability to establish a soil seed reserve following disturbance. However, it is difficult to predict the absolute number of seeds needed in the soil seed reserve to maintain a remnant *E. salmonophloia* population. This is because for recruitment *E. salmonophloia* relies on the co-occurrence of large scale disturbance and favourable rainfall in the first summer following germination. The co-occurrence of these events may be quite infrequent (Section 4.4). As a consequence the relationship between the number of seeds in the soil reserve and the number of recruits is not linear. Obviously in remnants where no seed is incorporated into the soil seed reserve following a disturbance no recruitment will occur. However, in cases where seed is incorporated into a soil seed reserve the number of seedlings which establish may be more sensitive to rainfall patterns following the disturbance and conditions within the remnant than to the number of seeds in the soil seed reserve. A greater number of seeds in the soil reserve does not necessarily increase the probability of seedling recruitment (Section 2.4). It would therefore appear that changes in the size of the soil seed reserve would have to be enormous for this to be affecting recruitment in the wheatbelt remnants.

A number of factors may reduce the probability of *E. salmonophloia* seedlings establishing in remnant woodlands following large scale disturbances. These include soil degradation, loss of mycorrhizal symbioses, grazing by domestic livestock and feral rabbits and increased competition from introduced annual plant species. These will be discussed individually below.

Livestock grazing and trampling in many remnant *E. salmonophloia* woodlands has resulted in soil compaction (Norton and Hobbs, unpublished data). As a consequence penetration of the soil by the roots of young seedlings may be impeded and their ability to utilise soil water and nutrients at depths lower in the profile will be reduced (Passioura 1991). During dry periods, when water in the surface soil is more limiting, seedlings with poorly developed root systems are therefore likely to be more stressed than seedlings with deeper, more well developed root systems. Soil compaction not only reduces the ability of the roots to provide the shoot with water and nutrients but may also induce the roots to send hormonal signals to the leaves which inhibit growth (Passioura 1991). Furthermore soil compaction reduces water infiltration rates; this is particularly noticeable in heavily grazed remnants during heavy winter rain when water can be observed running across the soil surface in sheets. By contrast in remnants which are not degraded by grazing little run-off is observed and infiltration rates are clearly higher. As a result of soil compaction, soil water recharge is likely to be lower in heavily grazed, degraded woodlands and water availability may therefore be more limiting. Water availability is the main factor limiting the early growth of *E. salmonophloia* seedlings (Sections 7.3 and 7.4) and therefore any reduction in soil water availability brought about by soil compaction will adversely affect seedling establishment. Soil degradation is clearly a factor which may be preventing the establishment of *E. salmonophloia* seedlings following disturbance.

Mycorrhizal symbioses between roots and various fungi are common in *Eucalyptus* spp (Pryor 1956; Chilvers 1973; Malajczuk *et al.* 1975; Warcup 1975). The mycorrhizal symbiosis is an alternative strategy to root growth which increases the uptake of poorly mobile soil phosphorus by increasing the volume of soil explored and lowering the concentration at which phosphorus is absorbed (Bowen 1981). The mycorrhizal symbiosis has not been studied in any detail for *E. salmonophloia* but observations of mycorrhizal roots on *E. salmonophloia* seedlings grown in the glasshouse confirms that the symbiosis occurs (Kyeremeh 1994). There have been no studies describing the effects of habitat fragmentation and degradation or the impact of surrounding land use on mycorrhizal populations in remnant *Eucalyptus* woodlands and forests. Negative impacts of these factors on mycorrhizal populations will obviously lower the probability of *E. salmonophloia* seedlings establishing. However, observations of mycorrhizal infection in approximately 40% of *E. salmonophloia* seedlings growing on soil collected from a limited sample of remnant woodlands suggest that the loss of this symbiotic association is not responsible for the lack of recruitment (Kyeremeh 1994). Clearly this is an important area for further research.

Livestock grazing in remnant woodlands may not only affect the ability of *E. salmonophloia* seedlings to establish following disturbance by changes to soil structure but also by direct grazing of the seedlings. Changes in the abundance of natural herbivores and their replacement with introduced herbivores has brought about a change in grazing regimes in Australian native vegetation communities. Grazing and trampling by domestic sheep and cattle has been shown to limit the recruitment of many woody perennial plant species including *Eucalyptus* spp. (Bryant 1971; Crisp and Lange 1976; Crisp 1978; Chesterfield and Parsons 1985; Gibson and Kirkpatrick 1989). Similarly it is well known that feral rabbits prevent the recruitment of many woody perennial plant species (Johnston 1968; Crisp and Lange 1976; Lange and Purdie 1976; Crisp 1978; Lange and Graham 1983; Cooke 1987; Auld 1990). Observations of *E. salmonophloia* seedlings following disturbances in unfragmented woodlands to the east of the wheatbelt indicate that recruitment can occur under some grazing pressure from domestic livestock and rabbits. However, it should be noted that the density of livestock and rabbits in these woodlands is a great deal less than in remnant woodlands. Domestic livestock and rabbit grazing is therefore another factor which may be preventing the establishment of *E. salmonophloia* seedlings in remnant woodlands following disturbance and is an important area for further research.

Finally the invasion of remnant *E. salmonophloia* woodlands by non-native annual plant species is widespread and may have reduced the probability of *E. salmonophloia* seedlings establishing following disturbance. These weeds have higher growth rates than woody perennial species and compete more effectively for limited soil water and nutrients (Hobbs and Atkins 1991). As a consequence they can prevent the establishment of native woody species (Hobbs and Atkins 1991). The importance of this competition has been recognised in Australia during attempts to re-establish woody species in degraded areas where non-native annuals are abundant (Goss 1986; Venning 1988; Buchanan 1989; Bird *et al.* 1990; Dalton 1990; Loney 1990). Increased competition with introduced annual plant species is another factor which may be preventing the establishment of *E. salmonophloia* seedlings following disturbance in remnant woodlands and is worthy of further research.

Clearly changes to the disturbance regime and/or changes in the ability of *E. salmonophloia* to regenerate successfully following disturbance can account for the lack of recruitment in remnant *E. salmonophloia* woodlands. Defining the relative importance of these factors is, however, beyond the scope of this thesis and requires further research.

In conclusion, the research presented in this thesis has documented the life history of *E. salmonophloia* and demonstrated that recruitment of seedlings occurs following large scale natural disturbances such as fires, floods, severe windstorms and droughts; recruitment in inter-disturbance periods is very rare. Prior to this investigation studies of disturbance and *Eucalyptus* forest and woodland dynamics had largely focussed on fire but the research presented here indicates that other forms of large scale natural disturbance are also important drivers of mediterranean climate *Eucalyptus* woodland dynamics in south western Australia. Evidently changes to the disturbance regime and/or changes in the ability of *E. salmonophloia* to regenerate successfully following disturbance are responsible for the lack of recruitment in remnant *E. salmonophloia* woodlands. Factors responsible for changes to these processes were discussed but it remains for future research to elucidate the relative importance of each. Experiments involving disturbance with and without modification of potential limiting factors will be required.

Management of *E. salmonophloia* woodland remnants in the wheatbelt of Western Australia must take into account the role of disturbance and include appropriate disturbance regimes to initiate seed regeneration of the dominant tree species. However, this presents a conundrum for conservation management as considerable adult mortality can occur but not all disturbances will lead to seedling recruitment, firstly because the rainfall pattern following the disturbance may not be favourable and secondly, because of changes in the ability of *E. salmonophloia* to regenerate due to soil degradation, grazing and weed invasion. Unfortunately it is not possible to predict when favourable rainfall will occur following a disturbance, but the impact of poor recruitment and high adult mortality on population size can be ameliorated by imposing disturbances at scales which do not endanger the whole population. It remains to be seen whether large-scale disturbances can be translated into smaller-scale management activities. The implications of the need for disturbance also need to be viewed from the perspective of landowners and local community groups who may be reluctant to lose adult trees in order to encourage seedling recruitment. The establishment of successful demonstration areas is required so that the benefits in terms of recruitment can be displayed. The changes in the ability of *E. salmonophloia* to recruit seedlings following disturbances are more easily overcome and may be achieved by ameliorating the effects of soil degradation, grazing and weed invasion. Clearly the development of cost effective techniques to overcome these problems is an important area of further research which will be of great benefit to the management of remnant *E. salmonophloia* woodlands and may also be relevant to similar woodland types elsewhere.

Finally, the understanding of *E. salmonophloia* woodland dynamics in the fragmented landscape of the wheatbelt has been significantly improved by an examination of the adjacent unfragmented system. Without such a comparison, the development of a clear picture of the dynamics of the woodland ecosystem would be much more difficult, if not impossible. In situations where an unfragmented system is no longer available as a reference area, it must be questioned whether it is possible to identify the processes which are important for the long term retention and management of the natural communities present in the fragmented system.

REFERENCES

Abbott, I., and van Huerck, P. (1985). Comparison of insects and vertebrates as removers of seed and fruit in a Western Australian forest. *Australian Journal of Ecology* **10**, 165-168.

Abensperg-Traun, M., and Smith, G. T. (1993). Predictable effects of agricultural development on the long term availability of hollows for animals: observations from the Western Australian wheatbelt. *Pacific Conservation Biology* **1**, 78-79.

Allee, W. C. (1949). Group survival value for *Philodina roseola*, a rotifer. *Ecology* **30**, 395-397.

Andersen, A. N. (1982). Seed removal by ants in the mallee of northwestern Victoria. In 'Ant-Plant Interactions in Australia.' (Ed R. C. Buckley.) pp. 31-44. (DR W. Junk: The Hague.)

Andersen, A. N. (1987). Effects of seed predation by ants on seedling densities at a woodland site in SE Australia. *Oikos* **48**, 171-174.

Andersen, A. N. (1988). Immediate and longer-term effects of fire on seed predation by ants in sclerophyllous vegetation in south-eastern Australia. *Australian Journal of Ecology* **13**, 285-293.

Andersen, A. N. (1989). How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia* **81**, 310-315.

Andersen, A. N., and Ashton, D. H. (1985). Rates of seed removal by ants at heath and woodland sites in southeastern Australia. *Australian Journal of Ecology* **10**, 381-390.

Andersen, A. N., and Yen, A. L. (1985). Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. *Australian Journal of Ecology* **10**, 25-30.

Arnold, G. W., and Weeldenburg, J. R. (1991). The distribution and characteristics of remnant vegetation in parts of the Kellerberrin, Tammin, Trayning and Wyalkatchem Shires of Western Australia. *CSIRO Division of Wildlife and Ecology Technical Memo.***33.** (CSIRO, Australia)

Ashton, D. H. (1975a). Studies of flowering behaviour in *Eucalyptus regnans* F. Muell. *Australian Journal of Botany* **23**, 399-411.

Ashton, D. H. (1975b). Studies of litter in *Eucalyptus regnans* forests. *Australian Journal of Botany* **23**, 413-433.

Ashton, D. H. (1976). The development of even aged stands in *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Botany* **23**, 413 - 433.

Ashton, D. H. (1979). Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Ecology* **4**, 265-277.

Ashton, D. H. (1981). Fire in tall open forests (wet sclerophyll forests). In 'Fire and The Australian Biota.' (Eds A. M. Gill, R. H. Groves and I. R. Noble.) pp. 339-366. (Australian Academy of Science: Canberra.)

Atkins, L., and Hobbs, R. J. (In press). Measurement and effects of fire heterogeneity in southwest Australian wheatbelt vegetation. *Calmscience*

Attiwill, P. M. (1994). The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management* **63**, 247-300.

Attiwill, P. M., Guthrie, H. B., and Leuning, R. (1978). Nutrient cycling in a *Eucalyptus obliqua* (L'Herit.) forest. I. Litter production and nutrient return. *Australian Journal of Botany* **26**, 79-91.

Attiwill, P. M., and Leeper, G. W. (1987). 'Forest Soils and Nutrient Cycles.' (Melbourne University Press: Melbourne)

Auld, T. D. (1990). Regeneration in populations of the arid zone plants *Acacia carnei* and *A. oswaldii. Proceedings of the Ecological Society of Australia* **16**, 267-272.

Bachelard, E. P. (1985). Effects of soil moisture stress on the growth of seedlings of three eucalypt species. I. Seed germination. *Australian Forestry Research* **15**, 103-114.

Barbour, M. G., and Lange, R. T. (1967). Seed populations in some natural Australian topsoils. *Ecology* **48**, 153-155.

Barrow, N. J. (1977). Phosphorus uptake and utilisation by tree seedlings. *Australian Journal of Botany* **25**, 571-584.

Battaglia, M. (1993). Seed germination physiology of *Eucalyptus delegatensis* R.T. Baker in Tasmania. *Australian Journal of Botany* **41**, 119-136.

Beard, J. S. (1990). 'Plant Life in Western Australia.' (Kangaroo Press: Kenthurst, New South Wales.)

Beard, J. S., and Sprenger, B. S. (1984). 'Geographical data from the vegetation survey of Western Australia'. *Vegetation Survey of Western Australia Occasional Paper* **2** (Vegmap Publications: Perth.)

Bell, D. T., Plummer, J. A., and Taylor, S. K. (1993). Seed germination ecology in southwestern Western Australia. *The Botanical Review* **59**, 24-73.

Bell, D. T., Vlahos, S., and Watson, L. E. (1987). Germination stimulation of seed of understorey species of the northern jarrah forest of Western Australia. *Australian Journal of Botany* **35**, 593-599.

Bellairs, S. M., and Bell, D. T. (1990). Temperature effects on the seed germination of ten Kwongan species from Eneabba, Western Australia. *Australian Journal of Botany* **38**, 451-458.

Berg, R. Y. (1975). Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* **23**, 475-508.

Bierregaard, R. O. J., Lovejoy, T. E., Kapos, V., dos Santos, A. A., and Hutchings, R. W. (1992). The biological dynamics of tropical rainforest fragments. *BioScience* **42**, 859-866.

Bird, R., Cumming, K. N., and Kearney, G. A. (1990). Research in direct seeding of trees in the 500-800 mm rainfall zone of Western Victoria. In 'Sowing the Seeds. Direct Seeding and natural regeneration conference proceedings.' pp. 65-74. (Greening Australia: Deakin, ACT.)

Bowen, G. D. (1981). Coping with low nutrients. In 'The Biology of Australian Plants.' (Eds J. S. Pate and A. J. McComb.) pp. 33-64. (University of Western Australia Press: Nedlands, Western Australia.)

Bradstock, R. A. (1991). The sensitivity of populations of fire-prone shrubs to variations in reproduction. *Bulletin of the Ecological Society of Australia* **21**, 57.

Bren, L. J. (1993). Tree invasion of an intermittent wetland in relation to changes in the flooding frequency of the River Murray Australia. *Australian Journal of Ecology* **17**, 395 - 409.

Brokaw, N. L. (1985). Treefalls regrowth and community structure in tropical forests. In 'The Ecology of Natural Disturbance and Patch Dynamics.' (Eds S. T. A. Pickett and P. S. White.) pp. 53-68. (Academic Press: New York.)

Brooker, M. I. H., and Kleinig, D. A. (1990). 'Field Guide to Eucalypts Volume 2.' (Inkata: Melbourne.)

Brown, N. A. C., Kotze, G., and Botha, P. A. (1993). The promotion of seed germination of Cape *Erica* species by plant-derived smoke. *Seed Science and Technology* **21**, 573-580.

Bryant, W. G. (1971). Grazing, burning and regeneration of tree seedlings in *Eucalyptus pauciflora* woodlands. *Journal of Soil Conservation New South Wales.* **25**, 121-134.

Buchanan, R. A. (1989). 'Bush Regeneration: Recovering Australian Landscapes.' (TAFE NSW: Sydney.)

Burrows, N., Gardiner, G., Ward, B., and Robinson, A. (1990). Regeneration of *Eucalyptus wandoo* following fire. *Australian Forestry* **53**, 248-258.

Burvill, G. H. (1979). The first sixty years, 1829 - 1889. In 'Agriculture in Western Australia 1829-1979.' (Ed G. H. Burvill.) pp. 4-17. (University of Western Australia Press: Nedlands, Western Australia.)

Carol, E. J., and Ashton, D. H. (1965). Seed storage in soils of several Victorian plant communities. *Victorian Naturalist* **82**, 102-110.

Chesterfield, C. J., and Parsons, R. F. (1985). Regeneration of three tree species in arid south-eastern Australia. *Australian Journal of Botany* **33**, 715-732.

Chilvers, G. A. (1973). Host range of some eucalypt mycorrhizal fungi. *Australian Journal of Botany* **21**, 103-111.

Chippendale, G. M. (1973). 'Eucalypts of the Western Australian Goldfields (and the Adjacent Wheatbelt).' (Australian Government Publishing Service: Canberra.)

Christensen, P. (1971). Stimulation of seedfall in karri. *Australian Forestry* **35**, 182-190.

Clarke, R. H. (1962). 'Severe local windstorms in Australia.' *CSIRO Division of Meteorological Physics Technical Paper* **13**. (CSIRO: Australia.)

Clayton-Greene, K. A., and Ashton, D. H. (1990). The dynamics of *Callitris columellaris/Eucalyptus albens* communities along the Snowy River and its tributaries in south-eastern Australia. *Australian Journal of Botany* **38**, 403-432.

Cooke, B. D. (1987). The effect of rabbit grazing on regeneration of sheoaks, *Allocasuarina verticilliata* and saltwater ti-trees, *Melaleuca halmaturorum*, in the Coorong National Park, South Australia. *Australian Journal of Ecology* **13**, 11-20.

Cowling, R. M., and Lamont, B. B. (1987). Post-fire recruitment of four co-occurring *Banksia* species. *Journal of Applied Ecology* **24**, 645-658.

Cowling, R. M., Lamont, B. B., and Enright, N. J. (1990). Fire and management of south-western Australian banksias. *Proceedings of the Ecological Society of Australia* **16**, 177-183.

Crawley, M. J. (1992). Seed predators and plant population dynamics. In 'Seeds: The Ecology of Regeneration in Plant Communities.' (Ed M. Fenner.) pp. 157-191. (C.A.B. International: Wallingford United Kingdom.)

Cremer, K. W. (1965). How eucalypt fruits release their seed. *Australian Journal of Botany* **13**, 11-16.

Cremer, K. W.; Cromer, R. N., and Florence, R. G. (1978). Stand establishment. In 'Eucalypts for Wood Production.' (Eds W. E. Hillis and A. G. Brown.) pp. 81-135. (CSIRO: Melbourne.)

Crisp, M. D. (1978). Demography and survival under grazing of three Australian semi-desert shrubs. *Oikos* **30**, 520-528.

Crisp, M. T., and Lange, R. T. (1976). Age-structure distribution and survival under grazing of the arid zone shrub *Acacia bukittii. Oikos* **27**, 86-92.

Dalton, G. (1990). Direct seeding in southern South Australia. In 'Sowing the Seeds. Direct Seeding and Natural Regeneration Conference Proceedings.' pp. 75-80. (Greening Australia: Deakin, ACT.)

Davies, S. J., and Myerscough, P. J. (1991). Post-fire demography of the wet-mallee *Eucalyptus luehmanniana* F. Muell. (Myrtaceae). *Australian Journal of Botany* **39**, 459-466.

Dexter, B. D. (1978). Silviculture of the river red gum forests of the central Murray flood plain. *Proceedings of the Royal Society of Victoria* **90**, 175 - 191.

Enright, N. J., and Lamont, B. B. (1989). Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *Journal of Ecology* **77**, 1111-1122.

Enright, N. J., and Lamont, B. B. (1992a). Recruitment variability in the resprouting shrub *Banksia attenuata* and non-sprouting congeners in the northern sandplain heaths of southwestern Australia. *Acta Oecologica* **13**, 727-741.

Enright, N. J., and Lamont, B. B. (1992b). Survival, growth and water relations of *Banksia* seedlings on a sand mine rehabilitation site and adjacent scrub-heath sites. *Journal of Applied Ecology* **29**, 663-671.

Farrington, P., Bartle, G. A., Watson, G. D., and Salama, R. B. (1994). Long-term transpiration in two eucalypt species in a native woodland estimated by the heat pulse technique. *Australian Journal of Ecology* **19**, 17-25.

Fitzpatrick, W. A. (1970). The expectancy of deficient winter rainfall and the potential for severe drought in the south-west of Western Australia. *Institute of Agriculture Miscellaneous Publication* **70/1**. (The University of Western Australia Agronomy Department: Nedlands, Western Australia.)

Gentilli, J. (1972). 'Australian Climate Patterns.' (Thomas Nelson: Australia.)

Gibson, A., and Bachelard, E. P. (1986). Germination of *Eucalyptus sieberi* L. Johnson seeds. I. Response to substrate and atmospheric moisture. *Tree Physiology* **1**, 57-65.

Gibson, N., and Kirkpatrick, J. B. (1989). Effects of the cessation of grazing on the grasslands and grassy woodlands of the Central Plateau, Tasmania. *Australian Journal of Botany* **37**, 55-63.

Gill, A. M. (1975). Fire and the Australian flora: A review. *Australian Forestry* **38**,

Goss, K. (1986). Greening the wheatbelt. *Landscope* **2**, 22-25.

Green, J. W. (1985). 'Census of Vascular Plants of Western Australia, 2nd edition.' (Department of Agriculture, Perth.)

Grose, R. J. (1957). A study of some factors associated with the natural regeneration of Alpine Ash, *Eucalyptus delegatensis* R. T. Baker, syn. *E. gigantea* Hook. f. *Forests Commission of Victoria Bulletin* **4**. (Victorian Forests Commission: Melbourne.)

Grose, R. J. (1960). Effective seed supply for the natural regeneration of *Eucalyptus delegatensis* R. T. Baker, Syn. *Eucalyptus gigantea* Hook. F. *Appita* **13**, 141-148.

Grose, R. J. (1962). Germination responses of seeds of Victorian eucalypts. In 'ANZAAS Jubilee Congress Proceedings.' pp. 1-15. (ANZAAS: Sydney, Australia.)

Groves, R., and Hobbs, R. J. (1992). Patterns of plant functional responses and landscape heterogeneity. In 'Biodiversity in Mediterranean Ecosystems in Australia.' (Ed R. J. Hobbs.) pp. 47-60. (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Groves, R. H., and Keraitis, K. (1976). Survival and growth of seedlings of three sclerophyll species at high levels of phosphorus and nitrogen. *Australian Journal of Botany* **24**, 681-690.

Harper, J. L. (1957). The ecological importance of dormancy and its importance in weed control. *Proceedings of the International Congress for Plant Protection* **4**, 415-420.

Harper, J. L. (1977). 'Population Biology of Plants.' (Academic Press: London.)

Harper, J. L., and Benton, R. A. (1966). The behaviour of seeds in soil. The germination of seeds on the surface of a water supplying substrate. *Journal of Ecology* **54**, 151-166.

Hester, A. J., and Hobbs, R. J. (1992). Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science* **3**, 101-108.

Hnatiuk, R. J., and Hopkins, A. J. M. (1980). Western Australian species rich Kwongan (sclerophyllous shrubland) affected by drought. *Australian Journal of Botany* **28**, 573 - 585.

Hobbs, R. J. (1991). 'Regeneration of Native Woodlands in Western Australia.' Report to World Wide Fund for Nature.

Hobbs, R. J. (1992). 'Biodiversity of Mediterranean Ecosystems in Australia.' (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Hobbs, R. J. (1993). Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt. *Biological Conservation* **64**, 193-201.

Hobbs, R. J., and Atkins, L. (1988). Spatial variability of experimental fires in south-west Western Australia. *Australian Journal of Ecology* **13**, 295-299.

Hobbs, R. J., and Atkins, L. (1991). Interactions between annuals and woody perennials in a Western Australian nature reserve. *Journal of Vegetation Science* **2**, 643-654.

Hobbs, R. J., and Hopkins, A. J. M. (1990). From frontier to fragments: European impact on Australia's vegetation. *Proceedings of the Ecological Society of Australia* **16**, 93-114.

Hobbs, R. J., Saunders, D. A., Lobry de Bruyn, L. A. , and Main, A. R. (1992). Changes in biota. In 'Re-integrating Fragmented Landscapes. Towards Sustainable Production and Nature Conservation.' (Eds R. J. Hobbs and D. A. Saunders.) pp. 65-106. (Springer-Verlag: New York.)

Hopper, S. D. (1993). Eucalypts. In 'Mountains of Mystery A Natural History of the Stirling Range.' (Eds C. Thomson, G. Hall and G. Friend.) pp. 71 - 82. (Department of Conservation and Land Management: Perth.)

Humphreys, F. R., and Craig, F. G. (1981). Effects of fire on soil chemical, structural and hydrological properties. In 'Fire and the Australian Biota.' (Eds A. M. Gill, R. H. Groves and I. R. Noble.) pp. 177-200. (Australian Academy of Science: Canberra.)

Humphreys, F. R., and Lambert, M. J. (1965). An examination of a forest site which has exhibited the ashbed effect. *Australian Journal of Soil Research* **3**, 81-94.

Jennersten, O. (1988). Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. *Conservation Biology* **2**, 359-366.

Johnston, T. N. (1968). The effect of sheep and rabbit grazing on regeneration of white cypress pine. *Australian Forestry Research* **4**, 3-12.

Judd, T. S. (1993). Seed survival in small myrtaceous capsules subjected to experimental heating. *Oecologia* **93**, 576-581.

Judd, T. S., and Ashton, D. H. (1991). Fruit clustering in the Myrtaceae: seed survival in capsules subjected to experimental heating. *Australian Journal of Botany* **39**, 241-245.

Kealley, I. (1991). Management of inland arid and semi-arid woodland forest of Western Australia. In 'Forest Management in Australia.' (Eds F. H. McKinnell, E. R. Hopkins and J. E. D. Fox.) pp. 286-295. (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Keeley, J. E. (1991). Seed germination and life history syndromes in the California chaparral. *Botanical Review* **57**, 81-116.

Keeley, J. E., and Keeley, S. C. (1987). The role of fire in the germination of chaparral herbs and suffrutescents. *Madrono* **34**, 240-249.

Keeley, S. C., and Pizzorno, M. (1986). Charred wood stimulated germination of two fire following-herbs of the California chaparral and the role of hemicellulose. *American Journal of Botany* **73**, 1289-1297.

Kuczera, G. (1985). Prediction of Water Yield Reductions Following a Bushfire in Ash Mixed Species Eucalypt Forest. *Melbourne and Metropolitan Board of Works Report No.* **MMBW-W-0014.**

Kyeremeh, S. (1994). 'The Edaphic Factors Affecting the Germination and Early Growth of Salmon Gum (*Eucalyptus salmonophloia*)' M.Sc. Thesis, School of Biological and Environmental Science, Murdoch University.

Lambeck, R. J., and Saunders, D. A. (1993). The role of patchiness in reconstructed wheatbelt landscapes. In 'Nature Conservation 3. The Reconstruction of Fragmented Ecosystems.' (Eds D. A. Saunders, R. J. Hobbs and P. R. Ehrlich.) pp. 153-161. (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Lamont, B. (1985). Gradient and zonal analysis of understorey suppression by *Eucalyptus wandoo. Vegetatio* **63**, 49-66.

Lamont, B. B. (1984). Specialised modes of nutrition. In 'Kwongan Plant Life of the Sandplain.' (Eds J. S. Pate and J. S. Beard.) pp. 236-245. (University of Western Australia Press: Nedlands, Western Australia.)

Lamont, B. B., Connell, S., and Bergl, S. M. (1991a). Population and seed bank dynamics of *Banksia cuneata*: the role of time, fire and moisture. *Botanical Gazette* **152**, 114-122.

Lamont, B. B., Maitre, D. C. L., Cowling, R. M., and Enright, N. J. (1991b). Canopy seed storage in woody plants. *The Botanical Review* **57**, 277-317.

Lamont, B. B., Klinkhamer, P. G. L., and Witkowski, E. T. F. (1993). Population fragmentation may reduce fertility to zero in *Banksia goodii* - a demonstration of the Allee effect. *Oecologia* **94**, 446-450.

Lange, R. T., and Graham, C. R. (1983). Rabbits and the failure of regeneration in Australian arid zone *Acacia* . *Australian Journal of Ecology* **8**, 377-381.

Lange, R. T., and Purdie, R. (1976). Western Myall *(Acacia sowdennii)*, its survival prospects and management needs. *Australian Rangelands Journal* **1**, 64-69.

Lobry de Bruyn, L. A. (1990). 'The Role of Ants and Termites in Modifying Soil Properties in Naturally Vegetated and Agricultural Environments'. Ph. D. Thesis, University of Western Australia.

Lodge, G. M. (1981). Establishment of warm and cool season native perennial grasses on the north-west slopes of New South Wales. II. Establishment and seedling survival in the field. *Australian Journal of Botany* **29**, 111-119.

Lodge, G. M., and Whalley, R. D. B. (1981). Establishment of warm and cool season native perennial grasses on the north-west slopes of New South Wales. I. Dormancy and germination. *Australian Journal of Botany* **29**, 121-133.

Loneragan, O. W., and Loneragan, J. F. (1964). Ashbed and nutrients in the growth of seedlings of karri (*Eucalyptus diversicolor* F.v.M.). *Journal of the Royal Society of Western Australia* **47**, 75-80.

Loney, B. (1990). Direct seeding in Western Australia-its status and future. In 'Sowing the Seeds. Direct Seeding and Natural Regeneration Conference Proceedings.' pp. 103-112. (Greening Australia: Deakin,ACT.)

Lourenz, R. S. (1981). 'Tropical Cyclones in the Australian Region, July 1909 to June 1981. Meteorological Summary.' (Bureau of Meteorology: Australia.)

Lush, W. M., Kaye, P. E., and Groves, R. H. (1984). Germination of *Clematis microphylla* seeds following weathering and other treatments. *Australian Journal of Botany* **32**, 121-129.

Main, A. R. (1987). Management of remnants of native vegetation - A review of the problems and the development of an approach with reference to the wheatbelt of Western Australia. In 'Nature Conservation: The Role of Remnants of Native Vegetation.' (Eds D. A. Saunders, G. W. Arnold, A. A. Burbidge and A. J. M. Hopkins.) pp. 1-13. (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Majer, J. D. (1980). The influence of ants on broadcast and naturally spread seeds in rehabilitated bauxite mines. *Reclamation Review* **3**, 3-9.

Malajczuk, N., McComb, A. J., and Loneragan, J. F. (1975). Phosphorus uptake and growth of mycorrhizal and uninfected seedlings of *Eucalyptus calophylla*. *Australian Journal of Botany* **23**, 231-238.

Marchant, N. G., Wheeler, J. R., Rye, B. L., Bennett, E. M., Lander, N. S., and Macfarlane, T. D. (1987). 'Flora of the Perth Region.' (Western Australian Herbarium, Department of Agriculture: Western Australia.)

McArthur, W. M. (1991). 'Reference soils of south-western Australia.' (Department of Agriculture, Western Australia: Perth.)

McArthur, W. M. (1992). History of landscape development. In 'Reintegrating Fragmented Landscapes. Towards sustainable production and nature conservation.' (Eds R. J. Hobbs and D. A. Saunders.) pp. 10-22. (Springer-Verlag: New York.)

McCullagh, P., and Nelder, J. A. (1989). 'Generalised Linear Models (2nd edition).' (Chapman and Hall: London.)

McFarlane, D. J., George, R. J., and Farrington, P. (1992). Changes in hydrological balance. In 'Reintegrating Fragmented Landscapes. Towards Sustainable Production and Nature Conservation.' (Eds R. J. Hobbs and D. A. Saunders.) pp. 146-186. (Springer-Verlag: New York.)

Minor, J. E., Peterson, R. E., and Lourensz, R. S. (1980). Characteristics of Australian tornadoes. *Australian Meteorological Magazine* **28**, 57 - 77.

Mott, J. J., and Groves, R. H. (1981). Germination Strategies. In 'The Biology of Australian Plants.' (Eds J. S. Pate and A. J. McComb.) pp. 307-341. (University of Western Australia Press: Nedlands, Western Australia.)

Northcote, K. H. (1971). 'A Factual Key for the Recognition of Australian Soils.' (CSIRO/Rellim: Glenside South Australia.)

Norton, D. A., Hobbs, R. J., and Atkins, L. (1994). Fragmentation, disturbance and plant distribution: mistletoes in woodland remnants in the Western Australian wheatbelt. *Conservation Biology* **In press**,

Nulsen, R. A., Bligh, K. J., Baxter, I. N., Solin, E. J., and Imrie, D. H. (1986). The fate of rainfall in a mallee and heath vegetated catchment in southern Western Australia. *Australian Journal of Ecology* **11**, 361-371.

O'Connell, A. M., Grove, T. S., and Dimmock, G. M. (1978). Nutrients in the litter of jarrah forest soils. *Australian Journal of Ecology* **3**, 253-260.

O'Connell, A. M., Grove, T. S., and Dimmock, G. M. (1979). The effects of a high intensity fire on nutrient cycling in jarrah forest. *Australian Journal of Ecology* **4**, 331-337.

O'Connell, A. M., and Menage, P. M. A. (1982). Litter fall and nutrient cycling in karri (*Eucalyptus diversicolor* F. Muell.) forest in relation to stand age. *Australian Journal of Ecology* **7**, 49-62.

O'Dowd, D. J., and Gill, A. M. (1984). Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology* **65**, 1052-1066.

Olsen, M., and Lamb, D. (1988). Recovery of subtropical rainforest following storm damage. *Proceedings Ecological Society of Australia* **15**, 297 - 301.

Parsons, R. F. (1968). An introduction to the regeneration of mallee eucalypts. *Proceedings of the Royal Society of Victoria* **81**, 59-68.

Passioura, J. B. (1991). Soil structure and plant growth. *Australian Journal of Soil Research* **29**, 717-728.

Pate, J. S., and Dell, B. (1984). Economy of mineral nutrients in sandplain species. In 'Kwongan Plant Life of the Sandplain.' (Eds J. S. Pate and J. S. Beard.) pp. 227-252. (University of Western Australia Press: Nedlands Western Australia.)

Pate, J. S., Dixon, K. W., and Orshan, G. (1984). Growth and life form characteristics of kwongan species. In 'Kwongan Plant Life of The Sandplain.' (Eds J. S. Pate and J. S. Beard.) pp. 84-100. (University of Western Australia Press: Nedlands, Western Australia.)

Pickett, S. T. A., Parker, V. T., and Fiedler, P. L. (1992). The New Paradigm in Ecology: Implications for Conservation Biology Above the Species Level. In 'Conservation Biology: The Theory and Practice of Nature Conservation Preservation and Management.' (Eds P. L. Fiedler and S. K. Jain.) pp. 65-88. (Chapman and Hall: New York.)

Pickett, S. T. A., and White, P. S. (1985). 'The Ecology of Natural Disturbance and Patch Dynamics.' (Academic Press: New York.)

Pierrehumbert, C. I. (1973). 'Short duration rainfall over south-west Western Australia.' *Proceedings Hydrology Symposium 1973, Perth August 8-11 National Conference Publication No.* **73/3**. (The Institute of Engineers, Australia: Perth.)

Portlock, C. C., Shea, S. R., Majer, J. D., and Bell, D. T. (1990). Stimulation of germination of *Acacia pulchella*: Laboratory basis for forest management options. *Journal of Applied Ecology* **27**, 319-324.

Pryor, L. D. (1956). Ectotrophic mycorrhiza in renantherous species of *Eucalyptus*. *Nature* (London) **177**, 587-588.

Raison, R. J. (1979). Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformation. A review. *Plant Soil* **51**, 73-108.

Renbuss, M. A., Chilvers, G. A., and Pryor, L. D. (1973). Microbiology of an ashbed. *Proceedings of the Linnean Society of New South Wales* **97**, 302-310.

Rice, S. K. (1993). Vegetation establishment in post-fire *Adenostoma* chaparral in relation to fine-scale pattern in fire intensity and soil nutrients. *Journal of Vegetation Science* **4**, 115-124.

Robberecht, R., Mahall, B. E., and Nobel, P. S. (1983). Experimental removal of intraspecific competitors-effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida*. *Oecologia* **60**, 21-24.

Runkle, J. R. (1985). Disturbance regimes in temperate forests. In 'The Ecology of Natural Disturbance and Patch Dynamics.' (Eds S. T. A. Pickett and P. S. White.) pp. 12-33. (Academic Press: New York.)

Russell, J. D., Fraser, A. R., Watson, J. R., and Parsons, A. W. (1974). Thermal decomposition of protein in soil organic matter. *Geoderma* **11**, 63-66.

Samson, D. A., Philippi, T. E., and Davidson, D. W. (1992). Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. *Oikos* **65**, 61-80.

Sanchez, P. A. (1976). 'Properties and Management of Soils in the Tropics.' (J Wiley and Sons: New York.)

Saunders, D. A. (1979). The availability of tree hollows for use as nest sites by white tailed black cockatoos *Calyptorhynchus* spp. *Emu* **79**, 215 - 227.

Saunders, D. A., Arnold, G. W., Burbidge, A. A., and Hopkins, A. J. M. (1987). 'Nature Conservation: The Role of Remnants of Native Vegetation.' (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Saunders, D. A., Hobbs, R. J., and Arnold, G. W. (1993). The Kellerberrin project on fragmented landscapes: A review of current information. *Biological Conservation* **64**, 185-192.

Saunders, D. A., Hobbs, R. J., and Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**, 18-32.

Saunders, D. A., and Ingram, J. A. (1987). Factors affecting survival of breeding populations of Carnaby's cockatoo *Calyptorynchus funereus latirostris* in remnants of native vegetation. In 'Nature Conservation: The Role of Remnants of Native Vegetation.' (Eds D. A. Saunders, G. W. Arnold, A. A. Burbridge and A. J. M. Hopkins.) pp. 249-58. (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Saunders, D. A., Smith, G. T., and Rowley, I. (1982). The availability and dimensions of tree hollows that provide nest sites for cockatoos (*Psittaciformes*) in Western Australia. *Australian Wildlife Research* **9**, 541-556.

Schafer, C. L. (1990). 'Nature Reserves. Island Theory and Conservation Practice.' (Smithsonian Institution Press: Washington, D.C.)

van Schagen, J. (1986). 'Ant-plant interactions in a Western Australian wheatbelt nature reserve.' *Natural Resources Project No.* **594**. (Curtin University of Technology: Bentley, Western Australia.)

Scougall, S. A., Majer, J. D., and Hobbs, R. J. (1993). Edge effects in grazed and ungrazed Western Australian wheatbelt remnants in relation to ecosystem reconstruction. In 'Nature Conservation 3: Reconstruction of Fragmented Ecosystems, Global and Regional Perspectives.' (Eds D. A. Saunders, R. J. Hobbs and P. R. Ehrlich.) pp. 163-178. (Surrey Beatty and Sons: Chipping Norton, New South Wales.)

Sivertsen, D. (1994). The native vegetation crisis in the central wheatbelt of N.S.W. *Search* **25**, 5-8.

Southern, R. L. (1979). The atmosphere. In 'Environment and Science.' (Ed B. J. O'brien.) pp. 183-226. (University of Western Australia Press: Nedlands Western Australia.)

Stoneman, G. L., Dell, B., and Turner, N. C. (1994). Mortality of *Eucalyptus marginata* seedlings in Mediterranean-climate forest in response to overstorey, site, seedbed, fertiliser application and grazing. *Australian Journal of Ecology* **19**, 103-109.

Tomkins, I. B., Kellas, J. D., Tolhurst, K. G., and Oswin, D. A. (1991). Effects of fire intensity on soil chemistry in a eucalypt forest. *Australian Journal of Soil Research* **29**, 25-47.

Venning, J. (1988). 'Growing trees for farms, parks and roadsides. A revegetation manual.' (Lothian: Melbourne.)

Walker, J., Raison, R. J., and Khanna, P. K. (1986). Fire. In 'The Impact of Human Activities on Australian Soils.' (Eds J. S. Russell and R. F. Isbell.) pp. 185-216. (University of Queensland Press: Brisbane.)

Warcup, J. H. (1975). A culturable Endogone associated with eucalypts. In 'Endomycorrhizas.' (Eds F. E. Sanders, B. Mosse and P. B. Tinker.) pp. 53-63. (Academic Press: London.)

Webb, L. J. (1958). Cyclones as an ecological factor in tropical lowland rainforest, north Queensland. *Australian Journal of Botany* **6**, 220 - 228.

Wellington, A. B. (1981). 'A Study of the Population Dynamics of the mallee *Eucalyptus incrassata* Labill.' Ph. D. Thesis, Australian National University.

Wellington, A. B. (1984). Leaf water potentials, fire and the regeneration of mallee eucalypts in semi-arid, south-eastern Australia. *Oecologia* **64**, 360-362.

Wellington, A. B. (1989). Seedling regeneration and the population dynamics of eucalypts. In 'Mediterranean Landscapes in Australia, Mallee Ecosystems and their Management.' (Eds J. C. Noble and R. A. Bradstock.) pp. 155-167. (CSIRO: Canberra.)

Wellington, A. B., and Noble, I. R. (1985 a). Seed dynamics and factors limiting recruitment of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. *Journal of Ecology* **73**, 657-666.

Wellington, A. B., and Noble, I. R. (1985 b). Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. *Journal of Ecology* **73**, 645-656.

Westoby, M., French, K., Hughes, L., Rice, B., and Rodgerson, L. (1991). Why do more plant species use ants for dispersal on infertile compared with fertile soils? *Australian Journal of Ecology* **16**, 445-456.

Yates, C. J., Hobbs, R. J., and Bell, R. W. (1994). Landscape-scale disturbances and regeneration in semi-arid woodlands of south-western Australia. *Pacific Conservation Biology* **In press**,

Zar, J. H. (1984). 'Biostatistical Analysis (2nd edition).' (Prentice-Hall: New Jersey.)

Zimmer, W. J. (1940). Plant invasions in the mallee. *Victorian Naturalist* **56**, 143-147.