Persistence mechanisms of *Erodiophyllum elderi*, an arid land daisy with a patchy distribution

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Declaration

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

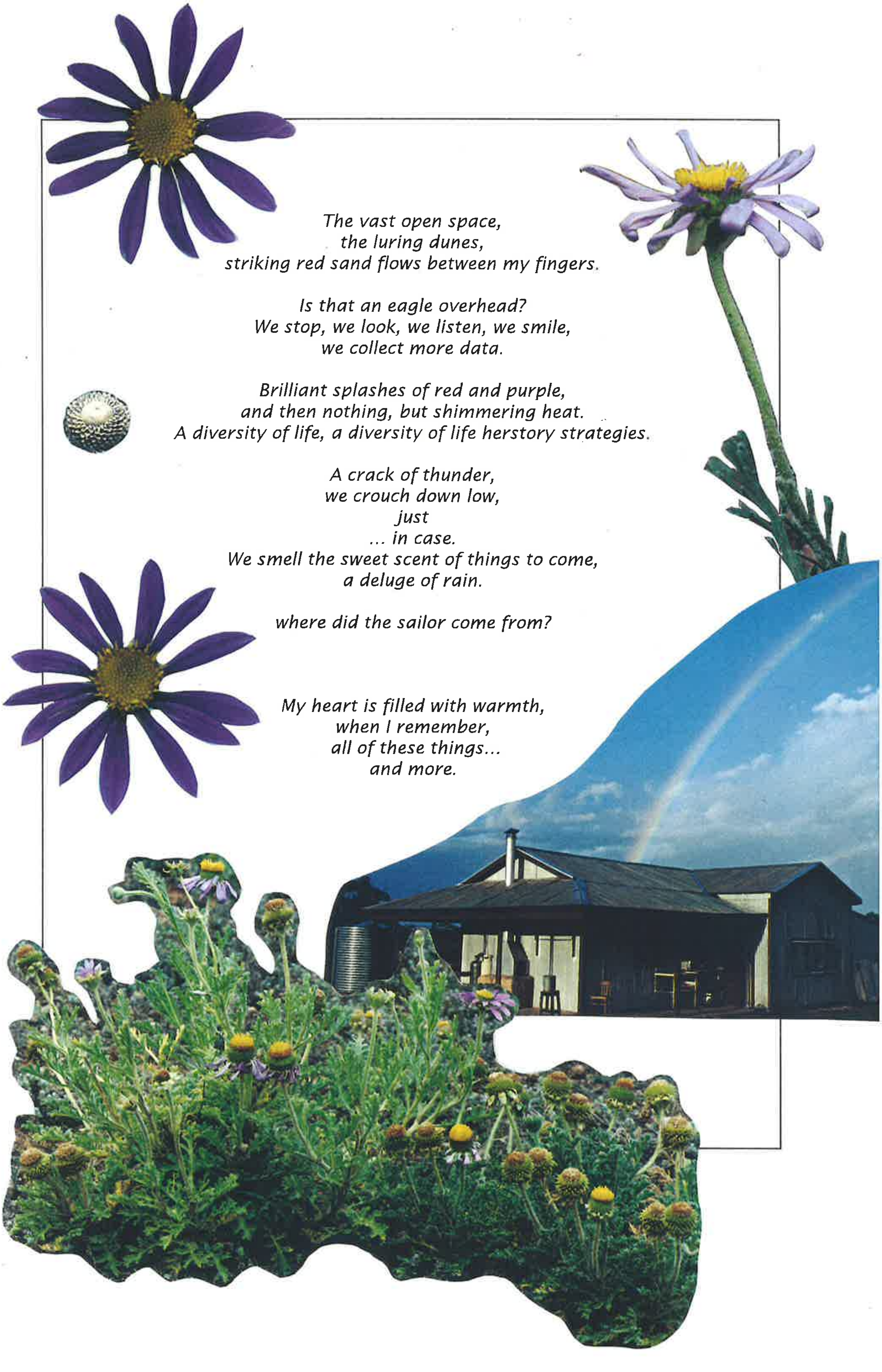
I also give consent to this thesis being available for photocopying and loan if accepted for the award of the degree.

Louise Emmerson

February, 1999.

Abstract

I investigate the persistence mechanisms of *Erodiophyllum elderi*, a short lived arid land daisy which inhabits low-lying areas in the north-east of South Australia. The topography of this region results in a series of *E. elderi* patches which vary in shape and size and are separated by distances of up to 10's of kilometres. *Erodiophyllum elderi* produces flowers which develop into hard woody capitula containing up to 130 seeds. Persistence mechanisms are investigated in terms of life history strategies and patchy population theory. Patchy population theory suggests that populations which are spread over space may have increased persistence if there is some degree of asynchrony between population fluctuations and if dispersal between populations occurs. *Erodiophyllum elderi* populations had highly synchronous dynamics due to similar environmental conditions over large areas. Results from this study indicate two persistence mechanisms operating on different time scales. Firstly, the seedhead allows within-patch, between generation persistence. Secondly, large dispersal events with infrequent deluges of rain may disperse seedheads between patches akin to the theoretical predictions of patchy population models. Such dispersal events which are only likely to occur every century or so, may enable temporally extinct populations to be recolonised. However, such effects remain purely speculative at this stage.



The vast open space,
the luring dunes,
striking red sand flows between my fingers.

Is that an eagle overhead?
We stop, we look, we listen, we smile,
we collect more data.

Brilliant splashes of red and purple,
and then nothing, but shimmering heat.
A diversity of life, a diversity of life herstory strategies.

A crack of thunder,
we crouch down low,
just
... in case.
We smell the sweet scent of things to come,
a deluge of rain.

where did the sailor come from?

My heart is filled with warmth,
when I remember,
all of these things...
and more.

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Contents

1. Introduction

Spatial heterogeneity is a feature of all natural ecosystems, and may be one of the most important factors influencing population dynamics (Kareiva 1990). Spatial heterogeneity can create a series of patches or 'local populations' when areas which are suitable for a species are surrounded by a matrix which is either less suitable or not suitable at all (Hanski and Gilpin 1991). Ecologists often study population growth and regulation without considering differences in the birth and death rates in different local populations (Pulliam 1988). Local populations are often considered to be independent of each other (although this is rarely stated explicitly) and a single local population is considered to be representative of all other populations. However, there is a growing body of theoretical research which suggests that differences between local population dynamics and dispersal between patches can be important for overall population persistence (eg. den Boer 1968; 1981; Hanski 1982; Hanski and Ranta 1983; Harrison and Quinn 1989; Chesson 1991; Hanski and Gilpin 1991; Hastings and Harrison 1994; Chesson 1998). Despite this, there is limited empirical research on the role of local populations on overall species persistence (Harrison 1991; Perry and González-Andújar 1993).

Most empirical studies of patchy populations (populations which inhabit a distinct series of patches) have focussed on animal populations rather than plants. This focus on animals is thought to be due to the emphasis of models on mobility and movement between patches (Perry and González-Andújar 1993) which make studying this aspect of animal populations more tractable. However, the patchy distribution of plant populations may be important for plant persistence. The empirical cases examined thus far are limited in number and are therefore not general (Harrison 1991). Clearly there is a need to examine patchy population theory for a wider range of species, in particular, we need to determine the relevance of models of patchy populations for plants. As the environment becomes increasingly fragmented, the importance of the patchy nature of populations becomes more relevant to our understanding of species persistence (eg. Menges 1991).

The purpose of this research is to examine the persistence mechanisms for the short-lived arid land daisy *Erodiophyllum elderi* and to determine the relevance of patchy population models for this species. In this chapter, I briefly outline advances in ecological thinking and ecological modelling with regard to patchily distributed populations. I then discuss mechanisms which produce heterogeneity for arid plant species, including variable resources and the effect of introduced herbivores. I then describe some adaptations of arid land species which allow them to exist in variable environments. Finally, I outline patchy population theory in the context of arid land ecology and provide an overview of my thesis.

1.1 THEORY OF PATCHY POPULATION PERSISTENCE

The fact that populations are heterogeneously distributed at some scale is one of the few certainties in ecology. However, it is generally less well known just how this patchiness affects population persistence either locally, or on a larger spatial scale. In some cases, a series of inhabitable areas (patches) are scattered throughout an otherwise uninhabitable area. Local populations which inhabit these patches may have different dynamics compared with the overall population (Strong 1986). If the populations inhabiting the series of patches are interconnected in some way, then this may increase species persistence (Hanski and Gilpin 1991).

The spatial limits of a population can be natural boundaries or artificial ones, set by the observer (Canny 1981; Wiegleb 1989). A *population* can be considered to be a collection of individuals of one species, either living in some specific area, or moving from area to area as a group. A *local population* is a group of individuals, within a population, distinguished in some way from the rest of the population (den Boer 1981; Hanski and Gilpin 1991). For sessile organisms, local populations inhabit a region called a *patch* and therefore, patches, or local populations, refer to specific localities. Individuals within a local population are much more likely to interact with each other through, for example, competition or reproduction, than with individuals from different local populations (Chesson 1998).

The term *metapopulation* is used to refer to a collection of local populations which are connected by dispersing individuals (Levins 1969; Hanski and Gilpin 1991). Most metapopulation models include the assumption that patches of suitable habitat occur as isolated areas (Hanski and Gilpin 1991). Local populations occupy a particular patch, and patches may or may not be physically connected. There is some degree of dispersal between local populations in a metapopulation.

1.1.1 Brief history of patchy population theory

Since the recognition of the importance of the spatial structure and the interconnectedness of populations in the pioneering work of Andrewartha and Birch (1954), there has been significant theoretical development of the ideas. Andrewartha and Birch argue that animal populations are not homogeneous in space and can consist of a number of partially independent local populations which are connected by immigration.

Although Island Biogeography theory (MacArthur and Wilson 1967) attempts to explain species diversity on a series of islands rather than single species population persistence, it also encompasses the idea of the interconnectedness of populations through dispersal. In mainland-island systems (a single species perspective of Island Biogeography), the mainland patch supplies propagules to islands of suitable habitat some distance from the mainland. In this system, the mainland patch is the only source of propagules and is never under threat of extinction. The rates of colonisation of the islands depend on the dispersal ability of the particular species and on the distance between the island and the mainland.

In a series of papers (Levins 1969; 1970; Levins and Culver 1971), the concept of a *metapopulation* is introduced and defined, and the first mathematical model of single-species metapopulation dynamics is constructed and explored. Metapopulation theory examines population persistence for a series of local populations without the necessity of a particular patch which remains immune from extinction, as is the case for the mainland patch in mainland-island systems. The overall persistence of these metapopulations can be increased through the recolonisation of temporally extinct patches by dispersal of propagules from neighbouring patches. The overall population essentially averages the local population dynamics over space and through time via dispersal between patches. The classic metapopulation framework has been extended and modified to examine mechanisms for the persistence of patchy populations (Hanski and Gilpin 1991; Harrison 1991; Perry and González-Andújar 1993; Day and Possingham 1995).

Because patchy population models focus on extinction and colonisation events, they can be difficult to apply to real populations (Harrison 1991). To make them more tractable, the focus can be shifted from extinction and colonisation events to simultaneous population fluctuations. If fluctuations in the size of local populations occur asynchronously, this can effectively 'spread the risk' over all local populations (den Boer 1981). Alternatively, if local population dynamics are synchronous, then local extinctions are also likely to occur simultaneously and therefore extinction events will be widespread.

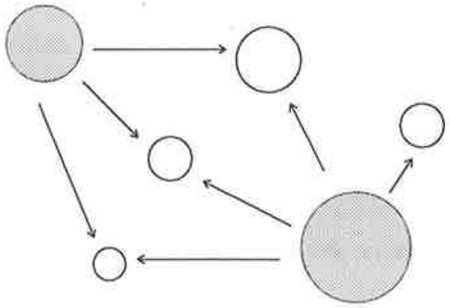
There are a range of possible frameworks for the persistence of patchily distributed species. These frameworks, or patchy population models, incorporate features from mainland-island systems and metapopulation theory. A description of the patchy population frameworks adapted from Harrison (1991) is given below.

1.1.2 Frameworks for patchy population persistence

1.1.2.1 Source-sink populations

Source-sink populations (Figure 1.1) assume two distinct types of populations: source populations and sink populations. Source populations are those which reproduce and contribute propagules to sink populations (Pulliam 1988). Sink populations, on the other hand, can not sustain themselves through time without the contribution of immigrants from source populations. The differences between source and sink areas may be due to a difference in habitat quality (Dias 1996). The local extinction of a subset of sink populations has little effect on the regional persistence of the species (Harrison 1991) because the sink populations have little influence on overall birth and death rates as they depend on source populations for propagules. The mainland-island system is a special case of the source-sink system, where there is a single source population (mainland) for the sink (island) populations.

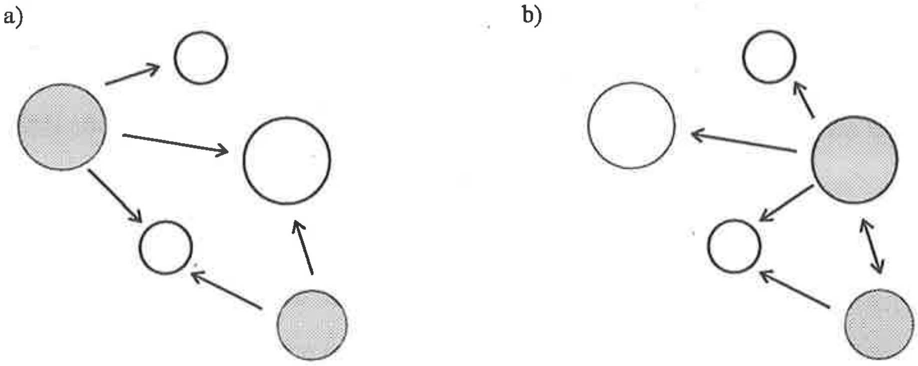
Figure 1.1: Example of a source-sink population where source patches (filled circles) provide propagules for sink patches (unfilled circles) through dispersal. Arrows indicate possible migration and subsequent colonisation through dispersal. Note that sink patches may be inhabited.



1.1.2.2 Classical metapopulations

In classical metapopulations (Figure 1.2), the population behaves like a source-sink model at any given time. The classic metapopulation framework differs from source-sink models because local populations can change between source and sink status (Figure 1.2 a and b). The overall metapopulation persists through a dynamic and regional balance between extinction and colonisation of local populations (Kareiva 1990; Harrison 1991).

Figure 1.2: Example of a classic metapopulation for time a and b. Source populations (shaded areas) do not necessarily remain source populations through time. Likewise for sink populations (unshaded area). Arrows indicate possible migration and subsequent colonisation through dispersal.

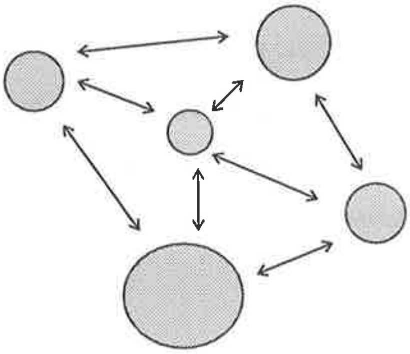


1.1.2.3 Patchy populations

Populations which are divided into discrete areas with frequent dispersal between patches are called 'patchy populations' (Figure 1.3). The high rates of dispersal between patches creates a single, highly interconnected population with no potential for either independent local population dynamics or local extinction (Harrison 1991). In this system there are no source and sink populations.

Although the term 'patchy population' is used to describe the above system by Harrison (1991), I use it to refer to the more generic case of populations which are divided into discrete patches unless explicitly stated.

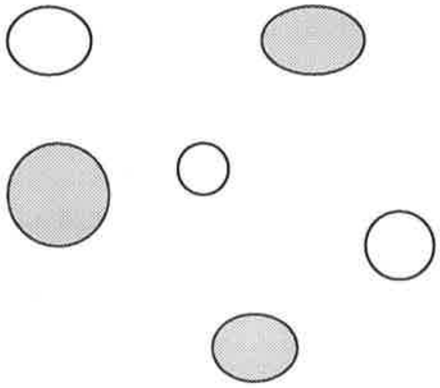
Figure 1.3: An example of a patchy population where dispersal between patches occurs frequently, and results in a lack of independence between populations. Arrows indicate migration and possible colonisation through dispersal.



1.1.2.4 Regionally declining populations

Regionally declining populations are a series of more-or-less independent populations. Although Harrison (1991) refers to these populations as non-equilibrium populations, this seems an overly specific definition. Regionally declining populations typically have local populations which are too isolated for migration between them to allow recolonisation. If these populations are not self-sustaining in the long term, regional decline must occur. Any dispersal occurring between local populations does not prevent extinction because of the overall decline of the population. These populations are therefore highly vulnerable to extinction because local populations can not be 'rescued' by propagules from neighbouring populations. Regionally declining populations are usually a product of the fragmentation or deterioration of a habitat (Harrison 1991).

Figure 1.4: Example of a regionally declining population where local populations are more-or-less independent. Local extinctions occur as part of an overall regional decline of the species. Shaded areas are occupied and unshaded areas are unoccupied patches.



1.1.3 Important parameters for persistent patchy populations

The two main factors which influence overall persistence of patchy populations are dispersal between patches and the degree of asynchrony in the temporal extinction of local populations. Classical metapopulation persistence depends on dispersal between populations which either rescues declining local populations or recolonises empty patches. For this to occur there must be some degree of asynchrony in local population fluctuations because if fluctuations were synchronous all populations are likely to become extinct simultaneously. In a similar way to classical metapopulations, source-sink systems require dispersal from source patches into sink patches. However, source-sink systems require a refuge source patch which is immune from extinction (Harrison 1991) rather than simply requiring asynchronous fluctuations. In contrast to both of the above systems, dispersal between populations occurs readily for 'patchy populations' in the sense of the term described by Harrison (1991).

1.2 THE PERSISTENCE OF REAL PATCHY POPULATIONS

There are few studies which have examined the persistence of real populations in the context of patchy population concepts. This is partly due to the difficulty of examining colonisation and extinction processes (Harrison 1991). However, the extension between synchronous populations dynamics and synchronous extinction events (den Boer 1968; 1981) allows us to examine a wide range of species in terms of patchy population theory by examining their long term population dynamics (Thomas 1991; Ranta *et al.* 1995). Species which have been examined in terms of patchy population theory are typically short-lived species with a high rate of population turn-over, including, butterflies (Thomas 1994), *Daphnia* (Hanski and Ranta 1983), moths and aphids (Hanski and Woiwood 1993) and a range of birds (Ranta *et al.* 1995). There is a paucity of data for patchily distributed plant species.

Furbish's lousewort (*Pedicularis furbishae*) is an example of a plant species which has been studied in a metapopulation framework (Menges 1990). Furbish's lousewort grows on river banks in northern Maine and relies heavily on dispersal of seeds along the river. Local population dynamics of *P. furbishae* are highly variable and patches have a high turnover rate. *P. furbishae* seeds have specific morphological characters which enhance dispersal, thus allowing colonisation of recently disturbed sites where competitors (inter-successional species) are temporarily extinct. Although there is some degree of asynchrony between populations, widespread catastrophic effects threaten Furbish's lousewort. Furthermore, the anthropogenic interference in the natural disturbance regime by changing the fluctuations of the river increase the threat to this species.

Collins and Glenn (1991) claim to show another example of colonisation and extinction dynamics in tallgrass prairies in north-eastern Kansas. Using eight years of data from 19 grassland communities, they examine species presence in terms of the core-satellite hypothesis described by Hanski (1982). They attribute the variable spatio-temporal dynamics to immigration and extinction events while failing to consider the role of the seed bank. Their failure to properly consider the seed bank means that what they term extinction and recolonisation may actually be seed dormancy and weather-dependent germination. Therefore, their study does little to further our understanding of patchy population theory for plant communities.

The studies conducted on real patchy populations, mainly animal populations, show that populations are not maintained by mutual recolonisation, but by the repeated immigration from a mainland or source population (Harrison 1991). However, Harrison (1991) stresses that the empirical results obtained thus far are by no means general, and argues the need to test patchy population theory for other species. The general lack of information for patchily distributed plant species begs further examination of this theory for plant persistence. Therefore, I have chosen to examine the relevance of patchy population theory for a short-lived arid land species which grows in distinct patches scattered throughout parts of southern Australia.

1.3 HETEROGENEITY OF ARID LAND SPECIES

Patchy plant distributions are characteristic of arid and semi-arid ecosystems (Tongway and Ludwig 1994) and this patchiness makes them ideal for examining patchy population theory. Many factors influence the patchy nature of plant distributions, and these factors often interact making it difficult to identify causality. Physical characteristics can create a patchy population structure, for example, soil type, soil moisture, and topographical features (Ludwig *et al.* 1994). Other factors, such as directed dispersal moving seeds to favourable sites (Howe and Smallwood 1982), the patchy nature of resource accumulation (Noy-Meir 1973; Friedman and Stein 1980) or the preferential survival of plants in particular areas (Osborn *et al.* 1932) also contribute to spatial heterogeneity.

Resource patchiness can result in the patchy distribution of plants because sites suitable for germination and growth are interspersed in areas which are generally inhospitable (Noy-Meir 1973; Ludwig *et al.* 1994; Tongway and Ludwig 1994). As well as broad scale patches of vegetation across a landscape, a variety of processes contribute to smaller scale heterogeneity within patches such as seed accumulation (Osborn *et al.* 1932) and soil moisture differences (Kemp 1989). Both broad and small scales of resource patchiness can have important consequences for population persistence through the stages of germination, growth and establishment. The redistribution of resources, in particular, water, in arid regions can influence the patchy nature of plant populations through time and space.

1.3.1 Water - an essential resource

Water is often considered to be the most important factor shaping vegetation patterns within an arid region. Plant growth in arid regions of the world is closely controlled by the spatial and temporal distributions of rainfall (Friedel *et al.* 1990). Not only does water influence biological interactions, including competition between individuals (Goldberg and Novoplansky 1997) and seed germination patterns (Went 1949), water also directs the dispersal of propagules (Gutterman 1994) and the movement of nutrients to low lying areas (Noy-Meir 1973; Ludwig *et al.* 1994). Water in arid regions is often a limited resource, and the ability of plants to utilise this resource influences their distribution and abundance. An important aspect of water as a resource in arid regions is the fact that rainfall is characteristically low and unpredictable.

Rainfall in Australian arid areas is particularly variable and unpredictable compared with other arid regions of the world (Friedel 1991). Roving storm cells and precipitation redistribution by run-on and run-off processes contribute further to the temporal and spatial variability of water availability (Friedel *et al.* 1993). Although most rainfall events are too small to stimulate an immediate response in plant growth (Stafford-Smith and Morton 1990), infrequent deluges of rain over a period of days can cause substantial changes in both the physical and biotic environment (Stafford-Smith and Morton 1990; Friedel *et al.* 1993). Large rainfall events affect vegetation well beyond the short term increase in soil moisture (Friedel 1991) by changing the structure of the landscape and redistributing soil, nutrients, water and seeds. Therefore, large rainfall events contribute to the patchy distribution of plant populations.

The distribution of plant populations is dynamic, and can change with the spatial and temporal water availability in any particular region. Pulses of plant production in the Australian arid regions are often separated by dry spells, during which, herbage is largely absent from the landscape due to its dependence on rain for germination and successful establishment. During wet years, patches of herbland vegetation expand and coalesce while in the long dry intervening times, they shrink and break up into smaller and smaller units (Morton 1990). Water limitation and rainfall variability necessitate plants to have a range of life history strategies that allow their persistence in arid regions. Vegetation is highly adapted to, and governed by, both climatic and edaphic factors (Stanley 1983).

1.3.2 Living in a harsh environment - adaptations of desert species

Despite many years with unfavourable growth periods due to low rainfall, many desert inhabiting species have stable long term population dynamics. Due to environmental fluctuations, and the fact that species requirements are not identical, different species are favoured at different times. Therefore, 'short term instabilities' in years when conditions are poor for a particular species allow the co-existence of many species through time (Chesson and Huntly 1989). However, to persist through extended periods of unfavourable conditions, species need to be able to store the benefits obtained during favourable years (Chesson and Huntly 1988). Therefore, risk-spreading life-history traits can provide a buffer against unfavourable conditions (Chesson and Huntly 1988).

The two extreme forms of plants which grow in arid regions are 'endurers' and 'avoiders', although most species lie somewhere between these extremes (Stafford-Smith and Morton 1990). Perennial plants (endurers) persist as individual plants and may require unusual conditions for germination and establishment (Friedel *et al.* 1990). Perennial species tend to average over environmental fluctuations through the longevity of plants, while the population dynamics of avoider species often reflect environmental fluctuations (Noble 1977; May 1981). In contrast, ephemeral plants (avoiders) are only present during favourable conditions. Typically, short-lived avoider species respond rapidly to rainfall and have a short life span culminating in reproduction immediately prior death. Short lived plants typically invest less in roots, grow fast, use nutrients quickly, but are not drought tolerant. Avoiders achieve long term persistence by escaping harsh conditions with a long-lived seed bank (Kemp 1989).

Whatever strategy is utilised, there needs to be a long-lived life-history stage which prevents population extinction during unfavourable conditions. The ability to persist throughout unfavourable periods by storing the benefits obtained during suitable periods is termed the 'storage effect' (Chesson and Huntly 1989). The long-lived stages of short-lived species (eg. seed banks or below ground storage organs) have the potential to buffer populations against the effects of unfavourable environmental fluctuations (Chesson and Huntly 1989; Pake and Venable 1995; 1996). Dispersal and dormancy mechanisms of short-lived arid land species provide them with a means of escape in space or time (Venable and Lawlor 1980).

1.3.2.1 Dormancy breaking requirements: ensuring suitable conditions

The seeds of many arid land species require specific dormancy breaking mechanisms that ensure that not all seeds germinate at the onset of rain. Breaking dormancy is a crucial stage in the life cycle of a plant because seeds have much higher resistance to extreme environmental conditions than seedlings (Gutterman 1994). Although the details are somewhat unclear, seeds respond to factors such as light intensity, light spectrum, day length, temperature, humidity and soil moisture (Went 1949; Ghersa *et al*. 1992; Baskin *et al*. 1993; Cox and Conran 1996). Philippi (1993 a & b) claim that specialised dormancy breaking requirements are a bet-hedging adaptation to fluctuating environments.

Seed dormancy can ensure that the timing of seed germination varies both within a species and within a plant (Westoby 1981) effectively spreading the risk of germination in case of widespread post germination failure. A range in germination timing may also reduce negative effects between sibling seedlings (Inouye 1980). Species which hold their seed bank in maternal structures, such as seed pods or capsules, also have seed release patterns which prevent all seeds germinating concurrently (Gutterman 1972).

1.3.2.2 Dispersal strategies: ensuring a suitable residence

Dispersal is important for the transportation or restricted movement of seeds to sites suitable for germination and contributes to species patchiness. For example, *Antastica hierochuntia* - the True Rose of Jericho, an annual species from the Negev desert, has evolved mechanisms to enhance both short and long distance dispersal (Friedman and Stein 1980). Short distance dispersal is achieved via the release of *A. hierochuntia* seeds from the skeletons of dead plants during rainfall events. These seeds anchor to the ground after detachment near the adults plants, in an area which was clearly suitable for parental success. Long distance dispersal is also mediated by water, although it only occurs with large rainfall events which result in sufficient sheet water flow to carry seeds down to low lying areas (Friedman and Stein 1980). Consequently, these seeds are transported to areas which are likely to receive sufficient water for germination and establishment. In addition, the seeds are only released from the seed holding structures when conditions are favourable for germination.

Seeds display a range of morphological characters such as plumes, wings and thorns to utilise different dispersal vectors including water, wind and animals (Gutterman 1994). Most seeds of desert inhabiting species do not have characters enhancing long distance dispersal (Ellner and Shmida 1981). This may be due to the overwhelming advantages associated with remaining in the vicinity of a site which was suitable for the parent plants (or at least the mother) or alternatively, to the disadvantages of long distance dispersal. The first of these possibilities, termed the mother-site theory, is common for species inhabiting Israeli deserts, but is less common for central Australian species (Jurado *et al.* 1991). This may reflect a lower degree of small scale spatial heterogeneity in Australian arid regions than in Israeli deserts. If this is true, directed dispersal or restricted dispersal may not be as important in Australian systems.

1.3.3 Alien herbivores - heterogeneity modifying forces

The introduction of sheep into the Australian arid lands has had a profound influence on the vegetation and the natural patchiness of vegetation. Two sources of habitat variability exist: patterns arising from natural habitat variability and the overlying effect of disturbance which includes the effects of grazing (McIntyre and Lavorel 1994). Although disturbance is an important and widespread phenomena in nature (Pickett and White 1985), introduced disturbance forces such as herbivores may have detrimental effects on native flora and fauna. Sheep were introduced to large areas when the land was taken up by pastoral lease. In the north east of South Australia this occurred in the 1860's (Hall *et al.* 1964). Due to poor management practices of the time, introduced herbivores profoundly affected the vegetation (Osborn *et al.* 1932; Hall *et al.* 1964; Lange 1985). Overgrazing has resulted in the widespread degeneration of plant cover and a resulting loss in soil stability (Jessup 1948) both of which influence vegetation establishment, growth and seed dispersal patterns.

Through differential grazing effects and the natural variability in plant distributions, grazing can both increase species patchiness and decrease species patchiness depending on the scale examined. The effects of grazing are likely to differ throughout a paddock according to the proximity of watering points (Lange 1969; Lange 1985), the establishment of fences which restrict sheep movement, and the preferential grazing behaviour of sheep (Hall *et al.* 1964). Alien herbivores tend to concentrate in areas of high productivity and these are often completely grazed out (Hall *et al.* 1964; Morton 1990; Friedel 1991; Scoones 1995). Although this is unlikely to be important during years of good rainfall when vegetation is widespread, it may have dramatic effects at other times by reducing areas of high productivity for these herb species. Pastoral use often results in a reduction in plant cover, accelerated erosion and an increase in effective aridity (Stanley 1983). The effects of grazing on native Australian vegetation is exacerbated by droughts and rainfall irregularity (Morton 1990).

1.4 MERGING PATCHY POPULATION THEORY WITH ARID LAND ECOLOGY

Given the patchiness of many arid land species and the large body of theoretical research devoted to questions relating to the role of patchiness, it is important to ask whether arid land species persist through any of the mechanisms described in the first half of this chapter. Although not framed in the context of metapopulation theory, Morton (1990) describes a scenario for medium sized mammalian persistence through metapopulation processes, and the contribution of grazing to population decline. In this scenario medium sized mammals in the Australian arid lands moved between patches of vegetation searching for suitable forage. As with kangaroo populations, the medium sized mammal populations fluctuated with environmental conditions (Adamson and Fox 1982) resulting in temporal extinction from poor conditions. When conditions became favourable again, populations were re-established from extant neighbouring populations. The combination of the reduced available forage because of the grazing pressure from introduced herbivores, the pressure of introduced predators and drought conditions increased probabilities of local population disappearance (Morton 1990). Consequently, competition for forage between introduced herbivores and native fauna occurred to the detriment of the medium sized mammals.

The continued modification of the environment through sheep grazing has influenced the native Australian vegetation and, in some cases, has resulted in a decline in plant seed banks and species habitat range (Lange and Purdie 1976; Lange 1985; Landsberg *et al.* 1997). In fact, Lange (1985) claims that over 60 rare or endangered endemic flora are found in remnant vegetation patches within pastoral lands. The mechanism for persistence of these species is unknown, but may be through metapopulation processes.

In a model of an annual plant species in a harsh environment Perry and González-Andújar (1993) examined metapopulation process with varying levels of spatial and temporal heterogeneity and a range of dispersal abilities. They found that temporal heterogeneity had an adverse effect on species persistence when added to existing spatial heterogeneity, with the degree of this effect depending on the dispersal ability of the species. Strongly dispersing species were only slightly affected while those with no or moderate dispersal became extinct. This has broad implications for patchily distributed short-lived arid land plants. In an area which is highly spatially heterogeneous, and has temporal variability due to fluctuating rainfall, the ability to disperse between patches may have dramatic consequences on population persistence.

The implications of patchy population theory are greater than just issues of population persistence. Reserve design and conservation strategies can be greatly affected by patchy population structure (Harrison 1991). For example, the prominence of source-sink systems may have important consequences when choosing areas, or size of areas, to reserve. Investigators could easily be misled about the habitat requirements of a species if they happen to examine a sink patch instead of a source patch (Pulliam 1988; Dias 1996). As there have been calls to establish a reserve system which excludes grazing from areas of Australia's arid regions (Stafford-Smith and Morton 1990, Landsberg *et al.* 1997; Tiver and Andrew 1997), patchy population theory has direct application. We need to determine the extent to which populations depend on continued immigration for species persistence (as is the case for sink populations, Pulliam 1988), the degree that they depend on the exchange of populations allowing extinction and colonisation dynamics to occur, or alternatively, develop other, more relevant theories for patchy population persistence. In these latter scenarios migration between populations is essential to all local populations and not just the sink populations.

1.5 OBJECTIVES AND OVERVIEW OF RESEARCH

The aim of this research is to examine the persistence mechanisms of the short-lived arid land daisy *Erodiophyllum elderi* - The Koonamore Daisy. *Erodiophyllum elderi* grows in water courses and low lying areas in a series of distinct patches which vary in size and are separated by a range of distances. The main questions I ask are: Does *E. elderi* achieve population persistence through one of the frameworks outlined in this chapter? If not, then how does *E. elderi* achieve long term persistence? Through a series of experiments and surveys, I examine some of the parameters which are important for models developed for species with patchy distributions, namely population asynchrony and dispersal between patches. I also examine how introduced herbivores affect the population dynamics and persistence of *E. elderi*.

I examine soil characteristics and topographical features of the patches to determine whether populations are restricted to these areas due to the physical environment (chapter 2). If not, it is possible that the *E. elderi* distribution is limited by other processes such as dispersal or resource availability. Because grazing may result in widespread synchronised local extinctions, I examine the effect of grazing on the population dynamics of *E. elderi* in chapter 3. Specifically, I ask: How are *E. elderi* populations affected by grazing pressure?

I determine the degree of synchrony between a series of local populations by examining the long term *E. elderi* population dynamics in seventy years of photographic records (chapter 4). Specifically, I question whether population fluctuations are synchronous over a long period of time. If populations are synchronous, is this through dispersal between patches, or through other factors which influence *E. elderi* population dynamics, such as widespread environmental conditions or within population competitive interactions?

To determine whether dispersal contributes to synchrony of *E. elderi* populations, I examine the dispersal of *E. elderi* propagules (chapter 5). Ultimately I question whether propagules are likely to disperse between populations of *E. elderi*. If propagules disperse between patches, then does this increase metapopulation persistence? Alternatively, if propagules do not disperse between patches, do other mechanisms allow long term population persistence?

I examine the seed bank of *E. elderi*. to determine its role for within patch population persistence (chapter 6). Specifically, I ask: How important is the seed bank for long term persistence of local populations? What effect does storing seeds in maternal structures have on seed viability and germination rates? I also question the assumption of a constant germination fraction of seeds for annual species and develop a simulation model for *E. elderi* considering alternative seed release curves which are more appropriate for this species.

I investigate processes involved in seedling establishment in chapter 7. I consider whether the interactions between *E. elderi* seedlings and mature plants are facilitative or competitive. I consider the distribution of seeds and the effects of this distribution on seedling distributions. I also examine whether there is a seed-seedling site suitability conflict.

In the final chapter I integrate the results from my experiments and simulation model in terms of the theory of patchy populations and describe mechanisms for long term *E. elderi* persistence.

2. Field site and study species description

2.1 INTRODUCTION

A suite of underlying factors and processes influence the spatial arrangement of populations in arid regions. Abiotic factors include topography, soil type, water and nutrient availability (Reader and Buck 1986; Pantastico-Caldas and Venable 1993; Chambers and MacMahon 1994). Biotic factors such as competition (Friedman *et al.* 1977; Fowler 1986), facilitation (Friedman and Orshan 1975) and herbivory (Osborn *et al.* 1932; Bergelson 1990) also influence the ability of a plant to germinate, grow and reproduce. The combined effects of abiotic and biotic factors on plant distributions result in complex patterns that are often difficult to interpret.

In this chapter, I describe *Erodiophyllum elderi* (the Koonamore Daisy) and the Koonamore Station field site and examine factors that may influence the patchiness of the distribution of this species. I examine characteristics of patches where local populations of *Erodiophyllum elderi* inhabit to determine causative factors for *E. elderi* distribution. A number of variables were measured both in areas where *E. elderi* grow and in adjacent areas to determine whether physical features of patches are associated with the distribution of *E. elderi*. Specifically I ask: What is the topography of the patches? How is this topography likely to influence the spatial pattern of *E. elderi*? Are there differences in soil characteristics or the readily germinable seed bank inside patches compared to outside patches? Is there a difference in *E. elderi* seedling growth in soil collected inside a patch compared with outside a patch? How are soil characteristics, the readily germinable seed bank and seedling growth affected by sheep grazing pressure?

2.2 SPECIES DESCRIPTION

The Koonamore daisy (*Erodiophyllum elderi* F. Muell.) is a composite that generally flowers between April and November (Black 1986; Figure 2.1). The flowers develop into a woody capitula or seedhead, which contains many seeds held in by hard spiny bracts (a maximum of 136 seeds per seedhead recorded). *E. elderi* is a short-lived perennial plant displaying a typically opportunistic nature. Plants lose foliage during unfavourable conditions and, in some cases, re-sprout from the base when conditions become more favourable (Cunningham *et al.* 1992). The tendency of plants to re-sprout is poorly known as there have been no detailed studies of *E. elderi*. Although *E. elderi* is often locally abundant following years of good rainfall (Carrodus *et al.* 1965), at other times the plants are absent from the landscape. *E. elderi* was recently listed as an endangered species in New South Wales (Webb 1995).

Erodiophyllum elderi is restricted to floodplains and sandy or calcareous soils (Bindyeye soils) (Jessop 1981; Black 1986; Cunningham *et al.* 1992) and is primarily found on Quaternary alluvial deposits (Carrodus *et al.* 1965). After periodic flooding it often forms a dominant component of the ephemeral herbland communities (Carrodus *et al.* 1965; Cunningham *et al.* 1992). *E. elderi* is essentially a plant of flooded flats because the woody seedhead dispersal is well suited to flood waters (Osborn *et al.* 1935). The topography of the Koonamore region creates a series of low lying areas which are inhabited by *E. elderi*. Consequently, *E. elderi* inhabits a series of discrete patches which vary in size and shape and are separated by a range of distances which make it suitable for metapopulation studies.

There is a discrepancy in the literature about the distribution of *E. elderi*. While Cunningham *et al.* (1992) and Jessop (1981) suggest that the distribution is limited to the north-east of South Australia, Black (1986) claims it to be widespread, stretching from New South Wales through the Murray and Flinders regions, across the Eyre Peninsula and the Nullarbor, into Western Australia. There are two species in this genus and they are both endemic to Australia. The other species *E. anthocephalum* is restricted to a small region in Western Australia of similar latitude to *E. elderi*.

Very little is known about the basic biology of *E. elderi* and virtually nothing is known about its life history strategies. Apart from the establishment of a permanent quadrat investigating the reinvasion of perennials into an *E. elderi* population in 1925, no other studies of this species are known. Unfortunately readings on this quadrat were discontinued in 1931, and no conclusions were drawn about the extent to which perennials re-invaded the quadrat, if at all.

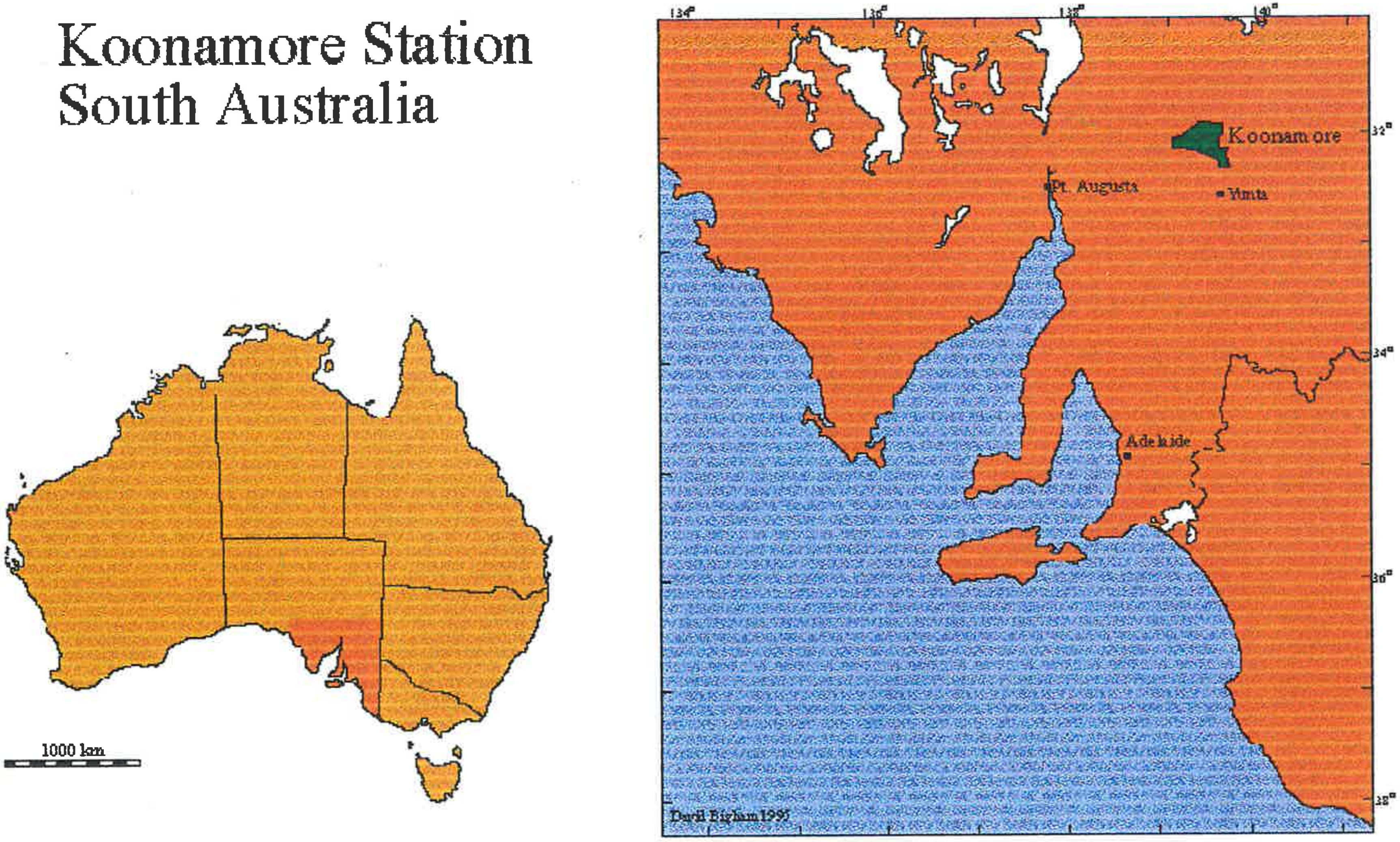
Figure 2.1: Diagram of *E. elderi* components, adapted from Black (1986). Flowering branch, hardened receptacular scale (bract), fruiting capitulum (seedhead), ray floret, bisexual disk floret, female disk floret, achene in vertical section.

2.3 SITE DESCRIPTION

2.3.1 Koonamore Station: vegetation, topography and soil

Koonamore Station (32°07'S, 139°22'E, altitude 200m) is located in the north-east of South Australia and is situated on a plain sloping gently towards Lake Frome (Figure 2.2). There are a series of three low hills on the station, namely Koonamore, Orama and Oopina which occasionally have steep rocky ridges. Between the hills, ridges of wind-blown sand lie across gently undulating plains of deep alluvial deposits (Carrodus *et al.* 1965). Koonamore Station is typically characterised by a gentle undulating topography (Jessup 1948).

Figure 2.2: Location map showing Koonamore Station in relation to Adelaide, South Australia and Australia.



There are many watercourses throughout Koonamore Station which only contain water immediately after heavy rainfall. Two major salt "lakes" or "pans" that rarely hold any water lie at the lowest sites of the property. The often well defined drainage channels fan out onto flood plains which reform again into channels further down the gradient before running onto one of the two major salt lakes (Carrodus *et al.* 1965).

The most common vegetation on the station is the shrub steppe described in Carrodus *et al.* (1965). This vegetation type is dominated by low shrubs usually 0.5 - 1 m tall, with semi-succulent leaves. These shrubs are usually separated from one another by a distance equal to, or greater than, the diameter of the plants. Ephemeral species throughout this region are often prominent after rains (Osborn *et al.* 1932; Wood 1958; Carrodus *et al.* 1965; Noble 1977) and there are many areas with tree species. For a detailed description of the vegetation of the area see Carrodus *et al.* (1965).

2.3.2 Rainfall and temperature

Although Koonamore homestead is a recognised Bureau of Meteorology weather station, the daily temperature is not recorded. Instead I present daily temperature from Yunta, the nearest Bureau of Meteorology site to Koonamore (32°35′S, 139°33′E, approximately 60 km S of Koonamore; Figure 2.2). Yunta temperature data was collected over a period of 29 years (1961-1990) while the rainfall records span 102 years (1888-1990). Statistics for the Yunta data are calculated from data extracted from the National Climate Centre from the Bureau of Meteorology. Temperature and rainfall are recorded for the 24 hours following 0900 hours for each day, a rain day has rainfall which exceeds 0.2 mm. Daily Koonamore rainfall data for 70 years (1923-1993) was obtained from the Bureau of Meteorology. Average monthly rainfall for Koonamore Station and the number of rain days per month were calculated for months which had complete records of daily observations.

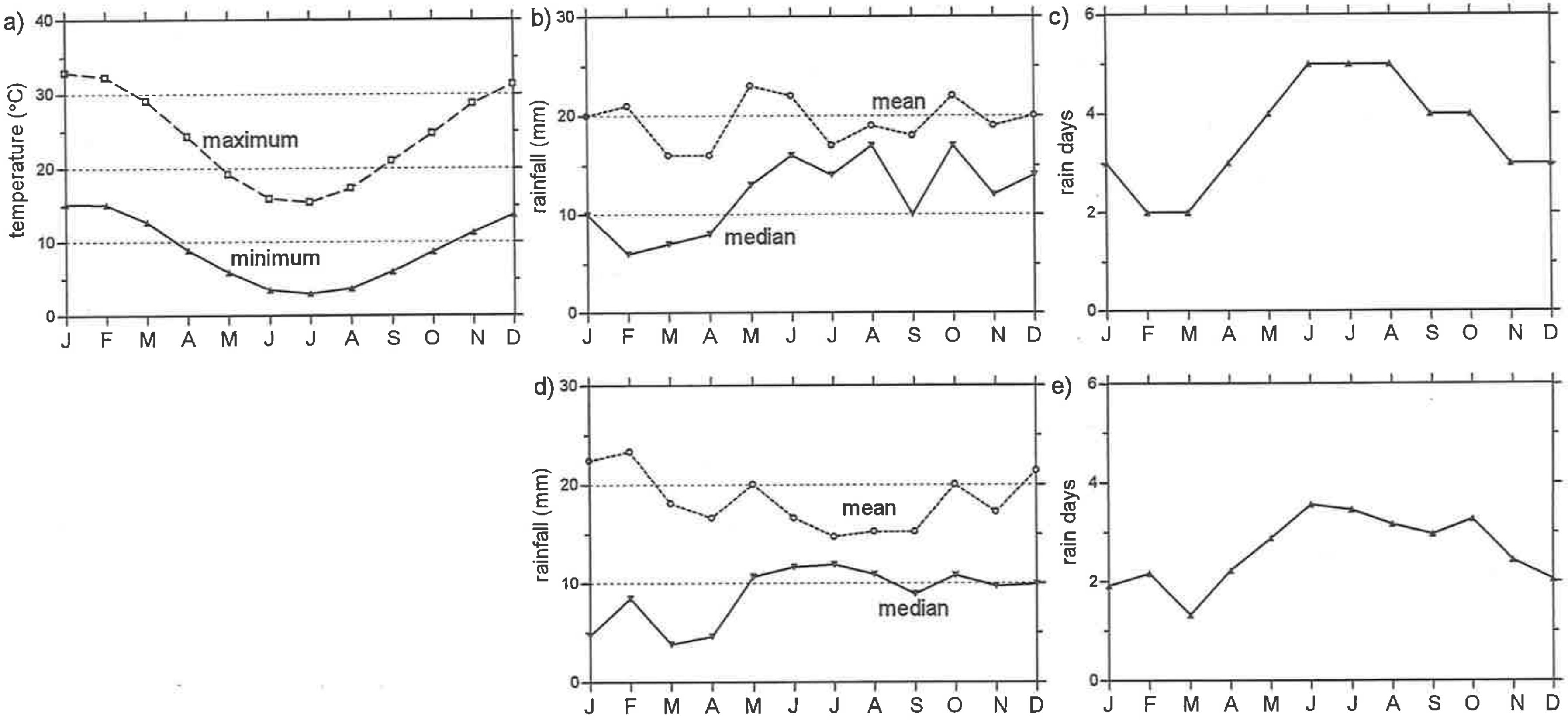
Yunta's average daily maximum and minimum temperatures show a strong seasonal trend with a peak during the summer months and a dip during the winter months (Figure 2.3 a). There was no seasonality for the average monthly rainfall for either Yunta or Koonamore (Figure 2.3 b & d) although the median values show a slight dip during the summer months. The lack of seasonality in the rainfall has been attributed to the area receiving falls from the fringes of the southern depression systems in winter, and the northern monsoon systems in the summer (Carrodus *et al.* 1965). This weather pattern tends to make the distribution of rainfall from local thunderstorms uneven. Koonamore has an average annual rainfall of 215.2 ± 14.60 mm (mean ± SEM based on 70 years of annual rainfall data). The number of rain days for Yunta and Koonamore is highest during the winter months June-August (Figure 2.3 c & e) with a lower number of monthly rain days during the summer months.

2.3.3 Koonamore Vegetation Reserve

The T.G.B. Osborn Vegetation Reserve (formerly the Koonamore Vegetation Reserve - henceforth I refer to it as the Reserve) was established in 1925 on Koonamore station by the University of Adelaide. An area of 390 hectares was fenced with rabbit- and sheep-proof fence at a time when the area had been severely overgrazed (Osborn 1925). At the time of fencing, virtually all of the original *Atriplex vesicaria* (bladder saltbush) bushes had been destroyed (Hall *et al.* 1964). Although the immediate removal of sheep occurred after fencing, the removal of rabbits did not really begin until the early 1970's when intensive rabbit eradication programs began (R. Sinclair, personal communication). At the time of fencing, a series of photo-points, permanent quadrats, and transects were established to monitor the recovery of the vegetation following the removal of sheep (Osborn 1925). Most of the readings in these quadrats focussed on species which are known to be important sheep fodder.

The Reserve and its surrounds are typically chenopod shrubland although there are areas with canopy species. The most common species for each of the life-forms are: trees - *Eucalyptus oleosa, Casuarina cristata, Myoporum platycarpum, Alectryon oleifolium, Acacia aneura, Santalum acuminata;* tall shrubs - *Eremophilla longifolia, E. sturtii, E. scoparia, Dodonea attenuata, Acacia burkittii, Senna spp.*; and low shrubs - *Atriplex vesicaria, A. stipitata* and *Maireana sedifolia* (Hall *et al.* 1964). Scattered amongst these areas are the ephemeral-herbland regions which display a wealth of diversity during the cooler winter months.

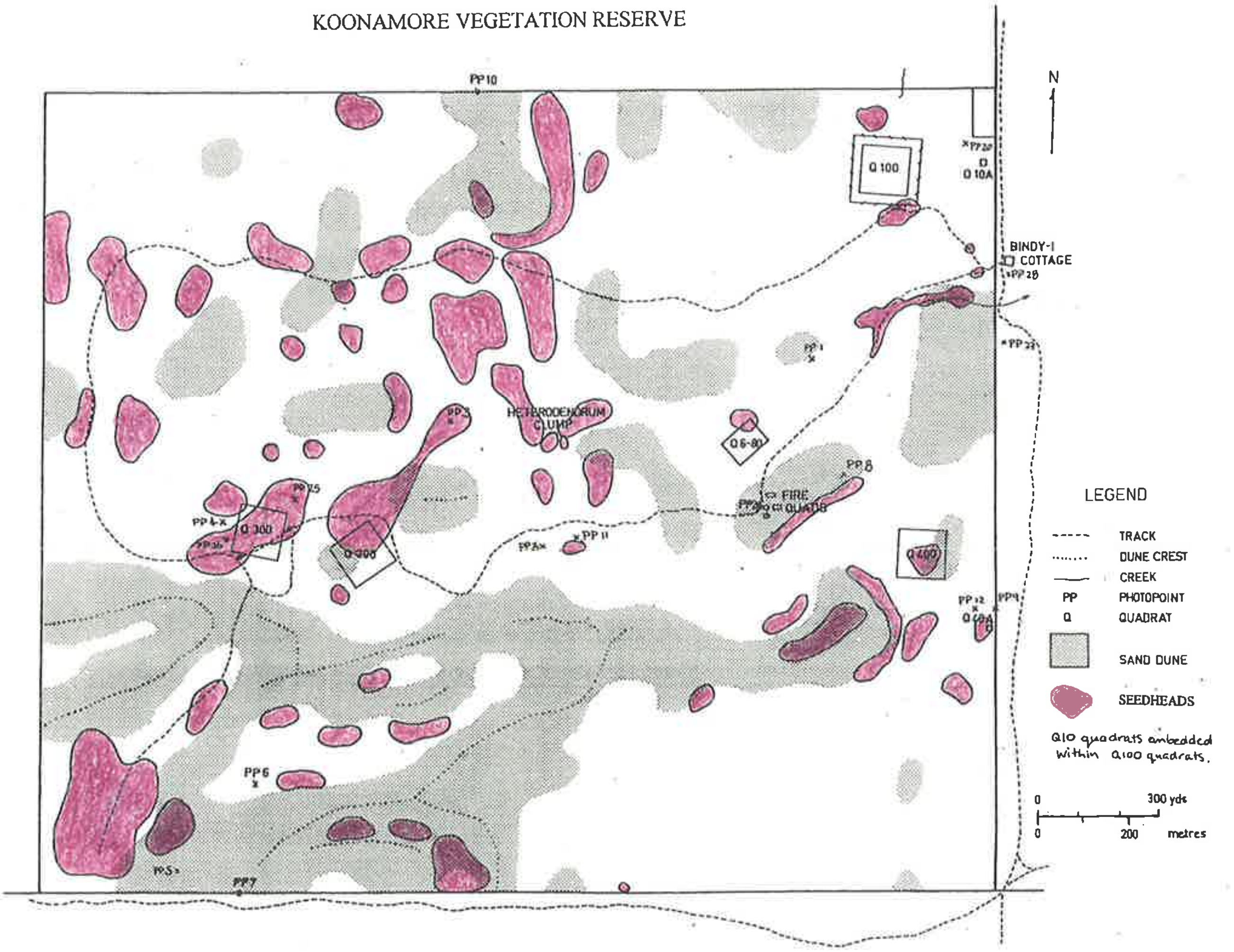
Figure 2.3: Data for Yunta Bureau of Meteorology station (32°35′S, 139°33′E), a) average daily maximum and minimum temperatures per month, b) rainfall per month, c) number of rain days per month, and Koonamore data for d) rainfall per month, e) number of rain days.



2.3.4 The distribution of *E. elderi* in Koonamore Vegetation Reserve

The entire Reserve was traversed along transects 15 - 20 m apart and the distribution of *E. elderi* seedheads were noted in December 1996. Seedhead distributions were mapped instead of plants as there were few living plants present at that time. This figure also shows the permanent photo-points, quadrats, transects and sand dunes in the Reserve (Figure 2.4).

Figure 2.4: Map of Koonamore Vegetation Reserve showing *E. elderi* seedhead distribution in December 1996. Also included are the permanent photo-points, quadrats, transects and sand dunes.



2.4 SITE DESCRIPTION

To examine *Erodiophyllum elderi* populations in a range of grazing pressures, six populations were chosen for investigation across Koonamore Station (Figure 2.5). Two populations were chosen in each of the three sheep grazing pressures: high grazing, intermediate grazing and low grazing (inside the Reserve). There are no sheep inside the reserve, virtually no rabbits but possibly an increased kangaroo population. Across this station, sheep tend to graze preferentially into southerly and south-westerly winds which prevail during summer months. This grazing behaviour results in the southern portion of paddocks, where the heavily grazed populations are situated, to be eaten out and trampled to a considerable degree (Hall *et al.* 1964). A central location post was positioned and a photo-point established in each of the six patches. These patches are examined in later chapters in this thesis.

High grazing pressure:

Patch 2 (Plate 2.1 a) is on the southern fence line of a heavily grazed part of South Lake Paddock. This patch is a low-lying basin surrounded by a *Maireana sedifolia* (bluebush) community and is often bare. Sheep graze heavily in this area as they move towards Southern Cross bore or smell water in Fife's dam across the fence in Koonamore Cross Paddock (L. MacLachlan, personal communication).

Patch 7 (Plate 2.1 b) is in Mustering Paddock 3 which is used as a holding paddock during shearing season. Once more the region of focus for this study was a patch growing along a southern fence line. Patch 7 is part of an extended patch which meanders along a watercourse towards Patch 6. This patch is bounded by sand dunes except on the southern side where a bluebush community exists on clayish soils. Sand dunes are also present on the southern side of the bluebush community.

Intermediate grazing pressure:

Patch 6 (Plate 2.1 c) is west of Patch 7, but on the other side of the fence in the northern section of Finn's Paddock. Hence the grazing pressure is less than in the heavily grazed patches, although sheep graze this area during times with northerly winds. This population grows in a large basin with a stand of *Eremophilla longifolia* growing toward the centre. The northern side of Patch 6 is bounded by a fence line with very few *E. elderi* on the other side. The area adjacent the fence on the northern side is infested with the introduced species *Marrubium vulgare* (horehound), which in turn is bounded by sand dunes on the northern, eastern and western sides. The southern side of this patch is bounded by the same bluebush community that borders Patch 7.

Patch 8 (Plate 2.1 d) is in Milang Cross Paddock (13 km from Bindy-i Research Centre) and is the most westerly patch studied. The population appears to follow a major drainage line and is the most extensive of the six patches studied. Within this patch there is a small clump of *Alectryon oleifolium* (bullock bush). The *E. elderi* patch is bounded by *Nitraria billardieri* and *Atriplex vesicaria* communities.

Low grazing pressure:

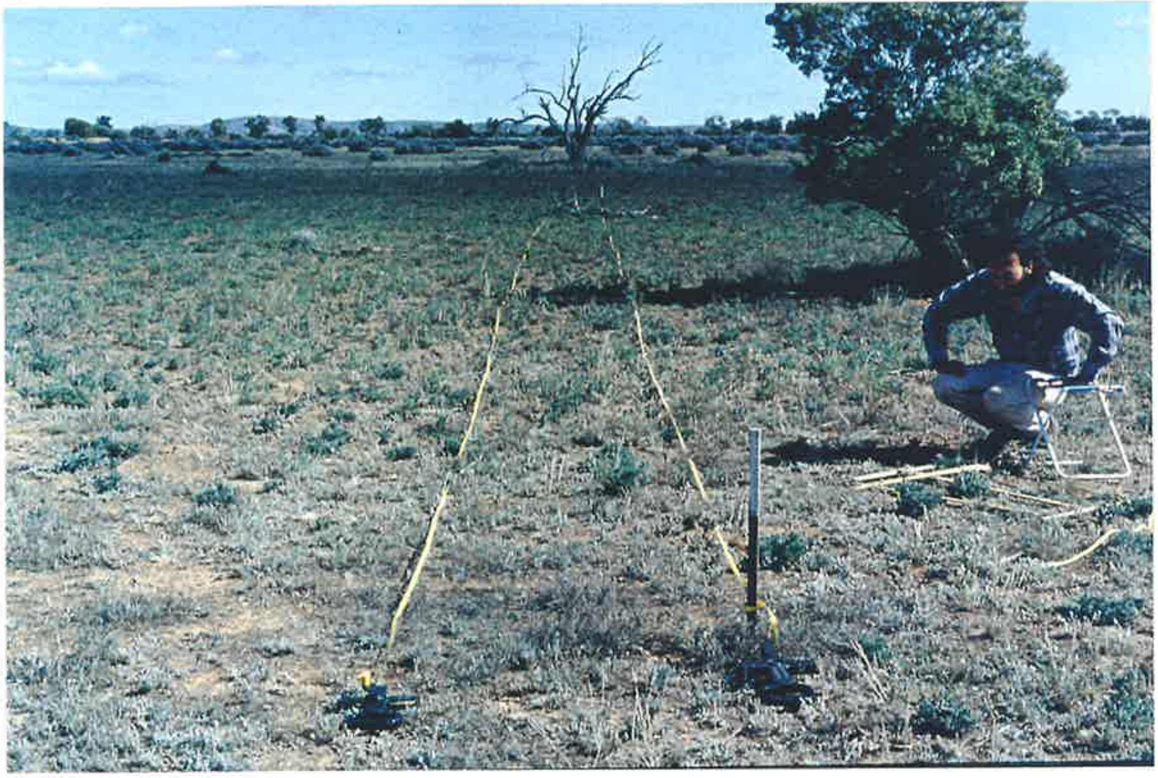
Patch 9 (Plate 2.1 e) is part of Q300, a permanent quadrat in the Reserve which is situated toward the western end in a low-lying region. This patch is bounded on the northern and southern sides by sand dunes, and a bluebush and saltbush community on the other sides. *Eremophilla longifolia* plants are scattered throughout the patch.

Patch 10 (Plate 2.1 f) is on the eastern side of the Reserve meandering along a watercourse. The area is sandy and is bounded by sand dunes in all directions except the southern, where a saltbush community grows. There are a few scattered *Myoporum platycarpum* trees within the *E. elderi* population. There is a well defined creek bed running from the easterly side of the patch although it rarely holds water.

Plate 2.1: Photos of the six *E. elderi* populations in November 1993.

High grazing pressure

a) Patch 2



b) Patch 7

Intermediate grazing pressure

c) Patch 6

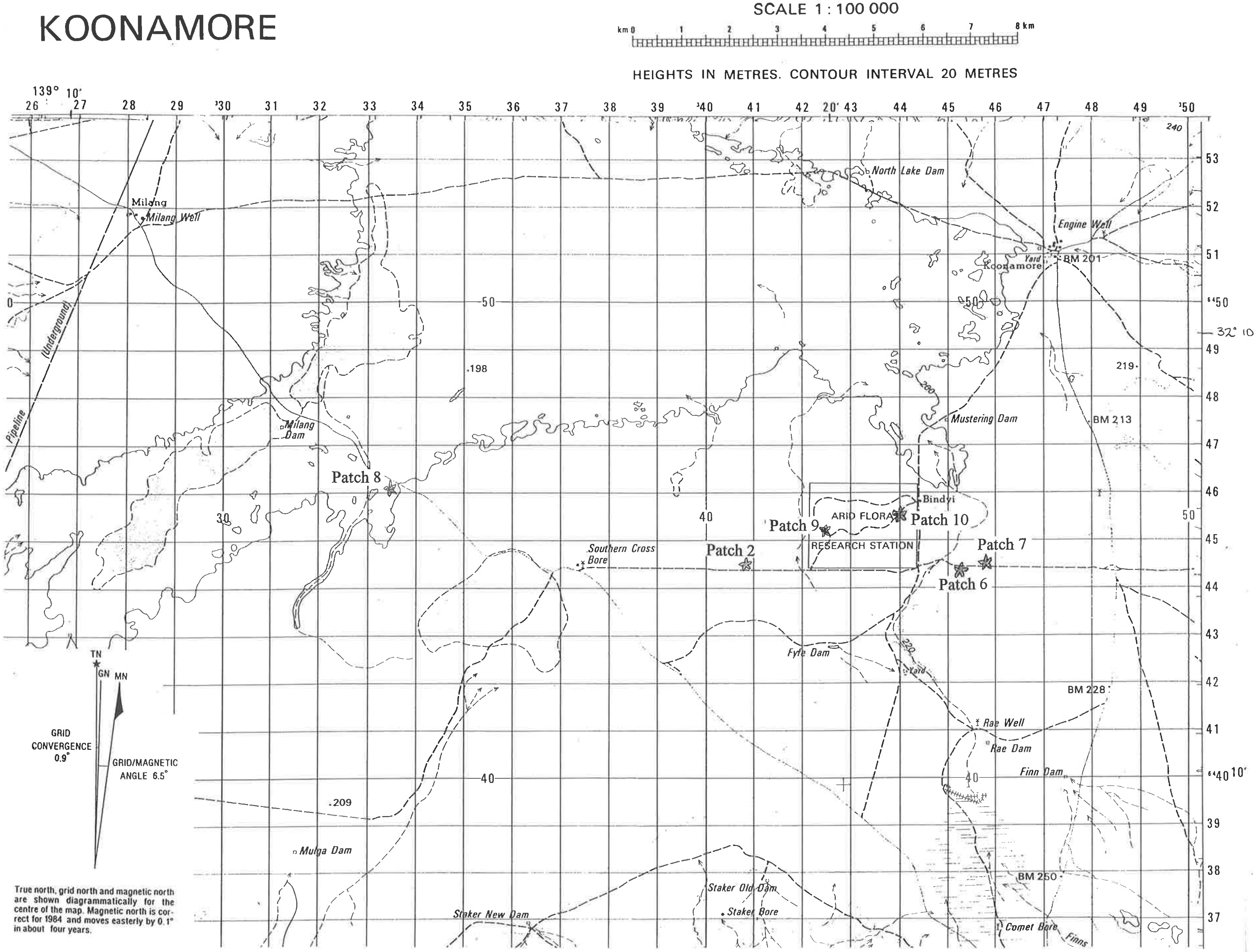
d) Patch 8

Low grazing pressure

e) Patch 9

f) Patch 10

Figure 2.5: Field site location map showing each of the six *E. elderi* populations across Koonamore Station, South Australia.



SHEET 6733 EDITION 1 NATIONAL TOPOGRAPHIC MAP SERIES

2.5 METHODS AND ANALYSES

2.5.1 Topographical details

Topographical gradients were measured along six transects for each patch described in section 2.3 to determine the topography of the patches. Radial transects were equally spaced centred on each location post, with the initial transect selected in a random direction in October 1994. Transects either extended from the location post to at least 15 m beyond the edge of the patch or reached 100 m and were well within the patch. The edge of the patch was considered to be a point with no living or dead *E. elderi* within a 3 m radius from the transect. Topographical measurements were made every 5 m along the transects.

Contour maps were created for each patch with the program Origin (Origin 1995). Points between topographical measurements along the transects were interpolated using the inbuilt kriging method. Patch edges and transect lines are marked on the contour plots.

2.5.2 Soil characteristics

To determine whether there was any difference between soil from inside and outside each of the six patches, *in situ* soil measurements were made. Soil from every 10 cm along a 1 m deep soil core inside and outside each patch was collected using a 10 cm diameter auger in March 1996. Soil texture, colour, pH and the presence of $CaCO_3$ was recorded. Texture was determined from the method of Northcote (1979), colour using the Munsell Soil Colour Chart (anonymous 1954), pH using a CSIRO laboratories field pH test kit and the presence of $CaCO_3$ by the reaction to 0.1N HCl where the presence of CO_3 leads to a reaction where gaseous $C0_2$ is visible.

2.5.3 Soil seed bank studies

Soil was collected to determine whether there was a difference in the readily germinable seed bank (RGSB) inside and outside each patch. Six 20x10 cm and 3 cm deep soil samples were collected from both inside and outside each patch in March 1993. The sample depth was chosen to represent the RGSB, as seeds in arid lands are normally stored within the top 2-3 cm of soil (Loria and Noy-Meir 1979/80;

Gutterman 1994). The inside patch samples were collected adjacent *E. elderi* plants for consistency. Six hundred grams of soil was weighed and placed in individual trays on the glasshouse bench and watered when necessary. All emerging seedlings were identified, recorded, and removed. The study was completed after two months which was two weeks after final seedling emergence. Data were analysed with MANOVA by species and position (inside or outside the patches).

2.5.4 Seedling germination

I conducted an experiment to determine whether the presence of *E. elderi* in the patches was restricted by either germination, survival of seedlings, or both. *E. elderi* seeds were planted 1 cm below the surface of the soil in five 40x40 cm quadrats inside and outside each patch on 5-Mar-1994 (germination occurs largely in the cooler winter months). Two seeds were planted per hole, with each 40x40cm quadrat having 10 holes and a total of 20 seeds. Seeding plots were monitored for seedling emergence every three months for the following year.

2.5.5 Growth of *E. elderi* seedlings in the glasshouse

To determine if there were differences in the growth of *E. elderi* seedlings in soil collected from inside and outside four patches I conducted a growth performance experiment. Soil was collected from four random quadrats (20x20 cm and 5 cm deep) inside and outside Patches 2 and 7 (high grazing - outside the Reserve), and Patches 9 and 10 (low grazing - inside the Reserve) on 20-Feb-1996. The soil was placed in pots and five *E. elderi* seeds were placed on the soil in each pot. Additional seedlings were germinated under identical conditions in petri dishes and transplanted to maintain a constant number of five seedlings per pot. All pots were watered equal volumes when necessary to ensure that water did not limit growth and that growth differences could not be attributed to different water regimes. The plants were harvested at the end of three months on 28-May-1996 before competitive effects became evident, and the above ground dry weight biomass was recorded for each pot. Data were tested for normality and homogeneity of variances. A two-way ANOVA was performed with patch and position (inside or outside) as factors followed by a Tukey post-hoc test.

2.6 RESULTS

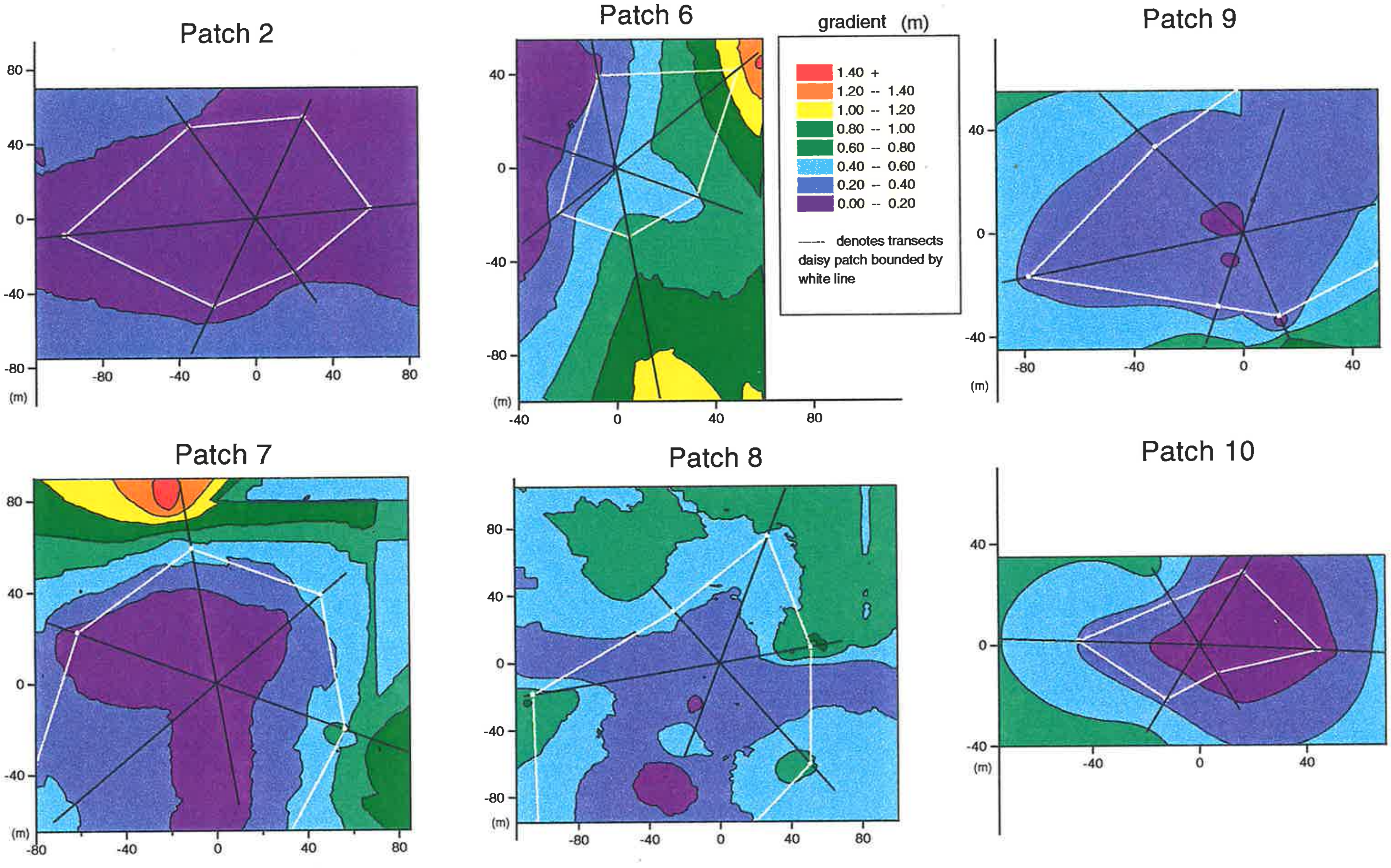
2.6.1 Topographical details

Topographical measurements indicate that the patches examined are all local depressions. These patches varied in size, shape and also the gradient of the patch slopes (Figure 2.6). Although the height between the top of the patch and the lower point differs between patches, *E. elderi* consistently grew in low-lying areas. Patch 6 was the only exception to the *E. elderi* population being at the lowest region because they were growing on the side of a basin. Other *E. elderi* populations in the region had a similar pattern to Patch 6 (personal observation).

2.6.2 Soil characteristics

There did not appear to be any consistent difference in any of the soil characteristics between inside and outside patches (Appendix 1, pages 185-187). Results were complicated by the lack of data for three sites due to the presence of a layer of rock inhibiting sampling below a depth of 20 cm. However, in half of the patches, $CaCO_3$ was not found inside the patch until a depth of 70 - 80 cm while outside the patch it was found at 10 - 20 cm depth or on the top. The pH varied between 8.0 - 9.5, and the three patches which showed a difference in $CaCO_3$ presence all had a higher pH outside the patch compared with inside the patch. In four patches the soil was more clayey inside the patches while the soil outside the patches were often sandier. The colour of the first layers of soil inside several patches were darker than the outside soil, although this was not consistent for all patches.

Figure 2.5: Topographical contour plots for each of the six patches showing patch boundaries (white lines) and transect lines (black lines). Contours based on data from the transect lines with all other values interpolated using the inbuilt kriging feature of Origin (Origin 1995).



2.6.3 Soil seed bank studies

Only three *E. elderi* seedlings germinated from the soil collected from inside the patches despite the samples being collected adjacent dead *E. elderi* foliage and none germinated from soil collected outside the patches. There was no difference between the readily germinable seed bank inside the patches compared with outside the patches (MANOVA, P=0.6896, F=0.8339, df_{num}=30, df_{den}=31; Table 2.1). However, there was a significant difference in the readily germinable seed bank between patches (MANOVA, P=0.0012, F=1.6090, df_{num}=150, df_{den}=175; Table 2.1). There was a significant effect of patch on seedling emergence for four species: *Lotus cruentus, Onopodium acualon, Oxalis corniculata, Schismus barbatus* (P<0.05; Table 2.2). In all cases there was a significant effect of patch (MANOVA, within columns: P<0.05, df_{num}=5, df_{den}=60). *Onopodium acualon* was found exclusively in the seed bank in Patch 7 while *Oxalis corniculata* was found exclusively in Patch 10. *Schismus barbatus* was found in high abundances in Patches 7 and 8 while there were few seedlings in the other patches.

Table 2.1: MANOVA results for readily germinable seed bank in soil collected inside the six *E. elderi* patches and outside patches.

Test	Pillai's Trace	Approx. F	df_{num}	df_{den}	$P\leq$
whole model	5.2176257	1.2332	330	451	0.0197
intercept	0.6980819	2.3892	30	31	0.0092
position	0.4466103	0.8339	30	31	0.6896
patch	2.8983929	1.6090	150	175	0.0012
position*patch	2.5929417	1.2568	150	175	0.0726

2.6.4 Germination of *E. elderi* seedlings

No germination within the seeded plots was recorded despite the fact that germination was observed in adjacent areas. If germination did occur, none of the seedlings survived to be recorded.

Table 2.2: Results for within species response to position and patch using the identity response matrix on within column differences after MANOVA.

Species	Pillai's trace	Exact F	df_{num}	df_{den}	$P \leq$
total abundance	0.1993954	1.3585	11	60	0.2164
Atriplex vesicaria	0.1549296	1.0000	11	60	0.4573
Boerhavia dominii	0.1428571	0.9091	11	60	0.5374
Carrichtera annua	0.2574346	1.8910	11	60	0.0586
Chenopodium cristatum	0.1549296	1.0000	11	60	0.4573
Crassula colorata	0.2535941	1.8532	11	60	0.0646
Eriochiton sclerolaenoides	0.0844444	0.5031	11	60	0.8938
Erodiophyllum elderi	0.1304348	0.8182	11	60	0.6222
Erodium cygnorum	0.1428571	0.9091	11	60	0.5374
Hordeum leporinum	0.234139	1.6676	11	60	0.1033
Lotus cruentus	0.4545455	4.5455	11	60	0.0001 ***
Daucus glochidiatus	0.1549296	1.0000	11	60	0.4573
Nicotiana glauca	0.1666667	1.0909	11	60	0.3840
Omphalolappula concava	0.122807	0.7636	11	60	0.6739
Onopordum acaulon	0.4926471	5.2964	11	60	0.0000 ***
Oxalis corniculata	0.2820513	2.1429	11	60	0.0303 ***
Schismus barbatus	0.3020473	2.3605	11	60	0.0170 ***
Scleroleana patenticuspis	0.1297044	0.8129	11	60	0.6272
Sida corrugata	0.1549296	1.0000	11	60	0.4573
Sonchus hydrophyllus	0.1549296	1.0000	11	60	0.4573
Stipa nitida	0.2415392	1.7371	11	60	0.0868
Swainsona formosa	0.1549296	1.0000	11	60	0.4573
Sisymbrium erysimoides	0.1827957	1.2201	11	60	0.2940
Tetragonia tetragonoides	0.1315123	0.8260	11	60	0.6148
Tribulus terrestris	0.2463768	1.7832	11	60	0.0772
Helipterum pygmaeum	0.1304348	0.8182	11	60	0.6222
Triodia sp.	0.1549296	1.0000	11	60	0.4573
unknown	0.1397059	0.8858	11	60	0.5588
Vittadinea cuneata	0.1270611	0.7939	11	60	0.6452
Zygophyllum sp.	0.1549296	1.0000	11	60	0.4573

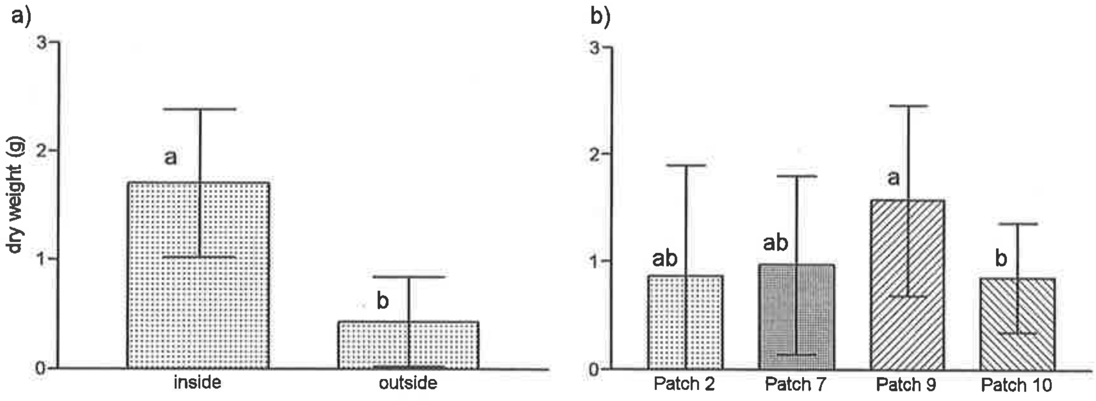
2.6.5 Growth of *E. elderi* seedlings in the glasshouse

E. elderi seedlings weighed more after three months when grown in soil collected from inside patches compared with those grown in soil from outside patches (ANOVA, patch, $P<0.0001$, F=50.37, df=3; Table 2.3; Figure 2.7 a). Seedlings weighed more when grown in soil from Patch 9 compared with Patch 10 (ANOVA, position, $P=0.0255$, F=3.70, df=1; Tukey, $P<0.05$; Table 2.3; Figure 2.7 b). Position accounted for 57.48% of the total variation while Patch only contributed 12.67% of the total variation.

Table 2.3: Two way ANOVA results for above-ground biomass of *E. elderi* grown in soil collected in each of the six patches studied both inside and outside patches (position).

Source	df	MS	F	*P*≤
patch	3	0.9452	3.700	0.0255
position	1	12.87	50.37	0.0001
interaction	3	0.1839	0.7201	0.5498
residual	24	0.2555		

Figure 2.7: Aboveground dry weight biomass of *E. elderi* seedlings grown in the glasshouse in soil collected from a) inside and outside patches, and b) in the four patches. Values are mean ± SD, different letters denote significant differences (Tukey, *P*<0.05).



2.7 DISCUSSION

Erodiophyllum elderi populations inhabit low-lying areas, creating a series of distinct patches which vary in size and shape. The low-lying areas result from the gentle undulating topography intermixed with sand dunes throughout Koonamore station (Carrodus *et al.* 1965). Although low lying areas are favourable for *E. elderi*, major floodplain areas may be detrimental (eg. Patch 6). Several sites had no *E. elderi* plants at the lowest point while plants were growing on the banks of the basin (personal observation). The lowest areas of basins could be inundated with water at times, which may bury the seeds too deeply for germination (eg. Ghersa *et al.* 1992) or provide waterlogged conditions which are unfavourable for *E. elderi* establishment.

Alternatively, run-on water from surrounding areas may modify soil conditions in the lower regions making them unsuitable for germination. Although run-on areas normally have increased nutrient concentrations (Ludwig *et al.* 1994) which benefits seedling growth, the accumulation of fine sediments may make these areas poor for establishment because the soils become crusty (J. Facelli, personal communication). The occasional filling of these low areas may result in dispersal of the seed bank up the basin bank away from the lowest point.

Although *E. elderi* seedlings were larger when grown in soil from inside patches, they also grew in soil from outside the patches. This suggests that factors other than soil differences, such as dispersal or moisture content, limit *E. elderi* distribution. There was no difference between soil from inside and outside patches in terms of soil pH, colour or $CaCO_3$ content although in some cases, the pH varied, and in others the depth to $CaCO_3$ varied. Seedling growth was lower in the sandy soil from outside some of the patches and in Patch 10, even under 'optimal' water conditions such as those provided in the glasshouse. Soil that has accumulated in lower areas may have a higher soil moisture content at times (Friedel *et al.* 1993) although this was not examined in the soil cores. As the ephemeral herbland communities are restricted to the low-lying regions, soil examination further away than considered may reveal differences between inside and outside the patches. In the absence of more thorough soil analyses which may reveal other differences, enhanced *E. elderi* seedling growth in soil from inside the patches is probably due to reduced growth in sandy soil and in some cases, nutrient differences.

There was no difference between the growth of *E. elderi* seedlings in soil collected from within the different patches. This is in contrast to the visual appearance of larger *E. elderi* plants in the lightly grazed areas (examined in Chapter 3). The lack of differences in *E. elderi* growth in soil from the different patches suggests that differences in the field are probably due to grazing effects or water moisture differences rather than physical soil differences. However, heavy grazing pressure over a long period of time is likely to change the soil condition substantially, in particular, soil compactness (Ludwig *et al.* 1994) which can affect seedling emergence. These effects which would be obvious in the field would be removed during the establishment of the glasshouse experiment. This may explain the lack of differences in seedling growth in soil from different patches.

Very few *E. elderi* seedlings emerged from the readily germinable soil seed bank despite collecting the soil from the base of *E. elderi* plants where a large seed density will most likely be if a soil seed bank exists. The seed bank for *E. elderi* appears to be held above ground in the hard woody seedheads. Although some species do hold the seed bank above ground (Gutterman and Ginott 1994, Gutterman 1994), most short-lived arid species typically produce a large seed reserve in the soil (Kemp 1989). The advantages of having an above ground seed bank are discussed in detail in Chapter 6. Preliminary germination trials showed no *E. elderi* seed dormancy, and therefore the lack of *E. elderi* seedlings emerging in soil collected from outside the patches suggests that none were present. The absence of *E. elderi* seeds in soil from outside the patches may be due to limited or directed dispersal which is examined in Chapter 5.

Many topographical features of the region influence the distribution of *E. elderi* although it is unclear which factors are the most important. Ultimately the spatial variation in plant density results from differences in either seed dispersal, seedling establishment, plant survival or reproduction (Reader and Buck 1986). Seedling establishment, plant survival and reproduction in relation to grazing pressure are examined in Chapter 3, while seedling-adult and seedling-seedling interactions which may influence growth and reproduction are examined in Chapter 7. Although *E. elderi* populations are restricted to the low-lying areas, there is no physical reason why these patches can not expand, except in the cases where the soil outside the patches is sandy. However, the effects of soil moisture content and seedhead dispersal limitation (examined in Chapter 5) could have a profound influence on *E. elderi* distribution.

3. The effects of grazing on population dynamics

3.1 INTRODUCTION

Grazing affects the germination, establishment, growth and reproductive phases of the life cycle of a plant directly and indirectly. In arid systems, germination can be influenced indirectly by the destruction of the soil crust during trampling (Osborn *et al.* 1932); a change in soil nutrients through the deposition of animal excreta; the location of seeds through influences on dispersal (Tremont 1994); and the availability of safe-sites, for example, through the removal of shrubs which may create suitable micro-sites. Once seeds have germinated, other processes become important, including defoliation and increased seedling mortality through trampling (Bergelson and Crawley 1992; Tremont 1994). Typically, grazing results in a decrease in vegetative cover (Williams 1985; McIntyre and Lavorel 1994; Landsberg *et al.* 1997) although this depends on the response of particular species within a community and whether the community has evolved under grazing or not (Mack and Thompson 1982; Oesterheld and Sala 1990).

To a large extent, the effects of grazing depend on the palatability of the species. The selective removal either of individual plants or particular species, due to differences in palatability, can lead to the competitive release of the remaining plants (Tremont 1994; McIntyre and Lavorel 1995). Additionally, the effects of grazing are not necessarily uniform for any given species at different sites (Bergelson and Crawley 1992; Landsberg *et al.* 1997). For example, in one community, a particular species may benefit from the selective removal of competitors, while in another community, this species may be the most palatable present and is therefore selectively grazed. Due to differences in palatability, species specific responses to grazing results in a change in species density along a gradient of grazing pressure away from watering points in many arid lands. This is referred to as the piosphere effect (Lange 1969). The effects of grazing on any particular species need to be examined at different sites experiencing a range of grazing pressures.

The individual responses to grazing may not be reflected at the population level. For example, while grazing can reduce population density, this does not necessarily result in a corresponding decrease in reproductive output (Bergelson and Crawley 1992) as the reproductive output of an individual plant may increase through reduced density-dependent effects. However, both individual and population level responses are likely to depend on differences in palatability, grazing pressure, and any variability between sites. In situations where there is an increase in density of plants with grazing, plants presumably gain more from competitive release, through the selective removal of competitors, than they lose through defoliation (Bergelson and Crawley 1992). While grazing is generally detrimental to plant survival or growth and affects plant size and shape (Landsberg *et al.* 1997), in some cases grazing may be beneficial. However, a positive individual response to grazing is uncommon (Bergelson and Crawley 1992) and if grazing pressure is strong, it will be to the detriment of the plant.

Prolonged effects of grazing can ultimately change the distribution and density of seed populations. Both short term ecological changes and long term evolutionary changes are two responses to a significant reduction in the reproductive output (Louda 1989). Seed banks reflect past and current selective pressures on both seed and seedling stages (Parker *et al.* 1989). As the Australian native vegetation is not adapted to the intense grazing pressure of introduced herbivores or the indirect effects of their presence (Osborn *et al.* 1932; Tiver and Andrew 1997), alien herbivores may be particularly detrimental to species persistence. The effects of grazing on seed production will be particularly important for highly palatable short-lived species, as they depend on the seed bank to maintain populations through adverse environmental conditions (Inouye 1980; Gutterman 1994). The seed banks of some short-lived Australian species have declined in response to grazing (Landsberg *et al.* 1997). It is clear that continual grazing effects on palatable species will most likely result in a decreased seed bank. Through the effect on seed banks, grazing may increase the probability of temporal extinction of local populations. The effect of grazing on the population dynamics and the seed bank of unpalatable or less preferred species is less clear.

In this chapter, I examine the effects of grazing on the ephemeral herbland communities at Koonamore Station, in the north-east of South Australia. These herbland communities, which inhabit floodplains and watercourses during good years of rainfall are heavily grazed (Hall *et al.* 1964). In particular, I focus on the often dominant species, *Erodiophyllum elderi* (Cunningham, Mulham *et al.* 1992). Although *E. elderi* is not preferred, sheep have been observed eating the flowers and chewing on seedheads (L. MacLachlan, personal communication; personal observation) and the long term effect of grazing on the *E. elderi* seed bank is unknown. Although *E. elderi* plants appear smaller in heavily grazed areas, the influence of grazing on the processes and stages of the life cycle has not been studied. In addition, the reduction in the size of plants is an individual response to grazing, and the population level response may be different.

I examined the effect of grazing pressure on the spatio-temporal dynamics of plants in six ephemeral herbland communities over a period of three years. Specifically, I ask: Does the density of grasses, forbs and *E. elderi* reflect palatability differences between these broad taxa according to grazing pressure? Does grazing affect *E. elderi* populations? If so, at what stage of the life cycle and through what processes does grazing affect *E. elderi*? Is the individual plant response in terms of biomass or reproductive output to grazing similar to the population level response? Does grazing have a long term effect on *E. elderi* populations by reducing the seed bank?, and finally, if grazing does reduce the seed bank, is it likely to increase temporal extinction rates of *E. elderi* populations?

3.2 METHODS AND ANALYSIS

To examine the spatio-temporal dynamics of six ephemeral herbland communities experiencing a range of grazing pressures, I monitored a series of permanent plots over a three year period. Three 5x5 m plots were randomly chosen in each patch described in Chapter 2, and within each of these plots, five 1x1 m quadrats were marked. All plants within the 1x1 m quadrats were counted unless large densities required sub-sampling of the quadrats. The permanent plots were established on 1-Mar-1994 with subsequent readings on 25-Aug-1994, 3-Mar-1995, 5-Sep-1995, 5-Mar-1996 and 30-Aug-1996.

3.2.1 Dung counts - a measure of grazing pressure

To determine the relative grazing pressure within the six patches, counts of animal dung were made in August 1996. Dung counts are known to provide a reliable estimate of grazing pressure (Lange 1985). Although the position of the patches within paddocks (described in Chapter 2) suggests grazing pressures to be within the broad classes of high, intermediate, and low grazing, grazing pressures are actually somewhere along a continuum. All dung was counted in the 1x1 m permanent plots described above although analysis was only conducted on sheep dung due to the negligible amount of dung from other animals. Dung abundances per m^2 were analysed with Kruskal-Wallis followed by Dunn's tests.

3.2.2 Densities of grasses, forbs and *E. elderi*

The density of grasses, forbs and *E. elderi* were examined to determine the spatio-temporal dynamics of the three taxa in the six communities which differed in their grazing pressure. The density of the three taxa were examined for within patch differences to determine whether any taxa dominates the patch, and between patch differences to determine whether differences were consistent between grazing pressures possibly indicating palatability differences. The ln(density+1) transformed densities of the taxa grasses, forbs and *E. elderi* in the 1x1 m permanent plots in each patch were analysed with a profile MANOVA using Jmp v3.1.4 (SAS 1995). The identity response matrix was used to test for within time differences according to patch and taxa. Tukey tests were performed to determine where differences were. Additionally, the density of mature *E. elderi* were examined to determine whether mature plants persisted through time.

3.2.3 Population dynamics of *Erodiophyllum elderi*

To determine whether *E. elderi* population parameters vary between patches and through time, individual *E. elderi* biomass and reproductive output was measured in the six populations. In each 1x1 m quadrat, *E. elderi* density, plant height, plant maximum width, plant perpendicular width to that maximum width and the number of flowers, buds and seedheads present on each plant were measured.

3.2.3.1 Non-destructive biomass estimation

To assess the above ground dry biomass of *E. elderi* plants in the permanent plots in a non-destructive way, a relationship was derived between biomass and plant height and width. To determine this relationship, the height (H), maximum width (W_m), and width perpendicular to the maximum width (W_p) were measured in the field for 116 plants which were not in the permanent plots. These plants were harvested and their dry weights recorded after being oven dried at 80°C for 24 hours. The relationship between the aboveground dry biomass of plants and the height and widths was examined using linear regression on natural logarithmically transformed data. Five different regressions were examined, including height, average width and additive and multiplicative combinations of height and width. The equation which gave the best prediction of biomass from height and width measurements was then used to predict non-destructive *E. elderi* plant biomass estimates.

3.2.3.2 Individual **E. elderi** *weight and reproductive output*

To determine if there were differences in individual *E. elderi* weight and reproductive output between patches, the size of plants and the number of seedheads on each plant in the permanent plots were recorded in March 1994. Separate one-way Kruskal-Wallis tests were conducted for biomass and reproductive output. Dunn's multiple comparison test was used to determine where differences between patches were.

3.2.3.3 Population response of density, reproductive output and biomass

To determine whether the per unit area density, biomass and reproductive output (number of seedheads) varied between patches, *E. elderi* density, biomass and reproductive output per m^2 were calculated from the permanent plot data. Data were analysed with MANOVA using the identity response matrix to determine significant effects within each variable. Tukey tests were performed on the natural logarithm transformed data for the significant variables to determine where differences between patches were. Data were analysed for March 1994 only, as future data collections included individuals from this time and hence lacked independence.

3.2.3.4 Transition between size classes

To determine whether *E. elderi* plants had different growth rates in the different patches, a series of transition matrices based on plant size and reproductive output were constructed. Transition matrices were constructed for the two six month periods between March 1994 and March 1995 and the matrix elements representing *E. elderi* growth, shrinking, remaining in the same category or dying were examined. *Erodiophyllum elderi* plants within the permanent plots were assigned to one of six categories according to their size and reproductive output (Table 3.1). In addition to the above-mentioned 5x5 m plots, *E. elderi* adjacent the permanent plots were monitored to ensure full category representation. This was necessary because *E. elderi* density varied across patches and although several patches had many *E. elderi* present in each category other patches had insufficient numbers in some categories.

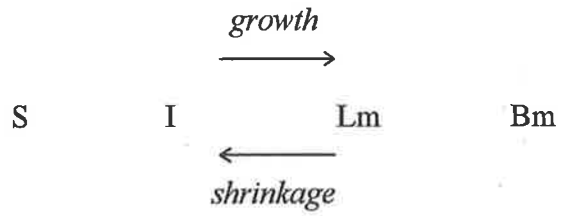
Table 3.1: Description of *E. elderi* plant categories according to their size, reproductive output and vitality.

Symbol	**inde**	**Category**	**Description**	**Reproductive status**
S	1	seedlings	≤5cm for any dimension	no seedheads
I	2	immature	generally <15cm for all dimensions	no seedheads
Lm	3	little and mature	≤15cm for all dimensions	seedheads present
Bm	4	big and mature	>15cm for any dimension	seedheads present
Pd	5	partially dead	>50% dead material	seedheads present
D	6	dead or dormant	above ground dead material	previous production may be present

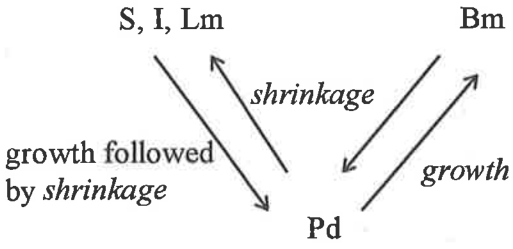
Transition matrices based on the *E. elderi* plant categories described in Table 3.1 were constructed for each patch for the two time periods of 1-Mar-1994 → 25-Aug-1994 and 25-Aug-1994 → 3-Mar-1995 (Table 3.2, page 52). Unfortunately, there were few small *E. elderi* plants present in all but the heavily grazed patches when the permanent plots were established and there are few plants represented in those categories in some of the patches. Transition matrices after 3-Mar-1995 were not constructed because there were few living *E. elderi* present in the patches and those that were present, died between readings. As the seed bank was not included in these transition matrices due to the difficulty in finding transition rates involving seeds, the traditional analysis of looking at the λ value (population growth rate) for each transition matrix was not possible. Instead I calculated a measure of *E. elderi* plant growth, shrinkage, remaining in the same category or death.

Figure 3.1: Possible transitions between categories for transition matrices constructed for each of the six *E. elderi* populations examined between March 1994 and March 1995.

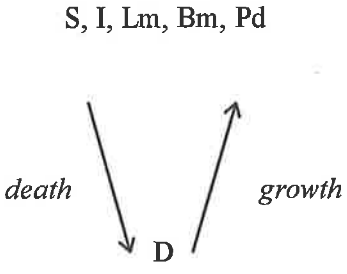
a) transitions between live stages (note: transitions possible between all categories for directions of both growth and shrinkage):



b) transitions including Pd plants:



c) transitions including individuals from category D:



Calculating transition probabilities

The probabilities of movement between categories shown in Figure 3.1 a, b, c are determined by the following equations for each patch:

The probability of shrinking from category i (s_i) is given by:

$$s_i = \begin{cases} \sum\limits_{j<i} p_{ij} + p_{i5}, & i = 1,\ 2,\ 3,\ 4 \\ \sum\limits_{j<3} p_{ij}, & i = 5 \\ 0, & i = 6 \end{cases}$$

where, p_{ij} is the probability of a transition from category i to category j and is estimated by dividing the number of plants making the transition from category i to j by the number of plants in category i.

The probability of plants shrinking between categories is:

$$s = \sum_{i=1}^{6} s_i p_i ,$$

where p_i is the probability of being in category i and is estimated by dividing the number of plants in state i by the total number of plants, and s is equivalent to the total number of plants shrinking between categories divided by the total number of plants.

The probability of growing (g_i) from category i is given by:

$$g_i = \begin{cases} \sum\limits_{j>i, j\le 4} p_{ij}, & i = 1,\ 2,\ 3 \\ 0, & i = 4 \\ p_{i4}, & i = 5 \\ \sum\limits_{j\le 5} p_{ij}, & i = 6 \end{cases}$$

and the corresponding probability of plants growing between categories is:

$$g = \sum_{i=1}^{6} g_i p_i .$$

The probability of no change from category i (n_i) is given by:

$$n_i = p_{ii}, \qquad i = 1,\ldots,5$$

and the probability of plants staying in the same category is:

$$n = \sum_{i=1}^{5} n_i p_i .$$

The probability of death from category i (d_i) is given by:

$$d_i = p_{i6}, \qquad i = 1,\ldots,5$$

and the probability of plants dying is:

$$d = \sum_{i=1}^{5} d_i p_i .$$

The proportions of the population growing, staying in the same category (no change), shrinking and dying within each patch were examined for each time period. These values do not include those individuals from the D (dead or dormant) category which had not re-sprouted after six months, as they were considered dead rather than dormant.

Table 3.2: Transition matrices constructed from *E. elderi* plants in the six populations for two time periods. Transition based on categories described in Table 3.1.

a) Transition matrices for each patch for the period 1 March 1994 → 25 August 1994.

Heavily grazed patches

Patch 2		*to*						
		S	I	Lm	Bm	Pd	D	*total*
	S	9	6	0	0	0	13	28
	I	0	25	2	0	1	7	35
from	Lm	0	22	3	1	4	10	40
	Bm	0	20	4	3	10	23	60
	Pd	0	3	2	2	1	14	22
	D	0	2	1	0	0	20	23
	total	9	78	12	6	16	87	208

Patch 7		*to*						
		S	I	Lm	Bm	Pd	D	*total*
	S	2	7	0	0	0	1	10
	I	0	10	1	0	2	1	14
from	Lm	0	12	0	0	3	1	16
	Bm	0	25	1	1	6	3	36
	Pd	0	0	0	0	0	6	6
	D	0	0	0	0	0	22	22
	total	2	54	2	1	11	34	104

Intermediate grazing pressure

Patch 6		*to*						
		S	I	Lm	Bm	Pd	D	*total*
	S	2	0	0	0	0	0	2
	I	0	6	1	0	0	0	7
from	Lm	0	3	4	2	1	2	12
	Bm	0	0	0	22	2	2	26
	Pd	0	1	0	3	4	7	15
	D	0	0	1	0	0	14	15
	total	2	10	6	27	7	25	77

Patch 8		*to*						
		S	I	Lm	Bm	Pd	D	*total*
	S	1	2	0	0	0	1	4
	I	0	4	1	0	0	2	7
from	Lm	0	3	8	0	0	1	12
	Bm	0	5	7	26	7	10	55
	Pd	0	3	3	9	4	6	25
	D	0	0	0	0	1	10	11
	total	1	17	19	35	12	30	114

Inside Koonamore Vegetation Reserve

Patch 9		*to*						
		S	I	Lm	Bm	Pd	D	*total*
	S	4	3	0	0	0	0	7
	I	0	4	1	0	0	0	5
from	Lm	0	5	3	0	0	1	9
	Bm	0	1	1	15	10	5	32
	Pd	0	0	0	4	4	6	14
	D	0	0	0	1	1	8	10
	total	4	13	5	20	15	20	77

Patch 10		*to*						
		S	I	Lm	Bm	Pd	D	*total*
	S	4	0	0	0	0	0	4
	I	0	5	1	0	0	2	8
from	Lm	0	6	1	1	1	1	10
	Bm	0	10	3	1	1	14	29
	Pd	0	3	1	1	0	7	12
	D	0	1	0	0	0	10	11
	total	4	25	6	3	2	34	74

b) Transition matrices for each population for 25 August 1994 → 3 March 1995.

Heavily grazed patches

Patch 2				*to*				
		S	I	Lm	Bm	Pd	D	*total*
	S	0	0	0	0	0	78	78
	I	0	0	0	0	0	82	82
from	Lm	0	0	0	0	0	12	12
	Bm	0	0	0	0	0	6	6
	Pd	0	0	0	0	0	16	16
	D	0	0	0	0	0	63	63
	total	0	0	0	0	0	257	257

Patch 7				*to*				
		S	I	Lm	Bm	Pd	D	*total*
	S	0	0	0	0	0	647	647
	I	0	1	0	0	0	53	54
from	Lm	0	0	0	0	0	2	2
	Bm	0	0	0	0	0	1	1
	Pd	0	0	0	0	0	11	11
	D	0	0	0	0	0	31	31
	total	0	1	0	0	0	745	746

Intermediate grazing pressure

Patch 6				*to*				
		S	I	Lm	Bm	Pd	D	*total*
	S	0	0	0	0	0	22	22
	I	0	2	0	0	0	9	11
from	Lm	0	2	0	0	0	6	8
	Bm	0	4	0	4	8	13	29
	Pd	0	0	0	0	0	7	7
	D	0	0	0	1	0	22	23
	total	0	8	0	5	8	79	100

Patch 8				*to*				
		S	I	Lm	Bm	Pd	D	*total*
	S	0	0	0	0	0	271	271
	I	0	0	0	0	2	16	18
from	Lm	0	0	0	1	1	17	19
	Bm	0	2	1	0	12	22	37
	Pd	0	0	0	1	0	13	14
	D	0	0	0	2	3	22	27
	total	0	2	1	4	18	361	386

Inside Koonamore Vegetation Reserve

Patch 9				*to*				
		S	I	Lm	Bm	Pd	D	*total*
	S	0	0	0	0	0	10	10
	I	0	8	0	0	1	4	13
from	Lm	0	1	1	0	1	2	5
	Bm	0	1	1	0	11	7	20
	Pd	0	1	0	0	2	12	15
	D	0	0	0	0	0	19	19
	total	0	11	2	0	15	54	82

Patch 10				*to*				
		S	I	Lm	Bm	Pd	D	*total*
	S	0	0	0	0	0	132	132
	I	0	4	0	0	0	25	29
from	Lm	0	1	0	0	0	5	6
	Bm	0	0	0	0	0	3	3
	Pd	0	0	0	0	0	2	2
	D	0	0	0	0	0	28	28
	total	0	5	0	0	0	195	200

3.2.4 Seed density and seedhead age class structure

To determine whether grazing affects the seed bank of *E. elderi*, seedhead densities were recorded in the six patches. Seedhead densities were recorded in terms of new seedhead production (on the plant, produced within the three previous years) and old seedheads (on the ground) in the fifteen 1x1 m permanent quadrats in each patch on 29-Aug-1996.

Seedhead densities were analysed according to age and total seed density for each patch. Seedhead densities were analysed within each age category of new and old according to patch with separate one-way ANOVAs on ln(density+1) transformed data followed by Tukey comparisons.

Erodiophyllum elderi seedhead densities were converted to total seed densities per m^2 using the average number of seeds per seedhead stage class as determined in section 6.3.1. The ln(seed density+1) transformed seed densities per m^2 were analysed within each patch using a one-way ANOVA followed by a Tukey's test. The age of seedheads and the density of seeds within the seedheads are discussed in detail in Chapter 6.

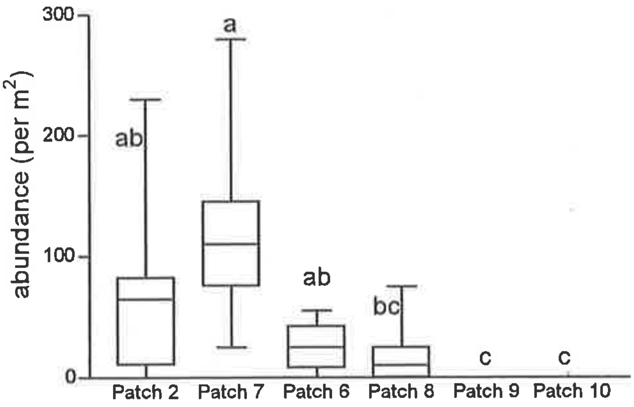
All data were tested for normality and homogeneity of variances and were transformed where necessary. Data were analysed with GraphPad PRISM v 2.0 (PRISM 1995) except for MANOVA tests which were calculated using Jmp v 3.1.4 (SAS 1995).

3.3 RESULTS

3.3.1 Dung counts - a measure of grazing pressure

Dung densities corresponded to the expected grazing pressures from the position of the patches within the paddocks and in relation to watering points across Koonamore Station (described in Chapter 2). Patch 7 had the highest sheep dung abundances (Kruskal-Wallis, $P<0.0001$, $\chi^2=63.93$, n=6; Figure 3.2). Patch 2 had the second highest dung abundances which were statistically higher than abundances in Patches 8, 9 or 10. There was no statistical difference in sheep dung abundances between Patches 6, 8, 9 and 10. No sheep dung was found inside the Reserve.

Figure 3.2: Sheep dung abundances recorded in the permanent plots in each of the six patches in August 1996. Boxes show mean, 25th and 75th percentiles and whiskers extend to maximum and minimum values. Letters denote significance differences (Dunn's test, $P \leq 0.05$).



3.3.2 Densities of grasses, forbs and *E. elderi*

Densities of grasses, forbs and *E. elderi* varied significantly between times (MANOVA, time: $P \leq 0.00001$, $df_{num}=5$, $df_{den}=245$; Table 3.3). The significant three way interaction time*taxa*patch indicates that differences between taxa (*E. elderi*, grasses or forbs) within the patches were not consistent through time (MANOVA, $P \leq 0.00001$, $df_{num}=50$, $df_{den}=1260$; Table 3.3).

Table 3.3: Profile MANOVA results for ln(density+1) of *E. elderi*, forbs and grasses in each patch for 25-Aug-1994, 3-Mar-1995, 5-Sep-1995, 5-Mar-1996 and 30-Aug-1996. Data are ln(density+1) transformed.

	Pillai's	approx. F	df_{num}	df_{den}	Prob>F
all within interactions	2.925	20.9022	85	1260	0.0000
time	0.936	722.7689	5	248	0.0000
time*taxa	0.902	40.9422	10	498	0.0000
time*patch	1.2997	17.7024	25	1260	0.0000
time*taxa*patch	1.8997	15.4410	50	1260	0.0000

Densities of *E. elderi*, grasses and forbs increased in all patches during the winter months (August-September) in each year (Figure 3.3 a, b & c). However, few of these plants survived until the summer recording (March) in any year. Densities of all taxa peaked in September 1995 in most patches which was most likely due to the high annual rainfall in that year. Despite the massive germination event in September 1995, few seedlings were present in summer.

There were considerably fewer *E. elderi* present in all patches in August 1996 than in either 1994 or September 1995 (Figure 3.3 a, b & c). Neither grass nor forb densities followed this pattern. The decline in *E. elderi* represented the rapid death of mature *E. elderi* plants over the three year period March 1994 to March 1996 (Figure 3.4). *E. elderi* recorded after August 1994 consisted largely of seedlings rather than mature plants. It appears that I monitored *E. elderi* at the end of a pulse of growth which was at its peak during my first field trip to the area in 1993 when *E. elderi* were flourishing throughout the region. This pulse of *E. elderi* occurred after 1992 which had the second largest annual rainfall recorded since the establishment of the Reserve (Figure 3.3 d).

Within patch differences

There were generally more forbs than either grasses or *E. elderi* at most times irrespective of grazing pressure (Figure 3.5). However, in March 1994 there was no difference between forbs and *E. elderi* in Patch 2 and in the Reserve (Patch 9 and 10), forb and grass densities were similar. Likewise, in August 1994 there was no difference between forb and grass density in Patch 9. The only occasion when forb densities were lower than either grasses or *E. elderi* was in Patch 7 in August 1994 when *E. elderi* densities were highest. *E. elderi* densities were typically lower than grasses or forbs in the Reserve. Grass and *E. elderi* densities varied through time but were generally similar within a patch.

Figure 3.3: Densities of a) *E. elderi*, b) grasses and c) forbs by patch through time and d) annual Koonamore rainfall from 1923-1996. Values plotted are mean ± SD based on fifteen 1x1 m permanent plots according to grazing pressures of high, intermediate and low.

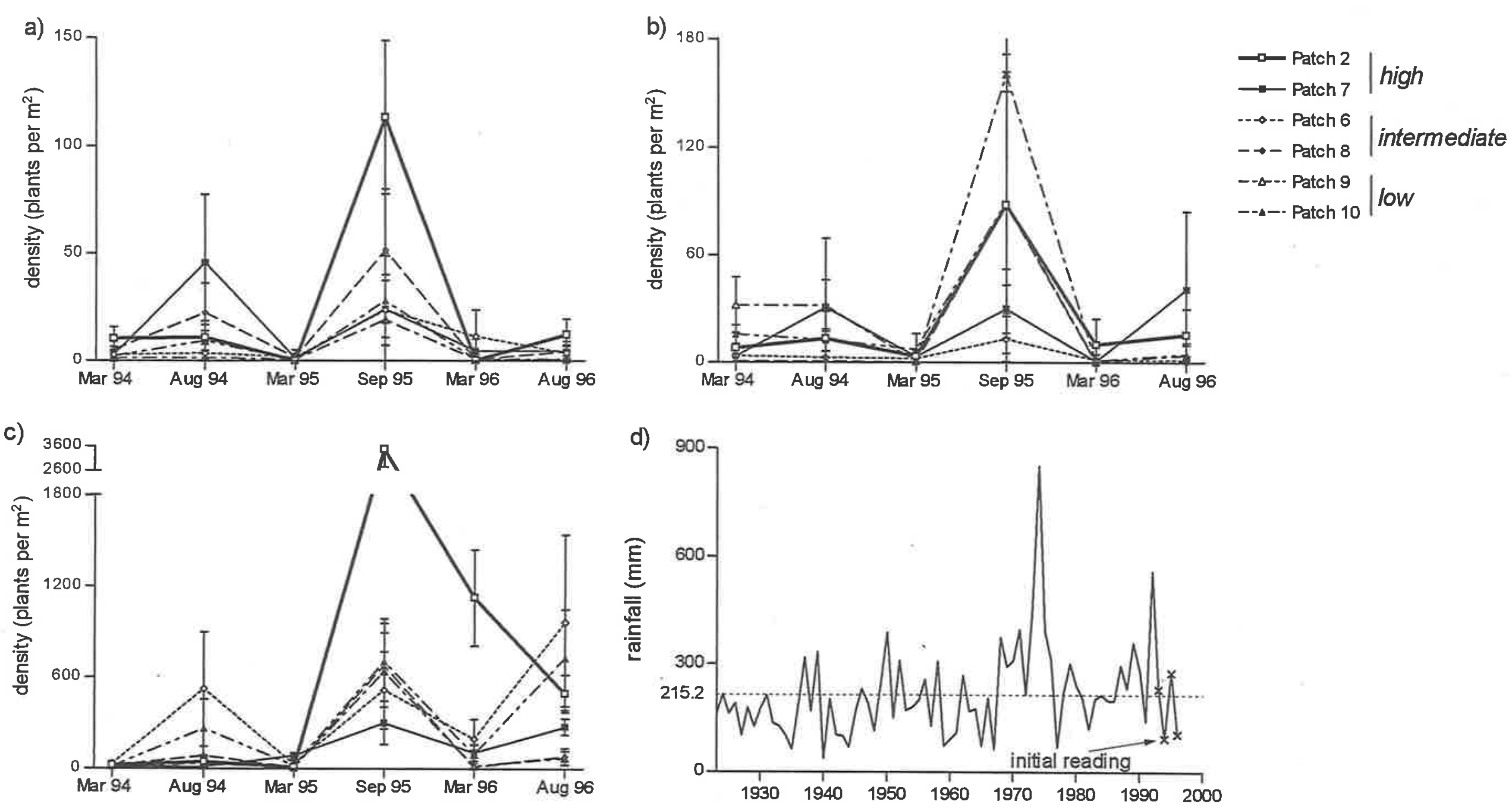
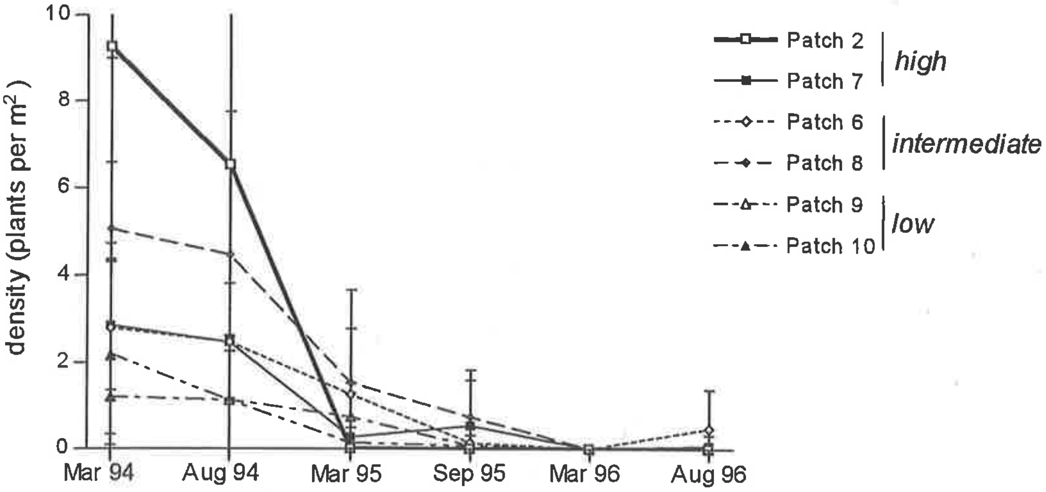


Figure 3.4: Mature *E. elderi* through time in each patch with different grazing pressures. Values plotted are mean ± SD based on fifteen 1x1m permanent plots.



Between patch differences

E. elderi, forb and grass densities were not consistent between patches (MANOVA, patch*taxa interactions, $P \leq 0.00001$, $df_{num}=10$, $df_{den}=252$ in all cases; Table 3.4 a, b and c). No patch had consistently highest densities for any taxa through time. *E. elderi* densities were highest in Patch 2 compared with other patches in March 1994 while they were lowest in Patch 6 and 9 in August 1994 (Tukey, $P<0.05$; Figure 3.5). There was no difference in *E. elderi* density between patches in March 1995, but in September 1995 there were more *E. elderi* in Patch 2 than in Patches 7, 9 and 10 with the fewest recorded in Patch 9. In March 1996, more *E. elderi* were recorded in Patch 6 than in Patches 2, 8, 9 and 10, while in August 1996 there were more *E. elderi* in Patches 2 and 7.

In general, there is a decrease in forb and grass density with decreasing grazing pressure in all years except 1994 when grass density was highest inside the Reserve. The exception to this trend is the density of plants in Patch 10 which were often higher than Patches 8 and 9 during the main germination period. The high grass densities inside the Reserve did not persist. In August 1996, and to a lesser extent in March 1996, the heavily grazed patches had highest grass densities.

Table 3.4: MANOVA results at each time for ln(density+1) of *E. elderi*, forbs and grasses in each patch. df_{den}=252 in all cases.

a) 1994

		1-March-1994			25-August-1994		
test	df_{num}	Pillai's trace	F Ratio	*P*≤	Pillai's trace	F Ratio	*P*≤
model	17	0.6556	28.220	0.00001	0.7960	57.838	0.00001
taxa	2	0.4421	99.850	0.00001	0.6242	209.311	0.00001
patch	5	0.198	11.808	0.00001	0.1276	7.370	0.00001
taxa*patch	10	0.4672	22.099	0.00001	0.6768	52.778	0.00001

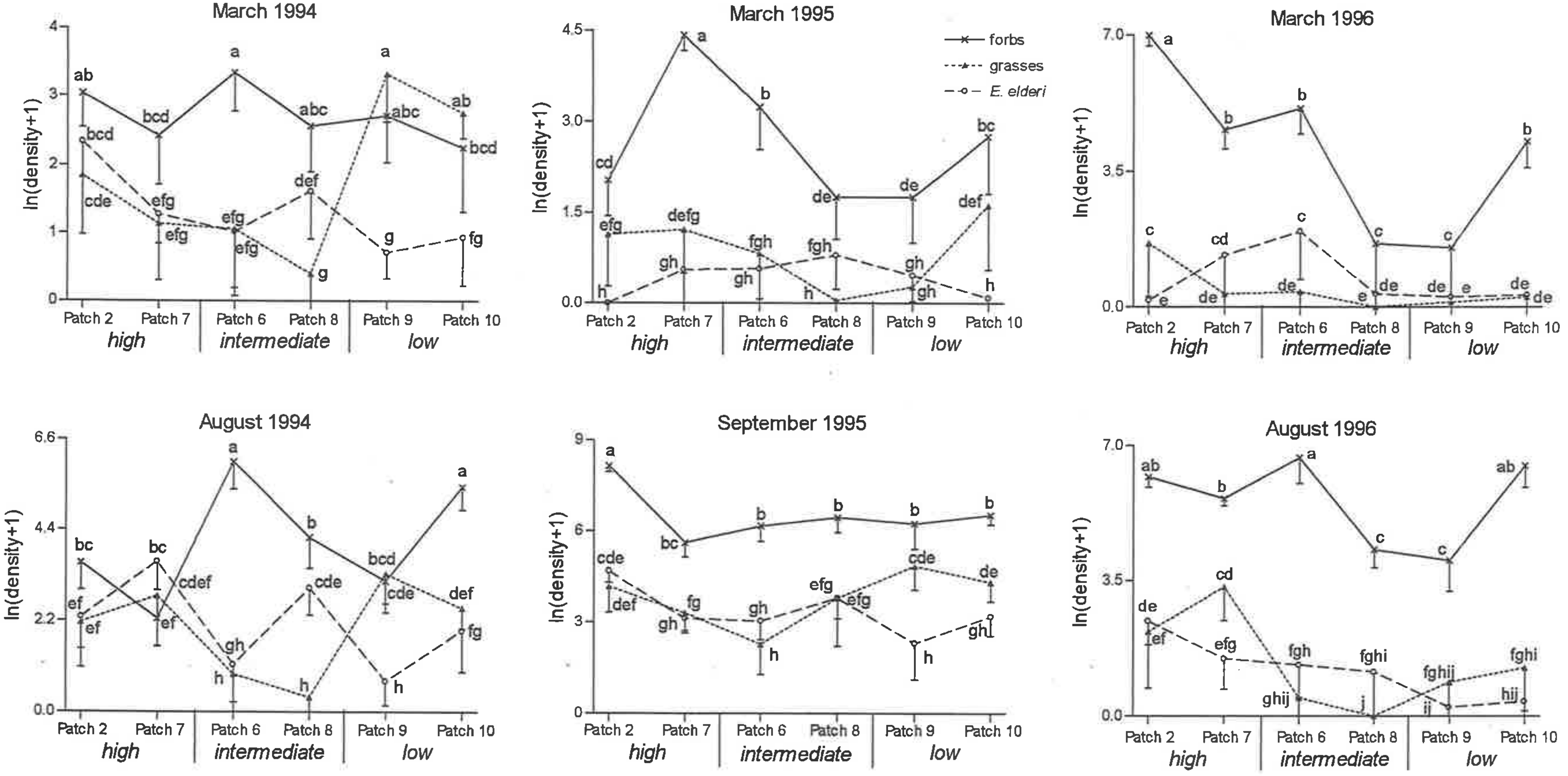
b) 1995

		3-March-1995			25-September-1995		
test	df_{num}	Pillai's trace	F Ratio	*P*≤	Pillai's trace	F Ratio	*P*≤
model	17	0.7751	51.092	0.00001	0.8314	73.102	0.00001
taxa	2	0.7031	298.441	0.00001	0.7898	473.495	0.00001
patch	5	0.3243	24.194	0.00001	0.4026	33.967	0.00001
taxa*patch	10	0.3743	15.072	0.00001	0.3331	12.591	0.00001

c) 1996

		6-March-1996			28-August-1996		
test	df_{num}	Pillai's trace	F Ratio	*P*≤	Pillai's trace	F Ratio	*P*≤
model	17	0.8566	88.556	0.00001	0.8935	124.348	0.00001
taxa	2	0.7928	482.219	0.00001	0.8719	857.663	0.00001
patch	5	0.5187	54.321	0.00001	0.4690	44.517	0.00001
taxa*patch	10	0.5167	26.940	0.00001	0.4112	17.601	0.00001

Figure 3.5: Densities per m^2 of *E. elderi*, grasses and forbs in each patch in high, intermediate or low grazing pressures in March 1994, August 1994, March 1995, September 1995, March 1996 and August 1996. Values are mean ± SD. Letters denote significant differences (Tukey test, $P<0.05$ on ln(density+1) transformed data).



3.3.3 Population dynamics of *Erodiophyllum elderi*

3.3.3.1 Non-destructive biomass estimation

The regression of biomass as a function of the sum of plant height and average width (r^2=0.8332, equation ii; Table 3.5) gave the best estimate of *E. elderi* plant biomass and was used for non-destructive biomass prediction. In general, equations based on *E. elderi* height and width were good predictors of aboveground dry biomass (Table 3.5; equations (ii), (iii) and (v)). The width of *E. elderi* plants predicted biomass better than plant height. However, because all equations have non zero intercepts, biomass estimates for values at the origin are misleading. The runs test showed no significant deviation from a straight line for all but equation iii (P>0.05).

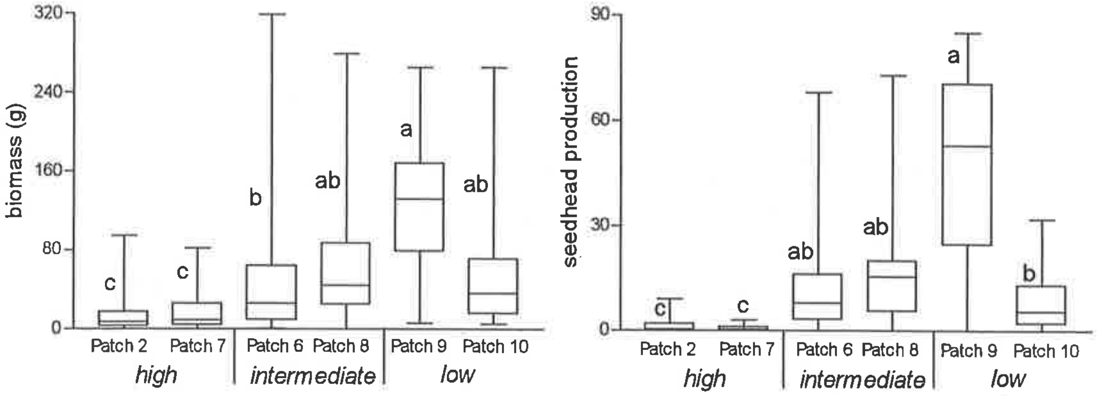
Table 3.5: Regression equations between above ground dry weight (B, g), height (H, cm), mean width (W_{ave}, cm) or maximum width(W_m, cm) and perpendicular width (W_p, cm).

Regression equation	df	r^2
i) $\ln B = -3.325 + 2.427 \ln H$	115	0.6417
ii) $\ln B = -5.466 + 2.426 \ln (H + W_{ave})$	115	0.8332
iii) $\ln B = -3.826 + 1.238 \ln(H * W_{ave})$	115	0.8231
iv) $\ln B = -2.683 + 1.953 \ln W_{ave}$	115	0.7825
v) $\ln B = -5.987 + 2.282 \ln(H + W_m + W_p)$	115	0.8300

3.3.3.2 Individual **E. elderi** *weight and reproductive output*

Individual *E. elderi* plants had lower individual biomass in the patches experiencing high grazing pressure than those subjected to lower grazing pressure (Kruskal-Wallis, P<0.0001, χ^2=138.5, n=6; Dunn's P<0.05; Figure 3.6). Likewise, the reproductive output per plant was lower for individual plants in the heavily grazed patches (Kruskal-Wallis, P<0.0001, χ^2=234.5, n=6; Dunn's P<0.05; Figure 3.6). The heavily grazed patches had lower mean and variances for both *E. elderi* reproductive output and biomass.

Figure 3.6: Biomass and seedhead production per *E. elderi* plant by patch in March 1994. Patches are in broad categories of high, intermediate, and low grazing pressures. Letters denote significant differences (Dunn's test, $P \leq 0.05$). Box shows mean, 25th and 75th percentiles and whiskers extend to maximum and minimum values.



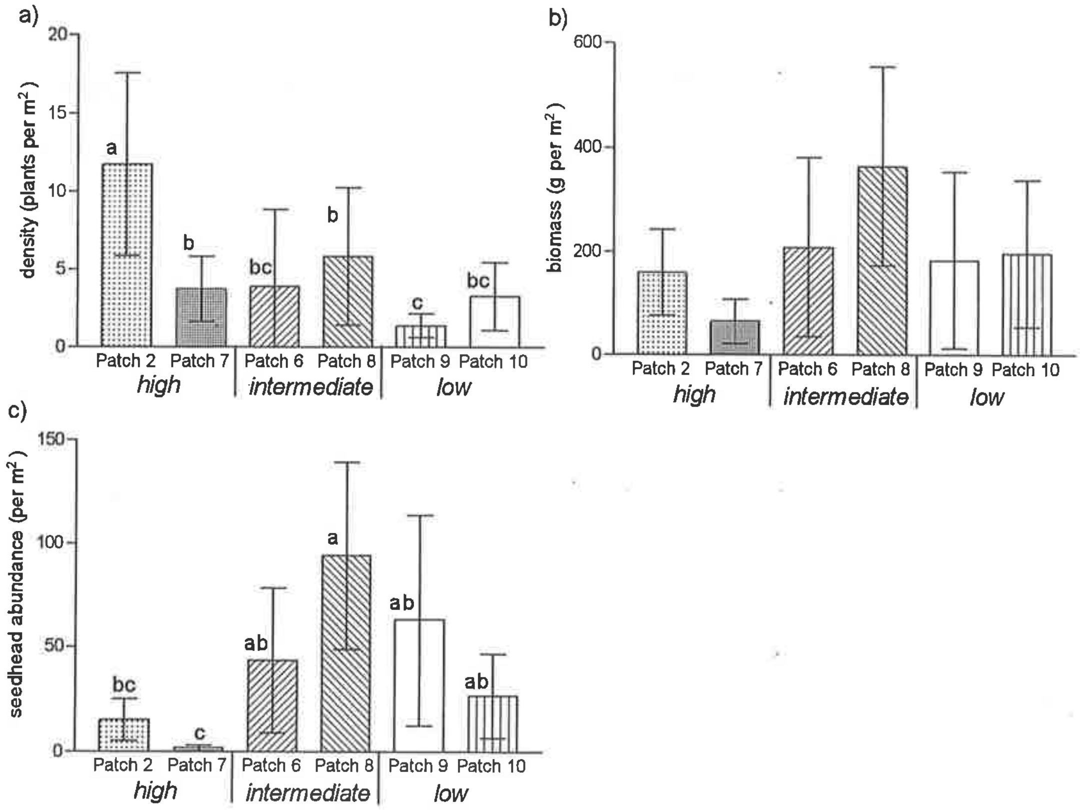
3.3.3.3 Population response of density, reproductive output and biomass

There were significant differences between patches of *E. elderi* density and reproductive output per unit area, but no difference between patches for the above ground biomass per unit area (MANOVA, within columns interactions, density: $P \leq 0.00001$, $df_{num}=1$, $df_{den}=77$; reproductive output: $P=0.0080$, $df_{num}=1$, $df_{den}=77$; biomass: $P=0.2352$, $df_{num}=1$, $df_{den}=77$; Table 3.6). The effect of patch was not consistent across the variables density, biomass and reproductive output. There was a higher density of *E. elderi* in Patch 2 than in all other patches, while the density in Patch 9 was significantly lower than Patches 2, 7 and 8 (Figure 3.7 a). Patches 9, 10 and 7 had significantly lower variances associated with *E. elderi* density (Bartlett's, $\chi^2=45.99$, $P \leq 0.0001$). There were no significant differences between patches for *E. elderi* biomass although the variance was lower in Patches 2 and 7 (Bartlett's, $\chi^2=30.6$, $P \leq 0.0001$; Figure 3.7 b). Seedhead production was highest in Patch 8, and lowest in Patch 7 and once more, the variances were lower in Patches 2 and 7 (Bartlett's, $\chi^2=104.6$, $P \leq 0.0001$; Figure 3.7 c). There was significantly higher seedhead production in Patches 8, 9, 6 and 10 than in Patch 7.

Table 3.6: MANOVA results for density, biomass and reproductive output per m^2 for March 1994 according to patch. Within column interactions from identity response matrix MANOVA results.

	Pillai's trace	Exact F	df_{num}	df_{den}	$P\leq$
patch	0.5038	25.3837	3	75	0.00001
intercept	0.6038	38.0943	3	75	0.00001
within column interactions					
density	0.3575	42.842	1	77	0.00001
biomass	0.0183	10.432	1	77	0.2352
reproductive output	0.0879	7.416	1	77	0.0080

Figure 3.7: *Erodiophyllum elderi* plant a) density, b) biomass and c) reproductive output from patches in broad categories of high, intermediate and low grazing pressures. Letters denote significant differences (Tukey's, $P\leq0.05$ on natural logarithm transformed data). Values are mean ± SD's.



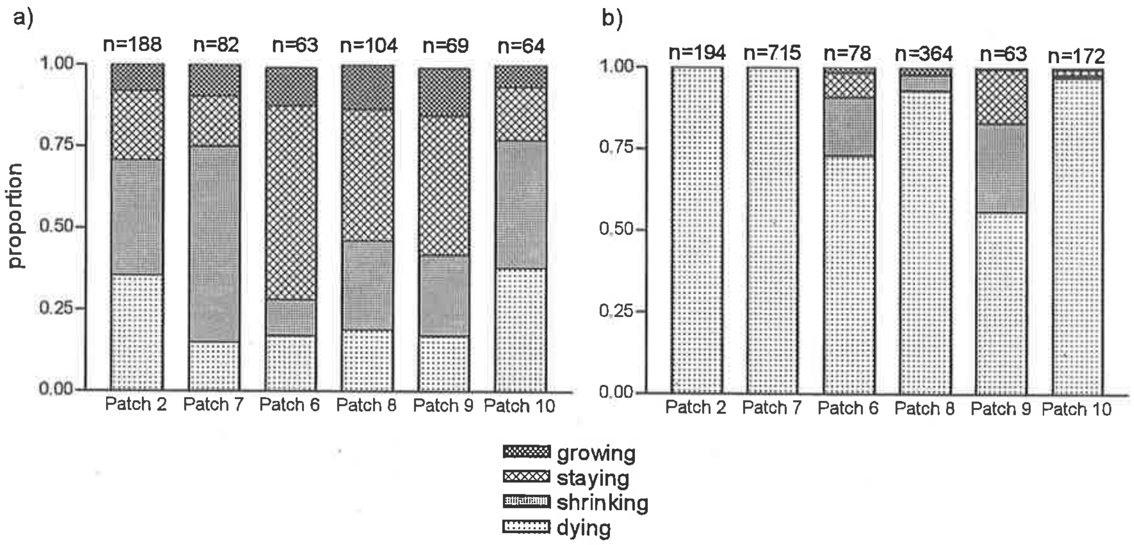
3.3.3.4 Transition between size classes

The proportion of *E. elderi* plants which changed between categories by either shrinking (that is parts of the plant died), growing or dying varied considerably between the patches in the period from March 1994 →August 1994 (Figure 3.8a). There was a lower proportion of individuals remaining in the same category in Patches 2, 7 and 10 (22%, 16% and 17% respectively) compared with Patches 6, 8 and 9 (60%, 41% and 43% respectively). The same three patches (2, 7 and 10) had more individuals which shrank between categories during that 6 month period than the other patches. There was little difference between the proportion of plants which had grown during the six month period. Patch 2 and 10 had the highest mortality rates (36% and 38% respectively) while all other patch mortality rates were below 20%.

During the period August 1994 →March 1995, nearly all *E. elderi* plants died in all patches (Figure 3.8 b). In most cases, *E. elderi* seedlings which had appeared in the permanent plots before the census in August 1994 did not survive until March 1995. Only one out of the 909 monitored plants survived in the heavily grazed patches (Patches 2 and 7). Patches 6 and 9 had the lowest proportion of plants die (73% and 56% respectively). Very few plants grew larger within this six month period and those that did were in Patches 6 and 8.

Very few *E. elderi* in the dead or dormant category re-sprouted from root stock (eight between March 1994 → August 1994, and a total of six re-sprouted between August 1994 → March 1995. Those with no above ground biomass within six months of initially being recorded as dead or dormant were considered dead rather than dormant.

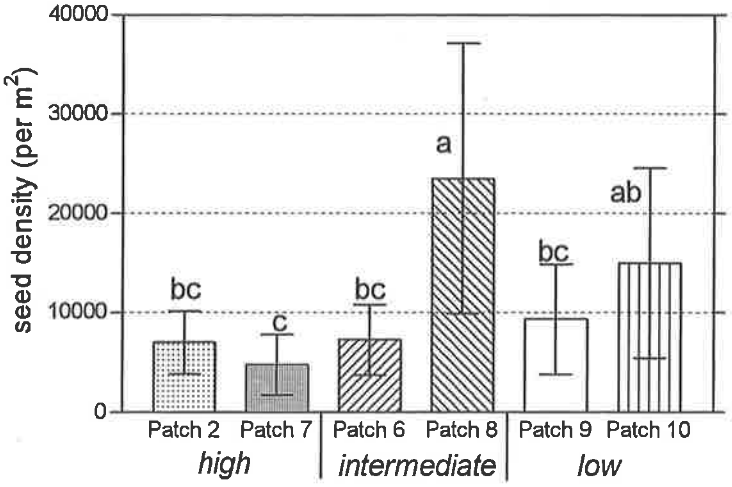
Figure 3.8: The proportion of *E. elderi* plants which died, shrank, remained in the same category or grew between a) March 1994 → August 1994 and b) August 1994 → March 1995. Values based on the number of plants indicated above patch bars.



3.3.4 Seed density and seedhead age class structure

The difference in *E. elderi* seed density between patches did not strictly correspond to patch grazing pressure (ANOVA, $P<0.0001$, F=10.92, n=6; Figure 3.9). Patch 8 had the highest seed density while the most heavily grazed patch (Patch 7) had the lowest. The large degree of overlap in seed densities between patches suggests that seed density values are highly variable. The two patches in the intermediate grazing pressure (Patches 6 and 8) had significantly different seed density values. Patches 8, 9 and 10 had the largest variances (Bartlett's, $\chi^2=54.68$, $P\leq0.0001$; Figure 3.9).

Figure 3.9: Total seed densities for each patch in the broad categories of high, intermediate and low grazing pressures. Values plotted are mean ± SD. Letters denote significant differences (Tukey, $P<0.05$ on ln(seed density+1) transformed data, N=15).

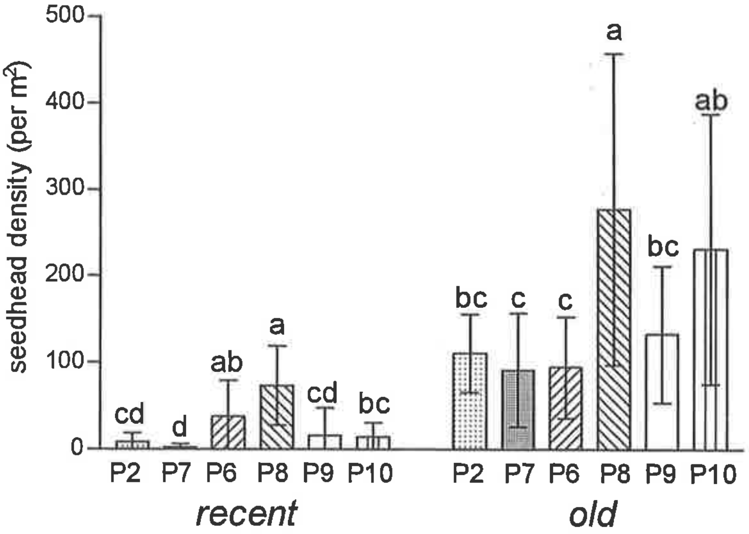


Erodiophyllum elderi seedhead densities differed between patches for both new and old seedheads (Table 3.7 a & b). The number of new seedheads was largest in Patch 8 and Patch 6 and lowest in Patches 2, 7 and 9 (Tukey, $P<0.05$; Figure 3.10). The variances were lower in Patch 2 and 7 than all other patches (Bartlett's, $\chi^2=77.66$, $P\leq0.0001$). Patch 8 and Patch 10 had the largest density of old seedheads and the largest variances (Tukey, $P<0.05$; Bartlett's, $\chi^2=42.19$, $P\leq0.0001$; Figure 3.10). Lower old seedhead density and variances were recorded in Patch 7, 6, 2 and 9.

Table 3.7: One-way ANOVA results for ln(density+1) transformed seedhead densities for a) new and b) old seedheads.

		a) new			b) old		
source	df	MS	F	P≤	MS	F	P≤
patch	5	21.06	14.44	0.0001	3.017	7.139	0.0001
residual	84	1.458			0.4227		

Figure 3.10: New and old *E. elderi* seedhead densities for each patch. Values plotted are mean ± SD. Letters denote significant differences (Tukey, $P<0.05$ on ln(density+1) transformed data within new and old seedhead age classes).



3.4 DISCUSSION

Grazing affected the density of grasses, forbs and *Erodiophyllum elderi* in the herbland communities and influenced the population dynamics of *E. elderi*. These effects are probably due to the influence of grazing on seedling germination patterns, the ensuing density-dependent effects in areas where seedling densities were large, the trampling and browsing effects of sheep, and the selective removal of palatable species which allowed competitive release of non-preferred species. Grazing reduced within patch variability of *E. elderi* density, seed density and seedhead production and through the reduction of seed bank input, has an overall negative effect on heavily grazed *E. elderi* populations. However, the fact that *E. elderi* populations persist despite long term heavy grazing suggests that grazing effects are unlikely to result in the widespread temporal extinctions of *E. elderi*, or these effects take longer than a century of grazing to become apparent.

While the density of grass was lower in the heavily grazed areas during the first year of this study, total seedling densities were often higher in the heavily grazed patches during the major germination periods. The initial lower grass density in heavily grazed patches may reflect the selective browsing of grass or the limited sites available for regeneration by seed due to the large area occupied by persistent grass basal areas (Tremont 1994). The massive emergence of seedlings in the heavily grazed patches after a big rain event was probably due to the increased bare area available for seedling emergence through trampling and soil destruction in these patches (McIntyre and Lavorel 1995). These germination patterns did not reflect palatability differences between grazing pressures which may be because the tiny seedlings were too small to be browsed. In contrast, all plants were large during the initial surveys when palatability preferences were apparent. Despite repeated massive germination there was a low survival of seedlings through to summer in all patches monitored. *E. elderi* seedlings emerged every year in August but survival until maturity never occurred in the heavily grazed patches.

Essentially the Koonamore flora is comprised of species displaying a winter germination strategy irrespective of grazing pressure during the three years examined. This is in contrast to the lack of seasonality found previously for short-lived species in the Koonamore Vegetation Reserve (Noble and Crisp 1979/80). However, Noble and Crisp concluded that five years of data is not enough to account for rainfall variability effects on vegetative growth and the limited duration of this study may not reflect long term patterns. Rainfall across this region typically displays no seasonality (Carrodus, Specht *et al.* 1965) and the predominance of winter germination recorded in this study probably reflects the effects of low temperature and low evaporation during the winter months.

During *E. elderi* pulses of growth such as the one examined in this study, *E. elderi* is locally dominant in the herb communities in terms of biomass. Because of their larger size, *E. elderi* plants may exert strong competitive effects on the smaller plants within the community during these pulses of growth. The conditions required for a pulse of *E. elderi* growth are not well known but are probably linked to high annual rainfall such as that occurring two years prior to the pulse examined in this study. Long term photographic records are examined to determine the synchrony between pulses of *E. elderi* and whether they are correlated with rainfall variables in Chapter 4.

Erodiophyllum elderi plants were more likely to shrink or die in the heavily grazed patches. This may be due to a) increased density-dependent effects due to higher seedling densities (Schupp 1995; Schupp and Fuentes 1995), b) poor root systems due to the smaller sized plants, c) decreased litter accumulation which may decrease favourable micro-sites (Facelli and Pickett 1991), or d) trampling effects during establishment and growth phases (Osborn *et al.* 1932; Tremont 1994). Although there was no visible evidence of sheep browsing *E. elderi* plants, this is another possibility which should be considered because it would also result in a reduced plant size and reduced survival rate. The effects of leaf litter on germination and growth of seedlings are examined in Chapter 7.

Although *E. elderi* plants are reported to re-sprout from the base when conditions improve (Cunningham *et al.* 1992), this is unlikely to be important as a long term population persistence mechanism. When environmental conditions allow *E. elderi* plants to re-sprout, they may have a competitive advantage over seedlings in the community due to size differences (Connell 1983; Goldberg and Werner 1983) as established root systems enable rapid growth. Under these circumstances, the re-sprouting plants will be able to reproduce quickly, adding input into the seed bank. It was not possible to examine the effects of grazing on the ability of plants to re-sprout as this phenomenon was so uncommon. However, the fact that *E. elderi* plants were smaller in the heavily grazed patches may suggest that they have smaller root systems and will thus be less likely to re-sprout once conditions become favourable.

The individual *E. elderi* plant response to the presence of grazing was the same as the population level response for seedhead production and to a lesser extent biomass. Although individual *E. elderi* plants are much smaller in heavily grazed patches, their density per unit area is greater, resulting in a similar biomass per unit area between patches. Despite the similarity between biomass per unit area in the different patches, the reproductive output per unit area was lower in the heavily grazed patches. The reduced seedhead production may reflect either the browsing of flowers by sheep in the heavily grazed areas or density-dependent effects on seedhead production due to the higher density of *E. elderi*.

Seedhead production in one of the intermediately grazed patches was higher on both an individual level and a population level than in any other patch examined. The first explanation for this pattern is increased resources for *E. elderi* growth and reproduction in this patch through the selective removal of other species within the community (McIntyre and Lavorel 1995). Such removal may cause competitive release of *E. elderi* because it is not preferred forage (Cunningham *et al.* 1992). Alternatively, *E. elderi* growth may be enhanced in the intermediately grazed patch due to physical characteristics of the patch which make it more suitable. Physical site differences, if they exist, are termed between patch variability (Chesson 1981).

Although the reproductive output per *E. elderi* plant is high inside the Reserve due to the large size of plants and the lack of browsing on flowers, the density of *E. elderi* plants was lower than in patches in the other grazing pressures. Due to the lower density of plants, seedhead production on a per unit area is lower than in the intermediately grazed Patch 8. Plants of all species were typically larger inside the Reserve which may result in strong competitive interactions.

It is difficult to explain the variation in seed densities between patches as many processes interact to produce this pattern. Grazing influences the dispersal and fate of seeds and fruits through the creation of bare ground (Tremont 1994), reduced vegetation cover (Watkinson 1978) and direct trampling effects. Seed dispersal inside the Reserve may be reduced because of the large amount of standing biomass which acts as seed traps. This would result in a large degree of patchiness in seed distribution, and hence *E. elderi* plant distribution (seedhead dispersal is examined in Chapter 5). Seedheads were scattered throughout the heavily grazed patch resulting in a reduced variance of seedhead density. However, there are areas in the heavily grazed patches with a large build-up of seedheads, although these areas of seedhead accumulation did not occur in the permanent plots. The high seedhead density in these areas could result in increased density-dependent effects after germination has occurred.

The reduced seedhead production in the heavily grazed patches was observed on both the individual level and on a population level. However, these heavily grazed populations persist despite this heavy grazing. The consequences of seed loss for a population varies with a) the degree of dependence on the seed bank, b) variation in seed escape through dispersal and predator satiation and c) the opportunity for compensation for this loss (Louda 1989). As *E. elderi* is a short-lived species, the seed bank is crucial for long term persistence and, therefore, seed protection from predators or compensation for years of low seedhead production, such as that recorded in this study, must have a role in *E. elderi* persistence in the heavily grazed areas. During years of high seedhead production it is possible either that grazing pressure on flowers is reduced because more palatable species are present, or that flower densities are sufficiently high that the grazing herbivore (predator) is satiated and there is still sufficient input into the seed bank. The reduced seed bank in the heavily grazed areas may suggest that the chance of local extinction is higher in these areas.

There are mechanisms which cause within patch variability in all but the most heavily grazed areas. For whatever reason, plants growing in particular sites within the low to intermediate grazed patches, grow better than plants in different locations within the same patch. The importance of areas of high productivity scattered throughout regions which are less suitable for plant growth and survival are well known for arid regions (Osborn *et al.* 1932; Noy-Meir 1973; Davidson and Morton 1981; Kemp 1989; Gutterman 1994; Schupp 1995; Schupp and Fuentes 1995). The positive association between the mean and variance for density, seedhead production and biomass shows that grazing exerts a strong effect on these variables (Garvey *et al.* 1998). Instead of a large variability in seedhead production, density, and biomass of plants, grazing has a homogenising and reducing effect on these variables. Through the reduction in spatial variability within patches, grazing may influence the long term patterns of the herbland communities in a negative way.

4. Long-term population dynamics

4.1 INTRODUCTION

The degree of synchrony between local population fluctuations may influence the overall population persistence of a patchily distributed species. From a theoretical perspective, metapopulation persistence occurs through the recolonisation of locally extinct patches via dispersal from extant neighbouring populations (Levins 1969; Hanski 1989). However, recolonisation can only occur if there is some degree of asynchrony in the temporal extinctions of local populations. If the dynamics of local populations are highly synchronous, then extinction events are likely to affect several small populations simultaneously (Harrison and Quinn 1989) or result in the extinction of the entire population. Therefore, when dispersal between local populations occurs, population asynchrony effectively spreads the risk of extinction over an entire metapopulation (den Boer 1968; 1981).

Although metapopulation models focus on asynchrony in terms of local extinctions, the synchrony of other population parameters may also influence metapopulation persistence. In real populations, temporal extinction and colonisation events are very difficult to study and the synchrony of other population parameters are studied instead (Thomas 1991; Ranta *et al.* 1995). Population size, for example, can be examined instead of local extinction events with the assumption that if the fluctuations in population size are highly synchronous between the series of local populations then extinction events are likely to be synchronous as well.

Dispersal is an important process which can increase population synchrony between a series of local populations through spatial averaging (Hanski and Woiwood 1993). Although dispersal increases synchrony, it increases the long-term persistence of a metapopulation through the recolonisation of temporally extinct local populations (Burgman *et al.* 1993) or prevents extinction of declining populations (Brown and Kodric-Brown 1977). Population synchrony is also unlikely to be detrimental to the metapopulation when all local populations are increasing. Hence, population synchrony only decreases metapopulation persistence if it results in highly correlated local extinctions (Hanski and Woiwood 1993). Therefore, it is important to consider the mechanism driving population synchrony and whether it affects metapopulation persistence adversely.

There is a paucity of long-term spatio-temporal data for real populations to test models of metapopulation persistence. Studies from a range of habitats show that synchrony between populations decreases as the distance between local populations increases and the ecological differences between sites increase (Thomas 1991; Hanski and Woiwood 1993; Heikkila *et al.* 1994; Ranta *et al.* 1995). Although synchrony decreases with increasing distance between populations for fish, bird and mammal populations across Finland, population processes were rarely completely independent of each other (Heikkila *et al.* 1994; Ranta *et al.* 1995). For example, if a local population increased in size in one location, population size was likely to increase simultaneously in other locations as well and conversely for population decline. In most cases, synchrony was increased through dispersal between populations, although it is likely that other factors were involved such as environmental conditions.

Although dispersal between animal populations often synchronises their dynamics, the effect of dispersal on the dynamics of plant populations is largely unknown. Dispersal for many arid plant seeds will only increase population synchrony between populations separated by small distances because their dispersal is typically limited (Ellner and Shmida 1981). The limited movement of seeds may make patchily distributed arid species highly vulnerable to local extinctions through low rates of recolonisation if they depend on metapopulation processes for long term persistence. However, infrequent and rare dispersal events may promote long term population persistence via dispersal between patches.

In addition to synchrony being driven by dispersal, widespread climatic conditions are also likely to create population synchrony. In arid systems, there are two scales of water availability which may influence population synchrony for species driven by rainfall (eg. ephemerals Went 1949). Spatial and temporal water heterogeneity is caused by variable rainfall across arid landscapes (Sharon 1972; Stafford Smith and Morton 1990; Friedel *et al.* 1993) and run-on areas accumulating water. While particular rain events in arid regions are variable across the landscape, the effects of drought or a particularly wet year are widespread (Chesson 1991; Hanski and Woiwood 1993). Spatial variability in rainfall may increase asynchrony between populations, while widespread effects of drought or wet years will most likely synchronise them. Rainfall heterogeneity may therefore be crucial for population persistence in arid areas depending on the degree to which it drives the population dynamics, the resulting degree of population synchrony, and the role that population synchrony has on long term species persistence. Other factors such as competitive interactions may also influence population synchrony as these are reported to change the dominance of species in arid regions (Noble and Crisp 1979/80).

In this chapter I investigate the long term population dynamics of a series of local populations of *Erodiophyllum elderi*. Specifically I ask: 1) Are the fluctuations of local populations of *E. elderi* synchronous? 2) Does the degree of synchrony between local populations decrease as the distance between populations increases? 3) How dependent are the population dynamics on rainfall? 4) What is the degree of rainfall heterogeneity over the same spatial scale? and 5) Are the dynamics of the broad taxa within the local populations correlated, or is there evidence of strong competitive effects which may influence population synchrony?

4.2 METHODS AND ANALYSIS

To determine the long term fluctuations of *Erodiophyllum elderi* populations I examined the visible biomass of *E. elderi* in the Koonamore Vegetation Reserve photo-records. The Koonamore Vegetation Reserve photo records began in 1926 and, although there are some years missing, is one of the most comprehensive photo series in an arid region in the world. However, the analysis of photographic records can be difficult because different cameras may be used from year to year, the angle of the photo may change and photos may be taken at different times of the day (Noble 1977; Noble and Crisp 1979/80). Therefore, I conducted a pilot study to determine the degree of accuracy of using photo records to estimate population fluctuations.

4.2.1 Photo-point comparison technique assessment

I conducted a pilot study in March 1994 to determine the accuracy of using photographic records to estimate the rank of the biomass of *E. elderi* populations by comparing rank biomass with actual biomass. At each of ten sites of variable *E. elderi* biomass and density, a 1x3 m area was pegged and photos were taken from different angles and distances (5 m directly in front of the 1 m edge of the pegged quadrat, 8.5 m at a 45° angle, and 16 m at a 45° angle). The above ground *E. elderi* biomass within the pegged quadrat was removed, dried in an oven at 80°C for 24 hours and then weighed.

Photos of the ten harvest sites were ranked in order of increasing biomass by a series of pair-wise comparisons. Each pair of photos were compared to determine which photo had the largest visible biomass of *E. elderi*. The ranks of all pairs were collated to determine the rank order of photos from highest to lowest biomass. The ranking procedure was repeated for photos from each distance and angle away from the pegged quadrat and then with photos from each site with randomly selected angles. This procedure was repeated a week later to check the consistency of the ranking values. The rank order of the photos was compared with the rank order of the actual biomass from the harvested areas using Spearman rank correlation.

4.2.2 Relationship between reproductive output and biomass

The relationship between the reproductive output and biomass of *E. elderi* plants was examined to determine whether comparing visible biomass in a photo was a useful indicator of reproductive output. I could not examine the reproductive output directly from the photo-records because seedheads were not always easily visible. The biomass of 116 individual plants was measured on 18-Aug-1994 after the number of seedheads on the plants were counted. The above-ground biomass of individual plants were harvested from four different populations to minimise the chance of a site specific relationship being detected. Harvested plants were dried in an oven at 80°C for 24 hours and their dry weights measured. The reproductive output per plant was correlated with the aboveground dry biomass with Pearsons Correlation co-efficient.

In this study I assume that if the number of seeds per seedhead varies, it increases with increasing biomass and will therefore be taken into consideration with larger biomass.

4.2.3 Long term photo-series

Because the ranking procedure of photos was successful for predicting the rank biomass of harvested areas, I was confident that I could use this method for the long term photo series. The long term KVR photo-records (1923-1994, based in the Department of Botany, The University of Adelaide) were examined to determine the ranks of biomass fluctuations for *E. elderi* populations. A total of ten series, representing eight different sites, had *E. elderi* visible. Photo-points were spread over an area of 390 hectares in the Koonamore Vegetation Reserve (Figure 2.4, page 26) and are described in Appendix 2, page 188.

Each of the ten photo series were ranked according to visible biomass of *E. elderi*, grasses and all other short-lived species. Although some individual grass and ephemeral species could be seen in photos, species could not always be identified. The species most likely to be in the photos (based on current species present and recorded notes on the photos) are grasses: *Stipa nitida* and *Schismus barbatus* and forbs: *Eriochiton sclerolaenoides*, *Dissocarpus paradoxa*, *Scleroleana patenticuspis*, *S. obliquicuspis*, *Salsola kali* and *Erodium cygnoreum*.

Instead of comparing each pair of photos for the entire series, I placed them into preliminary levels of high, medium, low or zero *E. elderi* biomass. I then performed a series of pair-wise comparisons (as described in section 4.2.1) of the photos within each level to obtain a sequential ranking. The photos at the high and low ends of each adjacent level were then compared to determine a sequential ranking of all photos in the photo-series. This rank order was then checked by pair-wise comparisons between adjacent photos to ensure that the rank order for the entire series was accurate. Photos with no *E. elderi* present were given equal zero ranking. This method deviates slightly from that of Noble (1977) by a preliminary placing into broad levels to reduce the time taken to make all comparisons. After several weeks the ranking procedure was repeated and found to be consistent.

Although large *E. elderi* plants were visible in the photos, *E. elderi* seedlings are not. However, because seedlings do not contribute to the seed bank at that stage, invisibility in the photos is not a problem. Both living and dead *E. elderi* material were considered in the estimates as it was not possible to distinguish between the two in black and white photos. Large dead *E. elderi* plants are often visible in photos for several years until they decay. Therefore, the presence of living biomass may be over-estimated and there may be years with a positive ranking when all the plants were actually dead. This is a common problem when examining photo series (Noble 1977). The colour photos from 1980 - 1994 were also examined as it was easier to see *E. elderi* in them and compared with the ranking for the same years for the black and white photo series.

The photo-point sites were examined in December 1996 to determine the direction of the photos with respect to the *E. elderi* populations. Although the initial photo records were taken at different times of the year, the latter photos were taken consistently during December (Appendix 3, page 189). I am confident that different photo times did not invalidate the technique. Unfortunately there was a large gap in the photo-records between 1932 and 1969 for many of the photo-points.

4.2.3.1 Synchrony of photo-point **E. elderi** *biomass dynamics*

The correlation between *E. elderi* biomass dynamics for each photo-point site was examined to determine whether the degree of spatial synchrony between *E. elderi* populations decreased as the distance between populations increased. Spearman rank correlations between the biomass ranks of all possible pair-wise combinations of photo-point sites were calculated. The Spearman rank coefficients were plotted as a function of distance between photo-points. Significance values were not assigned to the individual Spearman correlation values as correlations among all possible pairs of sites resulted in a lack of independence between some pairs of correlations in a similar manner to Thomas (1991).

At two of the sites (Q30 and Q40), photos are taken 10 m apart facing each other, providing two series of photos with partially overlapping fields of view. The correlation between *E. elderi* biomass ranks for each series within Q30 and Q40 were compared to determine whether photo-points separated by 10 m were ranked similarly. Because two photo stakes were in each of the Q30 and Q40 quadrats, there are two series of photos for each of these populations. The biomass dynamics within each site should therefore have similar dynamics. Spearman rank correlations were used to examine the degree of correlation between the photos within the same population.

4.2.3.2 Population dynamics of grasses and **E. elderi**

To determine whether the biomass of grasses and *E. elderi* fluctuated similarly through time within a site, I examined the biomass dynamics of the two taxa within each photo series. If the biomass fluctuations of the two taxa differ, it may indicate possible competitive interactions which may influence population synchrony between *E. elderi* populations or dissimilar responses to environmental variables. The proportion of years with *E. elderi* and grasses visible in the photos were calculated for each photo-point. The average proportion of years with *E. elderi* biomass visible was compared to the proportion of years with grass biomass visible using a paired t-test with pairing by photo-point. The proportion of years with *E. elderi* visible was calculated from the year after the first time they were observed within a photo series to ensure results were not biased by the possible colonisation of patches since the photo-records commenced. The correlation between the grass and *E. elderi* biomass dynamics within each photo-series was calculated using the Spearman rank correlation.

4.2.3.3 Correlation between biomass dynamics and rainfall

Correlations between the biomass ranks of the photo series and rainfall were conducted to determine the importance of rainfall as a driving factor for *E. elderi*, grass and forb population dynamics. Daily rainfall records for Koonamore Station were obtained from the South Australian Bureau of Meteorology. These records are largely continuous since 1888, although the ones post-1923 only are of relevance here. The occasional missing values were interpolated from the nearest neighbouring stations.

For each photo-point, the biomass ranks of *E. elderi*, grasses, and all forbs were correlated with rainfall. The following rainfall variables were calculated from the date of each photo: total rainfall in the previous 12 months, total rainfall in the previous 24 months, total rainfall 12-24 months previously, the number of rain days in the previous year, and the number of rain days with rainfall > 5 mm, > 25 mm, and > 50 mm in the previous year. Spearman rank correlation between each of these rainfall features and the biomass ranks for *E. elderi*, grasses and ephemerals were performed for each photo-point. The correlations were repeated for the *E. elderi* biomass dynamics from the year after they were first observed to ensure the data were not biased if colonisation had occurred since 1923.

The correlation coefficients between biomass dynamics and the rainfall variables for each photo point site were compared with one-way ANOVAs. Separate analyses were conducted for *E. elderi*, grasses and forbs to determine whether different rainfall variables affect the different taxa. Tukey post-hoc comparisons were used for each taxa group to determine where differences were.

4.2.4 Spatial rainfall variability

Rainfall was measured across an area slightly larger than the Reserve to determine whether the degree of spatial variability across that area. The rainfall in the six *E. elderi* patches described in Chapter 2 was monitored every few months between 17-Jun-1994 and 5-Apr-1997. The Patch 10 rain gauge was randomly assigned as the focal gauge to compare with all other rain gauges. This avoided making all possible pair-wise comparisons. Cumulative rainfall between readings were tested for normality and the correlation between rain gauge and the rainfall in Patch 10 were determined with Pearson correlation.

4.3 RESULTS

4.3.1 Photo-point comparison technique assessment

The correlation between photo biomass ranks and actual biomass was good with photos taken from the same angle and distance at both ranking sessions (Table 4.8). The correlation between actual biomass and biomass ranks of photos taken from different angles were less accurate (Table 4.8). Therefore, I decided that rank comparisons would be more accurate within a photo series rather than between photo series because of the range of angles and distances from the *E. elderi* populations in the Reserve photo series. Biomass for the harvest sites ranged from 54 g.dwt.m^{-2} to

716 g.dwt.m^{-2}. Estimates of actual biomass from the photo records were considered unreliable and were therefore not attempted.

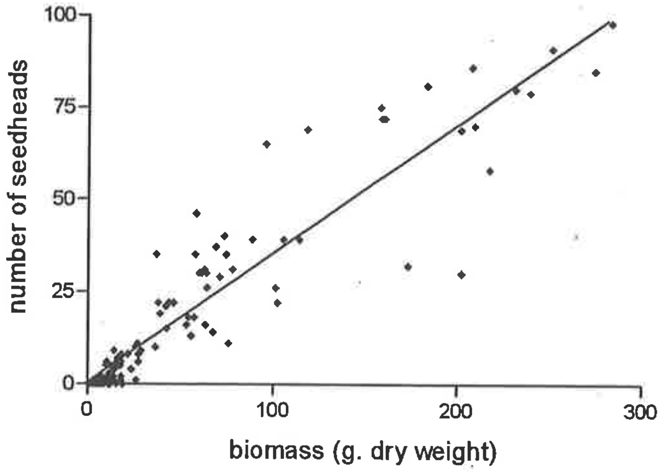
Table 4.8: Spearman rank correlations for harvest sites for the two ranking sessions. Photos were selected from random distances for the final column. In all cases d.f = 1, 8.

	16 m	8.5 m	5 m	random selection
ranking 1	r=0.891, *P*<0.001	r=0.867, *P*<0.002	r=0.842, *P*<0.004	r=0.685, *P*<0.035
ranking 2	r=0.867, *P*<0.002	r=0.903, *P*<0.001	r=0.891, *P*<0.001	r=0.673, *P*<0.039

4.3.2 Relationship between reproductive output and biomass

There was a strong correlation between *E. elderi* plant biomass and seedhead production (Pearson correlation, r=0.9348, P<0.0001, n=116; Figure 4.1). Therefore, the ranking of biomass of the photo-record corresponds also to a ranking of the reproductive output.

Figure 4.1: Relationship between reproductive output and biomass per plant for 116 *E. elderi* plants harvested from several populations in March 1994. Linear regression best fit included.



4.3.3 Long term photo series

Rank orders of the photo series biomass were very repeatable. The ranking of biomass within a photo series was the same when repeated several weeks after the initial ranking. The ranks of the colour photo series were also the same as the black and white photo series.

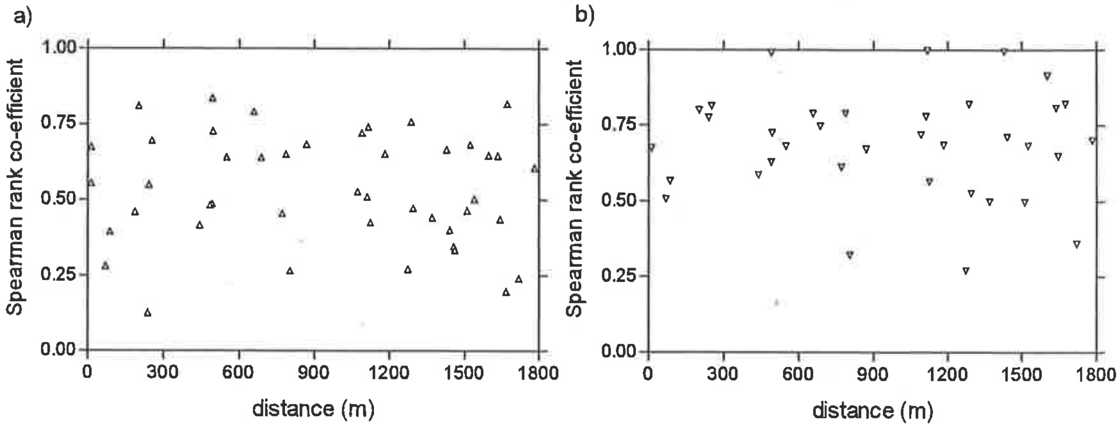
Individual *E. elderi* plants that were followed through time in several photo-series were not visible for more than 2-3 years. In all cases, this is likely to be an overestimate of their survival as dead biomass can remain relatively intact for several years (personal observation from photo-points described in Chapter 2).

4.3.3.1 Synchrony of photo-point **E. elderi** *biomass dynamics*

Biomass dynamics between *E. elderi* populations were highly synchronous. The degree of synchrony of the biomass dynamics of *E. elderi* populations did not decrease with increasing distance between populations (Figure 4.2 a). When the correlation between photo-points was calculated using *E. elderi* since first observation in each photo-point, the overall level of synchrony between populations increased (Figure 4.2 b). However, there was still no decrease in synchrony with increasing distance between populations.

There was a high degree of correlation between photo-points separated by 10 m within the same population for both *E. elderi* and grass dynamics (Spearman rank, $r=0.674$, $P=0.0002$ for Q30 *E. elderi*, $r=0.553$, $P=0.004$ for Q40 *E. elderi* and $r=0.823$, $P<0.0001$ for Q30 grasses, $r=0.853$, $P<0.0001$ for Q40 grasses, $n=25$ for all tests).

Figure 4.2: Spearman rank correlation coefficient between all pairwise comparisons of photo-points. *E. elderi* biomass dynamics plotted against distance between photo-points a) all years of photo-point data, b) data since the first observation of *E. elderi* within each photo-series.



4.3.3.2 Population dynamics of grasses and **E. elderi**

The proportion of years with *E. elderi* visible in the photos was lower than for grasses (t-test, t=10.70, df=7, *P*<0.0001; Figure 4.3). On average *E. elderi* were observed in the photo-points 25% of the time with grasses visible 76% of the time. In contrast, there were at least some short-lived forbs visible 95% of the time.

Erodiophyllum elderi were visible 30% of the time when examining photo-series from the year after daisies were first observed in each photo-point. In some of the photo-points, *E. elderi* plants first appeared well after photo records began (Appendix 3, page 189). The maximum continuous time with no *E. elderi* visible between photos in a photo-point was 14 years in PP8 between 1975-1989.

Grass and *E. elderi* biomass dynamics were positively correlated in all populations (Table 4.9), although this varied between populations (Spearman r, r=0.744, for PPQ6-80NW, and r=0.407, for PP8). The presence of grass did not necessarily mean that *E. elderi* were visible, although the converse is true, and when *E. elderi* were visible, grass were also visible.

Figure 4.3: The proportion of years with biomass visible in the photo series for *E. elderi* and grasses. Values include mean ± SD, n=8.

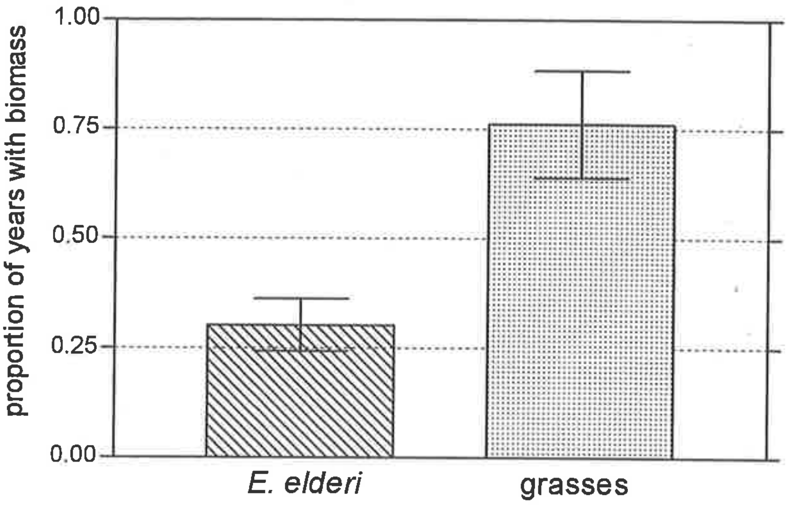


Table 4.9: Spearman rank correlation between grass and *E. elderi* biomass ranks for each photo-point. Values are Spearman r, n and *P* for each correlation.

Photo-point	Sr	n	*P*≤
PP8	0.407	31	0.0230
PP4	0.472	43	0.0014
Q6-80 NW	0.744	27	0.0001
PP9 (KVR)	0.330	49	0.0210
Q30W	0.553	27	0.0030
Q40 NW	0.460	25	0.0210
PP3	0.489	47	0.0005
PP7 (KVR)	0.411	45	0.0050

4.3.3.3 Correlation between biomass dynamics and rainfall

The correlation between rainfall and the biomass dynamics of *Erodiophyllum elderi*, grass and ephemerals were highly variable (Figure 4.4 a-d). No statistical interpretation of the significance of individual Spearman rank correlation values were attempted due to the repeated analysis of the same data. As the photo-points differed in their strength of correlation between biomass ranks and rainfall, it is not possible to determine a single driving factor. However, rainfall 12-24 months before the photos were taken had the lowest correlation with any of the biomass considered (Figure 4.4 a-d).

Erodiophyllum elderi biomass ranks were not statistically correlated more strongly with any aspect of rainfall when all data were included (ANOVA, F=1.481, n=7, *P*=0.2042; Figure 4.4 a). However, when *E. elderi* biomass ranks were considered from the year after they were first observed in the photo-points the number of rainfall events greater than 50 mm was most highly correlated with the biomass dynamics (ANOVA, F=4.539, n=7, *P*=0.001; Figure 4.4 b). The rainfall 12-24 months previously and the number of rain days with more than 5 mm precipitation had the lowest average correlation with the biomass ranks of *E. elderi* in both cases.

Grass biomass dynamics were driven primarily by the previous 24 months rainfall (ANOVA, F=4.609, n=7, *P*=0.0009; Figure 4.4 c). Likewise, the previous 24 months rainfall was most strong correlated with the forb biomass ranks (ANOVA, F=2.917, n=7, *P*=0.0181; Figure 4.4 d). The response of the forbs to rainfall is similar to the response for grasses partly because the grasses contributed to the overall forb estimates. Rainfall in the previous 24 months had a strong effect whereas the rainfall 12 - 24 months previously had the weakest effect on forb dynamics.

Biomass dynamics for PP3 and the rainfall for Koonamore Station (Figure 4.5 a & b) show dips and peaks occurring at the same time for the relative biomass ranks of grasses and *E. elderi*. However, there were many years when no *E. elderi* were observed in the photographs. The rainfall during 1975 and 1988, when there were no *E. elderi* observed for 14 years continuously in PP3, did not seem particularly low compared with other years (Figure 4.5 b). The widespread lack of *E. elderi* observed across the Reserve in that period was immediately after Koonamore had received an annual rainfall of more than three times the average annual rainfall.

Figure 4.4: Spearman rank correlations of the biomass of photos against rainfall a) *E. elderi* biomass, b) *E. elderi* biomass since first observation, c) grass biomass, and d) forb biomass. Boxes show 25th, 75th and 50th percentiles and whiskers extend to maximum and minimum values. Different letters indicate significant differences (Tukey, $P<0.05$, after one-way ANOVA).

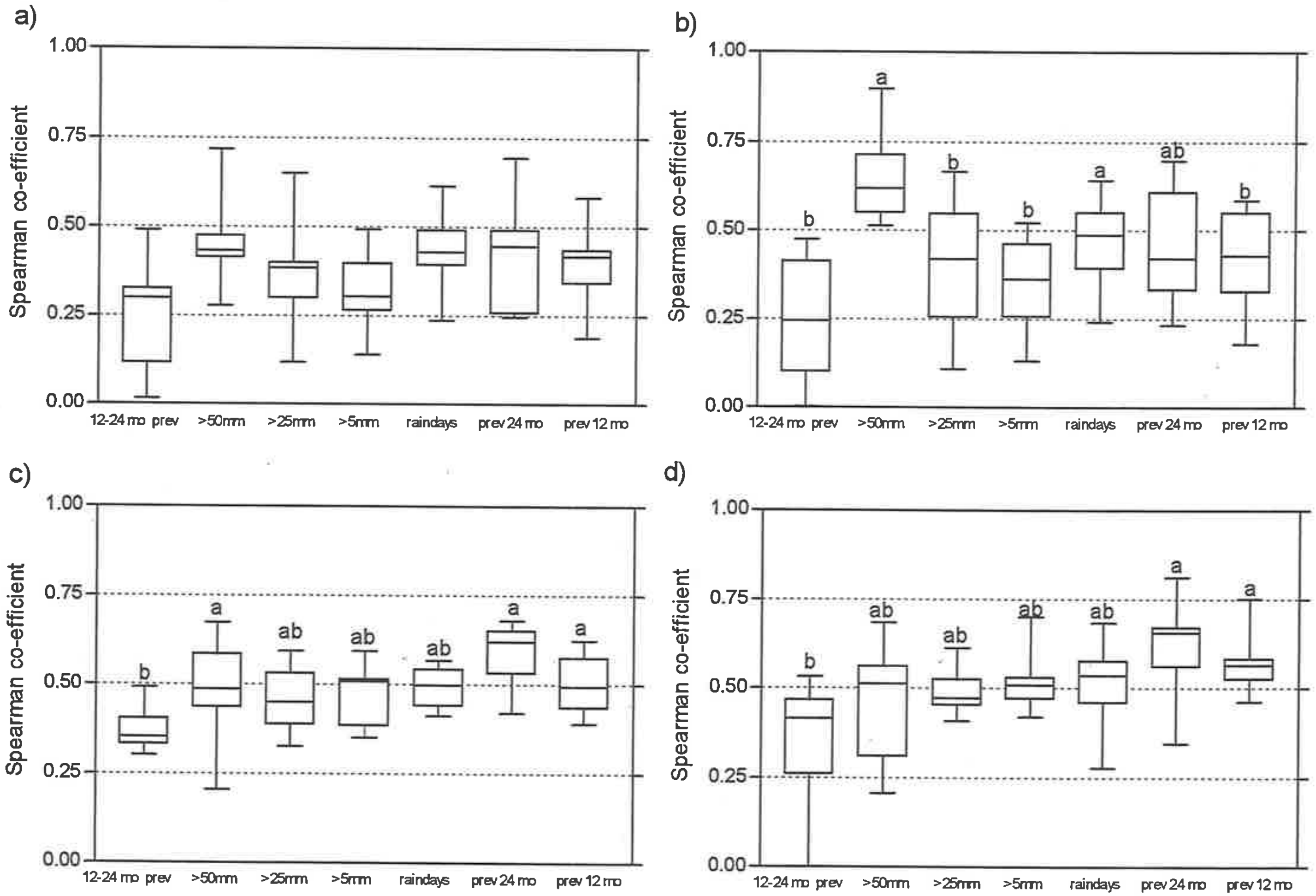
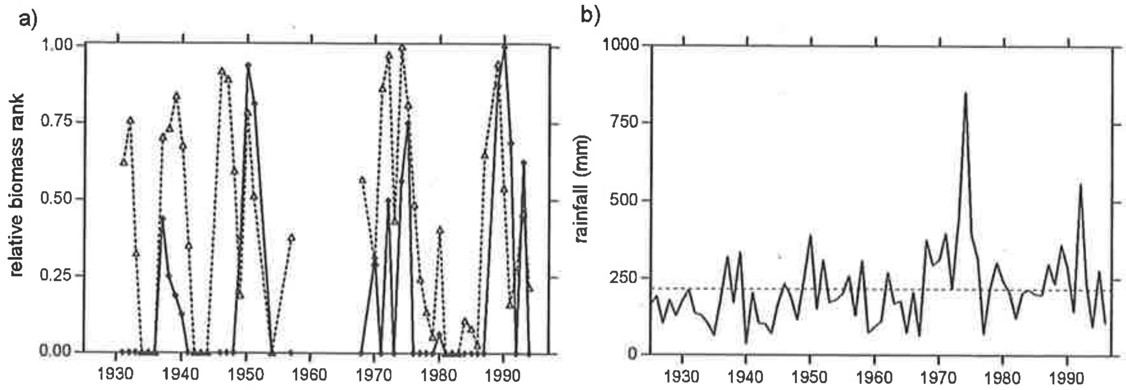


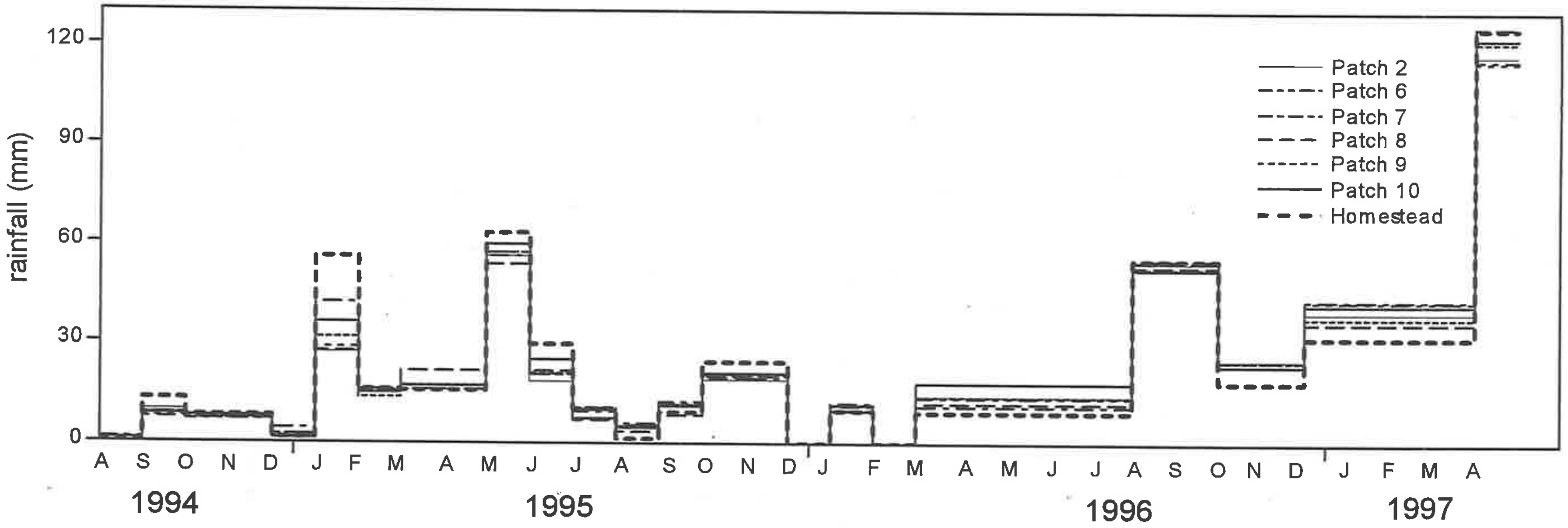
Figure 4.5: a) Example of *E. elderi* (solid line) and grass (dashed line) relative biomass ranks for PP3. Note that photos were not taken between 1953 and 1967, b) annual rainfall for same period with mean annual rainfall of 215 mm indicated with a dashed line.



4.3.4 Spatial rainfall variability

Rainfall in rain gauges separated by distances comparable with the size of the Reserve were highly correlated over the three years examined (Pearson correlation, r^2 ranged between 0.992 and 0.997 for correlation with Patch 10, n=22, $P<0.0001$; Figure 4.6). In addition to this, the rainfall in Patch 10 was highly correlated with the rainfall measured at Koonamore Homestead (Pearson correlation, $r^2=0.9757$, n=22, $P<0.0001$) which is the rainfall gauge used for correlation between rainfall and biomass dynamics. The two closest gauges (Patches 6 & 7) showed very little difference in cumulative rainfall between readings (average difference = 0.5 ± 3.11 mm, mean ± SD) except on one occasion when the difference was 13.5 mm (30-Jan-1995). The cumulative rainfall over a month and a half for this period in Patch 7 was much higher than in all other patches with rainfall ranging between sites from 27 - 42 mm. On two occasions, no rainfall was recorded in any patch after a period of several months.

Figure 4.6: Cumulative rainfall between field trips for each daisy patch. The vertical spread indicates the degree of rainfall variability while the width of the horizontal bars indicates the time between rainfall collection periods.



4.4 DISCUSSION

Erodiophyllum elderi populations had highly synchronous biomass dynamics which is probably due to their direct and rapid response to rainfall. Although there was a small degree of rainfall heterogeneity over the same spatial scale over a period of three years, it was not sufficient to create asynchronous population dynamics. Consequently, the basic premise of population asynchrony between local populations in metapopulation theory does not apply over the spatial or temporal scale investigated for *E. elderi*.

Synchrony of biomass dynamics between local *E. elderi* populations did not decrease as the distance between sites increased. This is in contrast to other taxa such as butterflies (Thomas 1991), beetles (den Boer 1981), microtine rodents (Heikkila *et al.* 1994), and British moths and aphids (Hanski and Woiwood 1993). In these studies, nearby populations were often synchronous and the degree of synchrony decreased as the distance between populations increased. Population synchrony between neighbouring populations was attributed to dispersal between populations (Thomas 1991; Heikkila *et al.* 1994; Ranta *et al.* 1995). As population synchrony for *E. elderi* appears to be largely due to its dependence on rainfall, synchrony is only expected to decrease when between population distances are sufficient for environmental conditions to vary between patches. However, other mechanisms such as dispersal between patches, competitive interactions within a population or physical differences between patches may also influence population synchrony. It is not possible to determine what effect dispersal has on population synchrony from the photo records. Within and between patch dispersal for *E. elderi* seedheads over a shorter time scale is investigated in Chapter 5.

The fact that *E. elderi* biomass dynamics were highly synchronous over seventy years of fluctuating rainfall suggests that extinction events are also likely to be highly correlated if driven by climate. The strong relationship between biomass and reproductive output suggests that seedhead production dynamics are also highly correlated between local populations and dependent on rainfall. Other researchers have recognised population synchrony as a feature of real populations due to correlated environments (Harrison and Quinn 1989; Gilpin 1990; Ranta *et al.* 1995) and have incorporated correlated extinction processes of nearby populations by extending classic metapopulation models (Gilpin 1990; Burgman *et al.* 1993).

Widespread climatic conditions synchronised *E. elderi* biomass dynamics over the spatial and temporal scales examined. There was no difference between the cumulative rainfall between the sites over the three years monitored which may explain the lack of asynchrony despite some variability between sites for particular rainfall events. Likewise, Sharon (1972) found long term averages did not vary over a region of about 80 km^2 in the southern Arava, Israel, even though individual rain events varied considerably. In addition, large differences in individual rainfall events in the Koonamore region are most likely to occur during summer, as summer rains tend to be larger and more variable than winter rains (Carrodus *et al.* 1965). Because of the high evaporation during these summer months, precipitation is unlikely to influence vegetation greatly and therefore spatial differences in rainfall events during summer months are less likely to have an impact on population dynamics.

Erodiophyllum elderi responded most strongly to the number of rain days in the previous year over 50 mm. In contrast, desert ephemeral germination can be enhanced with smaller rainfall events of 10 mm (Loria and Noy-Meir 1979-1980). Only 17 out of a total of 2129 rain days between 1923 and 1994 had more than 50 mm. It is unclear from the photo records which life history stage is affected by these large rainfall events. During the period March 1994 to August 1996 I found *E. elderi* seedlings present in the patches during winter, although no seedlings survived until the following summer (see Chapter 3). Therefore, the response to large rainfall events reflects processes involved with seedling survival.

The biomass dynamics of both *E. elderi* and grasses is correlated within a site due to their common response to rainfall. *E. elderi*, grasses and forbs all responded strongly to the previous years rainfall. While this was expected for forbs and grasses (Went 1949; Noble and Crisp 1979/80), the weak response of *E. elderi* to rainfall in the period 12 - 24 months previously implies an opportunistic response to precipitation. It is unclear whether grasses out-compete *E. elderi* during establishment phases in the low rainfall years or whether *E. elderi* simply have higher moisture requirements for successful establishment. Although grass and *E. elderi* biomass dynamics were positively correlated in all photo-points considered, the degree of correlation varied. In contrast, Noble and Crisp (1979/80) found that the dominance between grasses and forbs across Koonamore Vegetation Reserve changed between growth pulses. They attribute these results to local differences in seed availability and possibly the outcome of competitive interactions. The populations with the lowest correlation were in the south-eastern corner of the Reserve, and two of the three populations had *E. elderi* visible in more recent years only. The recent observation of *E. elderi* in those photo-points may suggest that those sites were colonised or re-colonised since the establishment of the photo-points.

Colonisation is one of the most important processes allowing metapopulation persistence, and also one of the most difficult to study. The increase in correlation between *E. elderi* biomass dynamics and rainfall when using records from the year after *E. elderi* were first observed in a photo-point, may reflect recent colonisation or recolonisation of the patches. Following this assumption, colonisation of five out of the eight populations examined may have occurred since 1925. The colonisation ability of a species will be crucial to its survival in a patchy habitat unless there are large, semi-permanent source patches (Ebenhard 1991). In addition, dispersal alone does not ensure persistence if a species is a poor coloniser (Hanski 1989). From an evolutionary point of view, there is a trade-off between being a good coloniser or being able to persist for a long time (Harper 1977). These issues are also important for species which are dependent on dispersing to and colonising disturbed sites (eg. the marine sea palm *Postelsia palmaeformis*, Paine 1979). Likewise, the long term persistence of Furbish's lousewort is crucially dependent on its ability to disperse to and colonise disturbed habitat (Menges 1990). In contrast to *E. elderi*, Furbish's lousewort has specific adaptations for seed dispersal. As colonisation is a difficult process to study, the position of *E. elderi* on the coloniser-persister scale is not well known.

The longest gap without detecting *E. elderi* in a photo series was 14 years. This suggests that either dispersal of propagules from neighbouring populations into these patches occurs within this time frame or other life-history traits buffer the effects of unfavourable environmental conditions (Chesson and Huntly 1988). For example, short-lived arid species may have a long-lived seed bank or below ground storage organs (Chesson and Huntly 1989; Pake and Venable 1996). Although *E. elderi* can re-sprout from the base when conditions become suitable after unfavourable periods (Cunningham *et al.* 1992), long term plant survivorship is unlikely to contribute to long term population persistence. Individuals which were clearly visible in the photos never survived longer than three years. Hence long term persistence within a population is most likely achieved via dispersal between patches or a long term seed bank. These possibilities are examined in Chapters 5 and 6 respectively. Other mechanisms such as long term seed banks (Gutterman 1994) and seed dormancy (Venable and Lawlor 1980) may contribute to the long term persistence of *E. elderi*.

Population synchrony in animal populations is often driven by dispersal between populations (Ranta *et al.* 1995). In contrast, the widespread effect of climatic conditions is of overwhelming importance to population synchrony for *Erodiophyllum elderi* and probably many other short-lived arid species. Although dispersal between populations may contribute to synchrony, its effect will probably be highly localised because arid plants rarely have adaptations for long distance dispersal (Ellner and Schmida 1981). If environmental conditions lead to local population extinction, then correlated extinctions are likely to decrease metapopulation persistence as they are likely to occur over a widespread region. As *E. elderi* populations persist after many years with no visible plants, either dispersal between patches occurs, or there is an alternative strategy for long term within-patch persistence. Persistence mechanisms for sessile organisms must therefore involve either very long distance dispersal between areas which are uncorrelated, or they must achieve long term within patch persistence.

5. Seedhead dispersal within and between patches

5.1 INTRODUCTION

The movement of seeds to sites suitable for germination and growth is important for seedling success in patchy environments because a large proportion of the environment is hostile. The distribution of plants therefore reflects both seed dispersal patterns and underlying patterns of site suitability. Both long distance dispersal processes (between patches) and short distance dispersal processes (within patches) are important for species with patchy distributions. Long distance dispersal allows the colonisation of new areas (Winn 1989) but has an element of risk, as few propagules reach suitable sites (Venable and Lawlor 1980). Short distance dispersal moves seeds away from the immediate vicinity of parent plants, therefore reducing the chance of density dependent interactions with adult plants or siblings (Howe and Smallwood 1982). Although short distance dispersal has some advantages, it does not lead to rapid population expansion or between patch movement.

Population growth is averaged over space and through time by between-patch dispersal and the recolonisation of temporally extinct local populations (Levin *et al.* 1984). In addition, a local population may benefit by receiving propagules from a neighbouring patch during times when it is unable to produce any itself (Pulliam 1988). However, obtaining empirical evidence of inter-patch dispersal events can be difficult because they may be rare or require particularly unusual conditions. Hence, many modelling attempts have been made to determine when, how many and how often seeds should disperse in terms of evolutionary strategies (Venable and Lawlor 1980; Levin *et al.* 1984; McPeek and Holt 1992).

There is a disparity between the morphological characters of fruits and seeds of many arid land plants which inhibit long distance dispersal and the theoretical prediction that long distance dispersal is necessary for the persistence of populations with patchy distributions. The size and shape of a propagule influences both the frequency and distance of seed dispersal. Structural characters such as plumes, wings or thorns, or fleshy fruits promote dispersal through wind, water and animals (Gutterman 1994).

Short distance dispersal is more common than long distance dispersal for many arid plant seeds due to a lack of dispersal enhancing characters (Ellner and Shmida 1981). Some seeds have structures which promote dispersal by more than one agent while other species have an obvious absence of dispersal enhancing characters (Gutterman 1994). However, the absence of obvious dispersal promoting characters does not preclude dispersal by either biotic or abiotic agents (Howe and Smallwood 1982). Reduced long distance dispersal in many desert species may suggest an extremely low benefit of long distance dispersal rather than a benefit of short distance dispersal (Ellner and Shmida 1981).

The alteration of dispersal processes may have important consequences on species distributions and population dynamics. Alien herbivores have affected many aspects of Australian native plant populations including plant abundance, size and distribution (Lange 1969; Lange 1985; Morton 1990; Friedel *et al.* 1993; Tongway and Ludwig 1994). The effect of alien herbivores on seed dispersal processes has largely been ignored, although their influence on the fate and dispersal of many seeds is recognised (Tremont 1994). Direct and indirect effects on seed dispersal are likely to influence dispersal patterns of many Australian arid species due to the introduction of new grazers and the increased pressure from native grazers. It is unclear whether introduced herbivores affect long distance dispersal, short distance dispersal or both.

There are two distinct phases in the seed dispersal process. The first phase typically involves seeds or propagules falling to the ground from the parent plant and is affected by fruit morphology (wings, plumes, etc.) or the presence of a fleshy pericarp. The second phase, involving the movement once the propagule has reached the ground, is one of the least studied phases in a plant's life cycle (Chambers and MacMahon 1994). Dispersal is difficult to study because seeds are often small and almost impossible to relocate, and there are typically large losses from the seed bank (Winn 1989). The first phase of dispersal is often limited in distance and duration (eg. Stamp and Lucas 1990) and therefore does not reflect the final fate of seeds or processes which are likely to be important for the long term persistence of species. In a recent review on dispersal, Chambers and MacMahon (1994) conclude that we know very little about a single day in the life of a seed, let alone a longer time scale.

The primary phase of dispersal is limited because *Erodiophyllum elderi* seedheads drop to the ground below the parent plant (personal observation). Therefore I focus on secondary dispersal of *E. elderi* seedheads. The objective of this part of my research was to examine the dispersal patterns of *E. elderi* seedheads. Specifically, I ask: Do seedheads disperse into patches, thereby contributing to the patchy nature of *E. elderi* populations? How are seedhead dispersal patterns affected by grazing pressure? Do introduced herbivores directly affect seedhead dispersal patterns? I question whether seedhead dispersal can occur away from a patch into a neighbouring patch allowing long term persistence through metapopulation processes. At the end of this chapter, I develop a theoretical framework to describe how dispersal patterns influence population persistence in terms of patchy population theory. Throughout this chapter, I explore *E. elderi* seedhead dispersal once they have reached the ground because of its importance from the perspective of long term population dynamics.

5.2 METHODS AND ANALYSIS

5.2.1 Pilot study to determine the effect of painting *E. elderi* seedheads

I painted *E. elderi* seedheads to enable their relocation following dispersal. To determine whether animals were attracted to the painted seedheads, thereby biasing dispersal patterns, I established a pilot study. In this study I examined whether painting seedheads increased the chance of seedhead removal. I constructed a series of 19 "corrals" (50x50 cm) bordered by bits of wood and rocks to simulate natural seed traps within each patch. The corrals eliminated seedhead dispersal through abiotic factors such as sheet water flow or wind but did not inhibit their removal by animals. Four coloured seedheads and four seedheads marked inconspicuously with a cross, sawn into the base of each seedhead, were placed into each of these corrals on 19-Oct-1994. Within each patch there was a total of 19 corrals, one for each different colour combination. Coloured and cross-marked seedheads were counted in the corrals on 17-Dec-1994 and 4-Feb-1995 and, when necessary, the corrals were reconstructed. Seedhead presence in the corrals was monitored for a total of four months, by which time I was confident that painting the seedheads did not increase their attractiveness to animals.

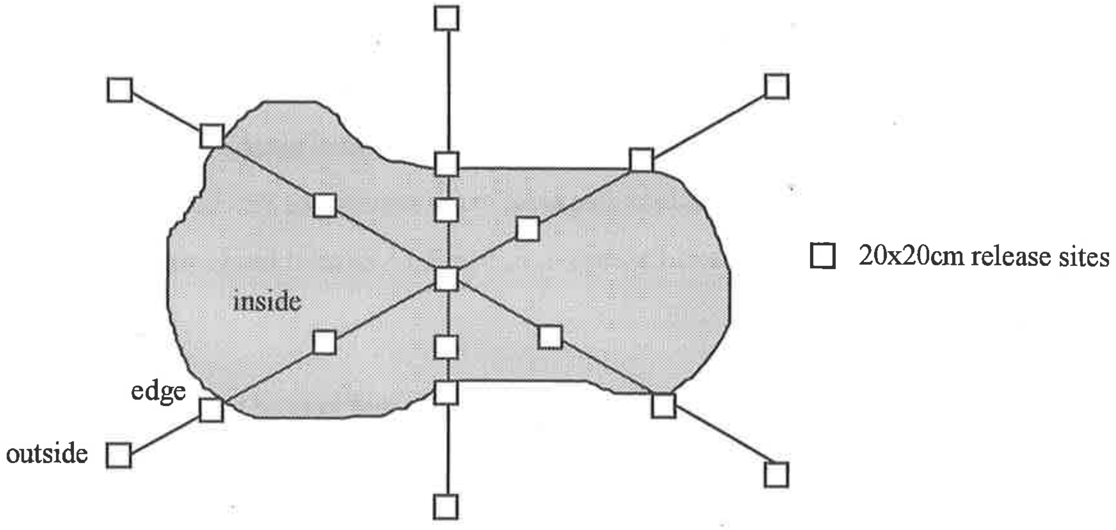
The abundance of seedheads remaining in the corrals were analysed using a means model ANOVA to test the average effect of painting and the difference in removal rate according to colour. The difference between the number of painted and cross-marked seedheads for each corral were logit transformed. Patches were used as replicates for colour.

5.2.2 Within and between patch dispersal

Seedhead dispersal patterns were monitored in six *E. elderi* patches to determine the effect of grazing pressure on dispersal patterns. To determine whether dispersal direction and distance depends on the initial position of seedheads within a patch, seedheads were released inside, at the edge and beyond the boundaries of each patch. The distance and direction of individual seedhead movement was monitored in each patch for nine months.

To determine seedhead release points within each patch, the distance to the patch boundary and the point midway to the edge of the patch were measured with six transects spaced 60° apart around each patch (Figure 5.1). Transects continued radially outward from the central location post until they were 15 m beyond the edge of the patch or reached 100 m and remained within the patch. Points were deemed to be in the patch if there was an *E. elderi* plant within 3 m either side of the transect line. At the midway point, the edge of the patch and the end of the transect (edge, inside and outside) as well as at the location post, 20 painted seedheads were deployed within a 20x20 cm area. There were a total of 19 release sites within each patch. The twenty seedheads deployed in each release site were painted with the same colour, requiring 19 different colour combinations of seedheads per patch to identify their origin. The two opposite corners of each release site were marked with pvc pipes protruding 10 cm above the ground.

Figure 5.1: An example of an *E. elderi* patch (shaded region) with release sites marked along transects spread 60° apart. Inside release quadrats are mid-way between the central post and the edge of the patch.



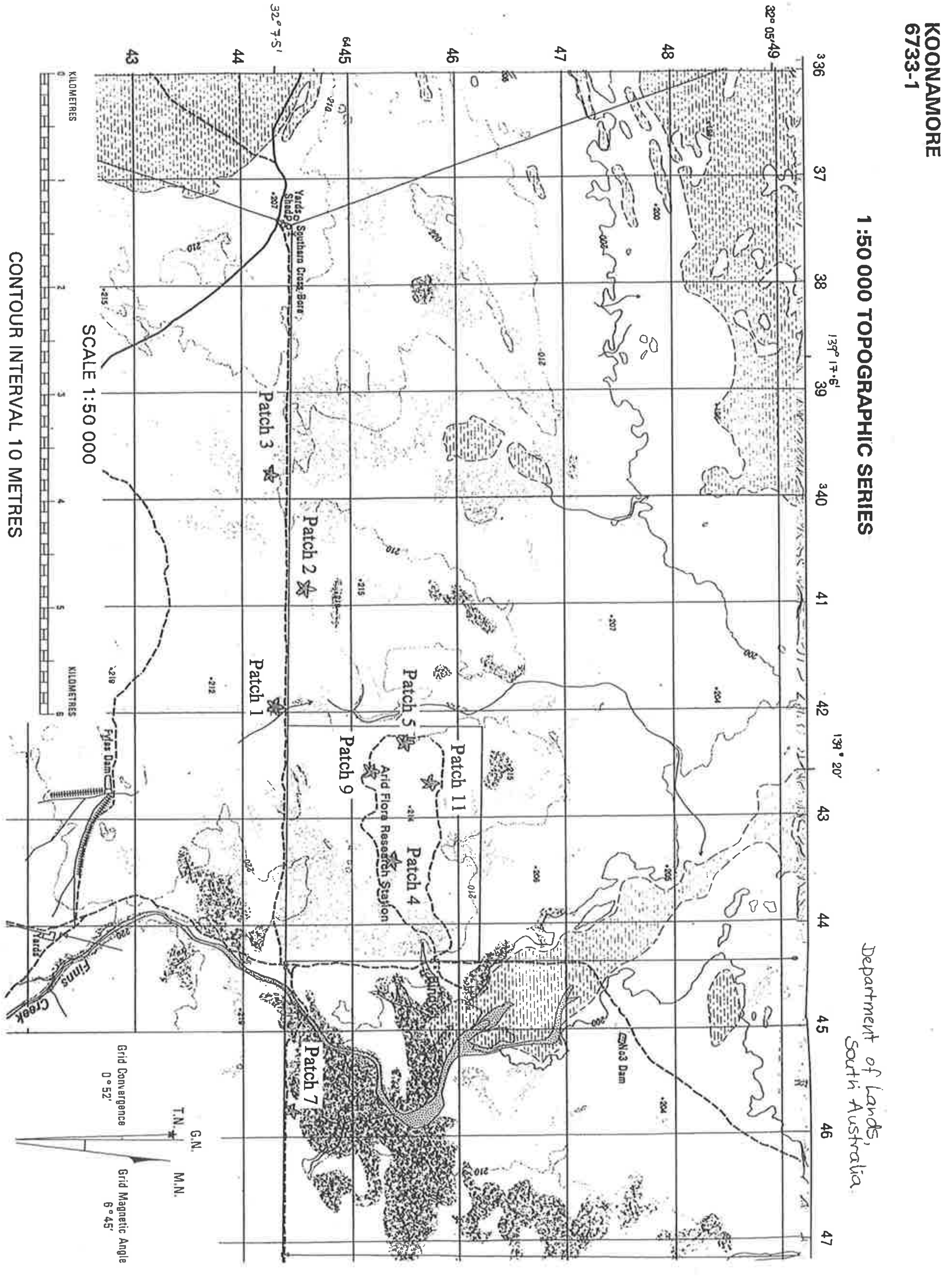
Seedheads were sprayed with fluorescent paint before deployment which made them visible during the day and at night with a portable UV lamp. Seedhead dispersal was measured by locating the seedheads at night with a portable UV lamp. A fluorescent painted rock was placed by the seedhead and the distance and direction each seedhead had moved from their release site was measured the following day using the rocks to relocate them. Seedheads were repainted after several months when the paint faded. The number of seedheads remaining in the release quadrat was noted at each time. Seedheads were released on 19-Oct-1994 and dispersal was measured on the 17-Dec-1994, 4-Feb-1995, 5-Mar-1995, 9-Jun-1995 and 17-Jul-1995 (2, 4, 5, 8 and 9 months respectively after deployment). Frequently measuring dispersal enhanced the ability to follow seedheads for a long time.

5.2.3 Seedhead dispersal on animal tracks

I performed a dispersal experiment to examine the effects of animal tracks directly because seedhead dispersal patterns in the first experiment had large variability within a patch depending on their proximity to animal tracks. Specifically, I ask: Is seedhead dispersal on animal tracks greater than off animal tracks both inside and outside the Reserve? Although many animals use tracks located outside the Reserve, they are mainly used by sheep (according to visible dung), while inside Reserve tracks are mainly used by kangaroos. Replicate tracks were located in *E. elderi* patches both inside and outside the Reserve, although there are fewer kangaroo tracks inside the Reserve than sheep tracks outside the Reserve. This experiment was conducted in areas with either high or low grazing pressure, because dispersal patterns in the previous experiment were not significantly different between patches outside the Reserve. Patches used for the track dispersal experiment were Patches 1, 2, 3, and 7 located outside the Reserve and Patches 4, 5, 9 and 11 located inside the Reserve (Figure 5.2).

Three well defined and recently used tracks were selected in each patch, and were searched for signs of fresh egesta and hoof/foot prints. Three release sites per track were established inside, at the edge and beyond each patch boundary which was consistent with the design of the first dispersal experiment. Twenty painted seedheads were released on the tracks and an additional twenty in the space immediately adjacent, but off the track. The distance and direction that seedheads moved, from both on and off the track release sites, were measured. Seedheads were released on 7-Mar-1995 and their movement monitored on 9-Jun-1995, 6-Sep-1995 and 31-Dec-1995 (3, 6 and 9 $^1/_2$ months respectively after deployment).

Figure 5.2: Location of *E. elderi* populations used in the track dispersal experiment. In each patch, seedheads were released on and off tracks and their movement monitored for a total of 9 ½ months.



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5.2.4 Analyses for the dispersal experiments

Data from both dispersal experiments were analysed with similar mixed model nested ANOVAs. Seedhead dispersal patterns were analysed separately in terms of the distance moved and the direction that they moved, either toward or away from the patch. Nested mixed model ANOVAs were conducted on data from the initial and final readings to minimise the reduction in power caused by repeated measurements for both experiments. For the within and between patch dispersal experiment, data were analysed for 2 months after deployment (17-Dec-1994) and 9 months after deployment (17-Jul-1995). For the seedhead dispersal on animal tracks experiment, data were analysed for 3 months after deployment (9-Jun-1995) and 9 ½ months after deployment (31-Dec-1995).

For the within and between patch dispersal experiment, data were analysed using mixed model nested ANOVAs with position (inside, at the edge or outside) nested within patch, and patch nested within grazing pressure. Patch was treated as a random factor with both grazing pressure and position within a patch as fixed factors. In the case of the track dispersal experiment, the same mixed model nested ANOVA was performed except position was replaced with treatment where seedheads were released on or off the tracks.

Distance

Data for average distance moved, maximum distance moved, and logit proportion moved per quadrat within each patch were checked for normality using the Shapiro-Wilks test and homogeneity of variances with Bartlett's test. In all cases there was some degree of skew because of the large number of seedheads which had not moved, even in patches with large dispersal distances. Therefore, mixed model nested ANOVAs (described above) and post-hoc tests were conducted on transformed data (Table 5.1). Although the rank transformation renders the data non normal, ANOVA is robust to deviations from normality (Zar 1984).

The number of rain days for Koonamore Station between each reading were plotted as histograms for comparison with seedhead dispersal patterns between the same time period. Rainfall was divided into categories of 0-5 mm, 5-10 mm, 10-20 mm and 20^+ mm.

In the case of the Track dispersal experiment, the effectiveness of pairing of the average distance moved per quadrat for the on and off track release sites were tested with the Pearson Correlation coefficient. This test determine whether there is a spatial component to the data which results in seedheads from each release pair moving similarly.

Table 5.1: Transformations of the release site values of a) within and between patch dispersal experiment and b) seedhead dispersal on animal tracks experiment.

	a) Within and between patch dispersal experiment	b) Track dispersal experiment
average distance moved	rank	rank
maximum distance moved	rank	ln(distance+10)
number of seedheads moving	rank	logit

N.B. The equation used for the logit transformation is given below.

Direction

To determine whether seedheads moved predominantly toward or away from patches both on and off tracks, the direction that the seedheads moved was examined. The number of seedheads moving away from the patch and towards the patch were logit transformed to improve normality using the following equation:

$$\ln(\frac{p}{1-p}), \qquad \text{where } p = \frac{(m+1)}{(n+2)},$$

where, m is the number of seedheads moving in particular direction and n is the total number of seedheads that could move.

The difference in logit transformed proportions of seedheads moving toward the patch compared with away from it (logit number toward - logit number away) were analysed with the nested mixed model ANOVA described above. For the track dispersal experiment the nested mixed model ANOVA was performed on the rank transformed differences. Release sites inside the patches were ignored for this analysis as it was not possible to determine their direction of movement.

Mean final differences in the number of seedheads moving toward compared with away from the patch were tested to determine whether seedheads moved mainly in either direction. To determine whether seedheads moved mainly toward or away from the patch, the mean of the quadrat differences were tested to determine a departure from zero. If mean difference > 0, seedheads moved predominantly toward the patch, and conversely if mean difference < 0, the seedheads moved predominantly away. Alternately, if there was no significant difference from zero, there was no predominant direction that seedheads moved. For the track dispersal experiment, the mean final differences were tested for both on and off track positions in each patch. In all but one case data conformed to normality and were analysed with a t-test, for the other case a Signed-rank test was used.

5.2.5 Germination of seeds from animal dung

To determine whether animal ingestion is another mode of transport for *E. elderi* seeds, the readily germinable seed bank of animal dung collected from within the patches was examined. Sheep have previously been browsing *E. elderi* flowers in these patches and the emergence of *E. elderi* seedlings would indicate, at least, that they can survive ingestion. Dung from sheep, rabbits, kangaroos and emus were collected on 3-Feb-1995 in Patches 7 and 6.

Dung was divided into 25 g amounts and mixed thoroughly with 500 g of potting mix after being loosely crumbled. The crumbled dung and potting mix were placed in containers in a glasshouse and watered. There were 6, 9, 13 and 18 replicates for emu, rabbit, kangaroo and sheep dung respectively. Seedling emergence was monitored for two months.

Total seedling emergence per pot was analysed due to the low germination for any particular species. Data were analysed using Kruskal-Wallis ANOVA by ranks as nil emergence values skewed the data, followed by Tukey's pairwise comparisons on ranks (Zar 1984).

Data were tested for normality and homogeneity of variances and transformed when underlying assumptions were not met. In some cases, transforming the data did not render the data normal or the variances homogeneous, and non-parametric tests were employed. All statistics were performed using the statistical software JMP (SAS 1995) except the Pearson Correlation Coefficients which were analysed with the statistical package PRISM (PRISM 1995).

5.3 RESULTS

5.3.1 Preliminary test to determine the effect of painting seedheads

There was no difference between the number of painted seedheads which were removed from the corrals and the number of cross marked seedheads at either two or four months (ANOVA, *P*>0.05, df=1; Table 5.2 a & b). However, colour did affect seedhead removal on 4-Feb-1995 (ANOVA, *P*=0.049, F= 1.718, df=18; Table 5.2 b), but the effect was probably because the yellow and pink seedheads had faded quickly in the sun. Data were re-analysed excluding these two colours and the effect was not significant (ANOVA, *P*=0.143, MS=0.078, F=1.439, df=16). As the dispersal patterns of yellow and pink seedheads was not unusual in the dispersal experiment, I was confident that there was no effect of painting seedheads on their removal but that light coloured seedheads would need to be repainted often.

Table 5.2: Means model ANOVA for seedhead dispersal controls for an overall effect of painting seedheads and specific colour effects for a) 17-Dec-1994 and b) 4-Feb-1995. Analysis performed on the logit difference between cross-marked and painted seedhead abundance left in corrals.

a)

source	df	MS	F	$P \leq$
mean	1	0.01	0.355	0.500
colour	18	0.023	1.037	0.428
error	95	0.022		

b)

source	df	MS	F	$P \leq$
mean	1	0.244	2.871	0.100
colour	18	0.147	1.718	0.049
error	95	0.085		

5.3.2 Within and between patch dispersal

The recovery rate for seedheads was very high (99%, 97%, 97%, 94% and 95% recovery for 2, 4, 5, 8 and 9 months respectively). Most of the seedheads which were not recovered were released in Patch 7 and were lost in sandy areas. In an attempt to find these seedheads the areas were raked and many seedheads were found buried in the sand. The movement of seedheads which had been covered in the sand were excluded from further analysis because the raking had moved them.

Distance

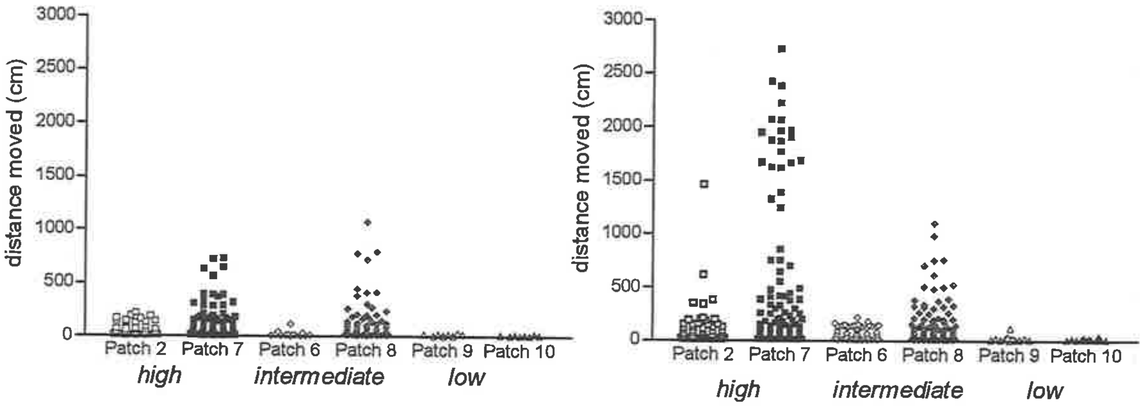
Seedheads did not disperse very far during the first two months after release (Figure 5.3 a). Most dispersal occurred between two and four months, subsequent dispersal between four and nine months was limited (Figure 5.3 b-d). Two significant rainfall events of 12 mm and 29 mm occurred during two and four months (Figure 5.4). Seedheads became trapped within the first few months by vegetation and other debris on the ground, were caught in depressions or stuck in the mud. Once seedheads were lodged they did not tend to move any further. Initial maximum distances moved by seedheads were 1075 cm outside the Reserve and 35 cm inside, while final maximum movement was 2750 cm outside the Reserve and 109 cm inside.

There was no significant effect of either grazing pressure or position nested within a patch on the average or maximum distance moved per quadrat initially (two way mixed model ANOVA, grazing pressure: P=0.1136, and P=0.1152, for average distance and maximum distance respectively; position: P=0.1266, df=12; Table 5.3 a and b). There was an initial effect of patch nested within grazing pressure on both average distance moved and maximum distance moved because seedheads moved further in Patch 8 compared with Patch 6 (ANOVA, P=0.0420, df=3 in both cases; Tukey, P<0.05, on ranked data; Table 5.3 a and b). There were no significant effects on the initial proportion of seedheads moving per quadrat (Table 5.3 c).

After nine months seedheads released outside the Reserve were more likely to move, and moved further, in terms of the average and maximum distances moved per quadrat and the number of seedheads moved per quadrat (ANOVA, P=0.0070, P=0.0043 and P=0.0242, respectively, df=2 in all cases, Table 5.3 a, b & c; Tukey, P<0.05 on ranked data). There was no significant difference between the two grazing levels outside the Reserve. The position where seedheads were released from within a patch did not affect their subsequent movement in terms of the average distance moved per quadrat, the maximum distance moved per quadrat or the number of seedheads moved per quadrat (ANOVA, P=0.4586, P=0.6626, P=0.4294, df=12 in all cases, respectively; Table 5.3 a, b & c).

The amount of variation explained by the ANOVA models increased from ≈37% in the first reading (2 months) to ≈45% by the final reading (9 months).

Figure 5.3: Individual seedhead movements throughout the course of the dispersal experiment experiencing different grazing pressures in each patch. Seedhead dispersal measured 2, 4, 8 and 9 months after deployment.



a) 2 months

b) 4 months

c) 8 months

d) 9 months

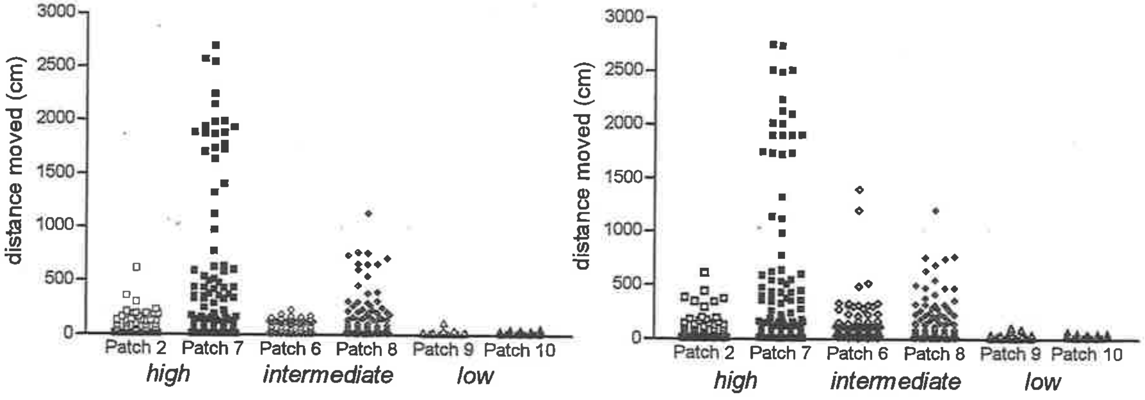


Figure 5.4: Histograms showing the number of rain days with rainfall between 0-5mm, 5-10mm, 10-20mm and 20^+ mm corresponding to the data collection periods for the dispersal experiment.

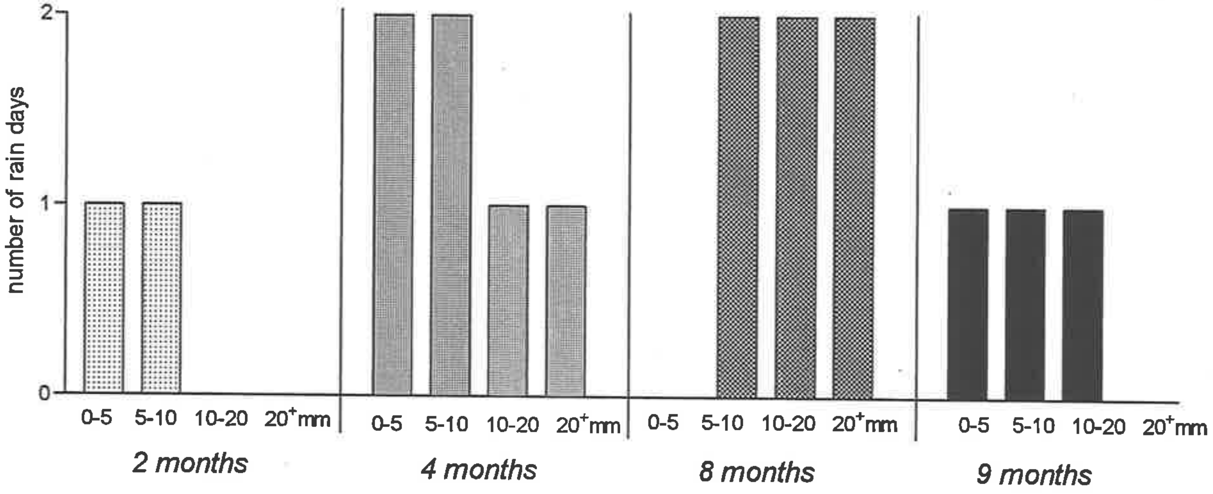


Table 5.3: Mixed model nested ANOVA results of rank transformed data of a) the average distance seedheads moved per quadrat b) the maximum distance a seedhead moved per quadrat and c) the number of seedheads moved from each quadrat for 2 months after deployment (initial) and 9 months after deployment (final).

a)

		initial			final		
source	df	MS	F	*P*≤	MS	F	*P*≤
model	17	2387.50	3.2876	0.0001	3247.15	4.8188	0.0001
grazing pressure	2	10082.7	4.8931	0.1136	20404	39.3974	0.0070
patch[grazing pressure]	3	2061.5	2.8387	0.0420	517.78	0.7684	0.5145
position[patch]	12	1111.28	1.5302	0.1266	671.28	0.9962	0.4586
residual	96	726.22			673.85		

b)

		initial			final		
source	df	MS	F	*P*≤	MS	F	*P*≤
model	17	2410.15	3.3381	0.0001	3126.94	4.4974	0.0001
grazing pressure	2	10047.2	4.8353	0.1152	19969.2	54.8226	0.0043
patch[grazing pressure]	3	2078.83	2.8387	0.0420	363.995	0.5235	0.6672
position[patch]	12	1155.37	1.5302	0.1266	547.15	0.7869	0.6626
residual	96	722.00			695.28		

c)

		initial			final		
source	df	MS	F	*P*≤	MS	F	*P*≤
model	17	2294.37	3.1281	0.0002	3368.66	4.9956	0.0001
grazing pressure	2	10138	6.5275	0.0807	19773	16.4154	0.0242
patch[grazing pressure]	3	1553.68	2.1183	0.1029	1204.9	1.7868	0.1548
position[patch]	12	1091.21	1.4878	0.1421	693.788	1.0289	0.4292
residual	96	733.47			3368.66		

Direction

There was no difference in the direction that seedheads moved (either toward or away from the patch) according to grazing pressure, patch nested within grazing pressure or the position within the patch (ANOVA, $P>0.05$ in all cases; Table 5.4 a & b). Movement was predominantly towards Patch 2 in the outside position which resulted in a borderline *P*-value (ANOVA, $P=0.0529$, df=6, $\alpha=0.05$; Table 5.4 b). This was probably because of the distinct basin shape of that particular patch resulting in good sheet water flow into the patch. The difference between the number of seedheads moving toward the patch compared with away was not significantly different to zero for all other positions in all patches for both the initial and final readings.

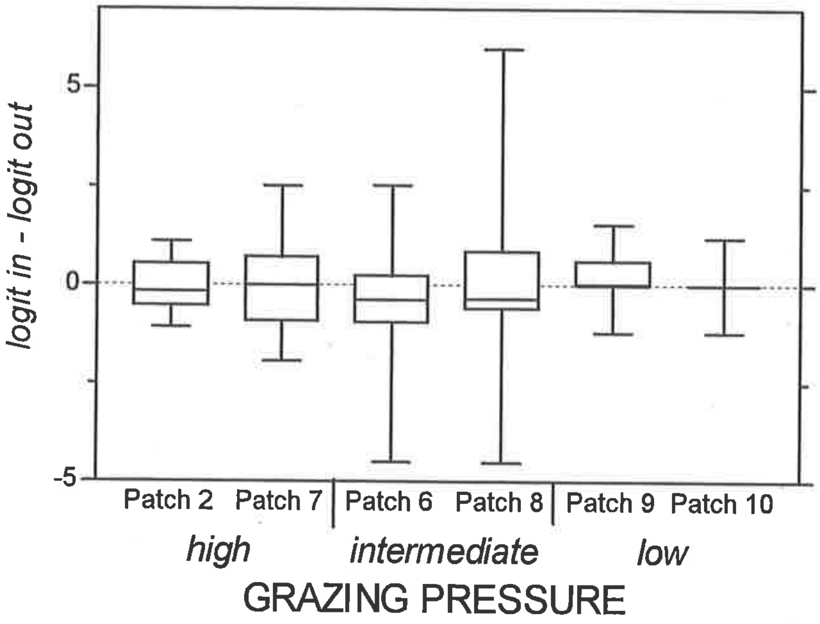
Table 5.4: ANOVA on the differences between the logit transformed number of seedheads moving toward compared with away from a patch. a) 2 months after deployment (initial) and b) 9 months after deployment (final).

		a) initial			b) final		
source	df	MS	F	*P*≤	MS	F	*P*≤
model	11	0.3014	0.2495	0.9919	2.7187	1.3281	0.2373
grazing pressure	2	0.1375	0.6432	0.5845	0.1109	0.1674	0.8532
patch[grazing pressure]	3	0.2120	0.1755	0.6672	0.6602	0.3225	0.8090
position[patch]	6	0.4018	0.3327	0.9165	4.6161	2.2560	0.0529
residual	50	1.2078			2.0470		

However, the differences between the logit transformed number of seedheads moving toward the patch compared with movement away from the patch was highly variable, particularly in Patches 6 and 8 (Figure 5.5). Although there was no consistent direction in which the seedheads moved within a patch, seedheads from within a release site often moved in the same direction. There were two main mechanisms observed which caused directional movement from within a release quadrat. Sheet water flow was evident by drift material banked up around the seedheads. This mechanism moved seedheads from the same release site down the gradient. In other cases, animals appear to have kicked seedheads, resulting in seedheads being scattered either toward or away from the patch.

Seedheads in patches outside the Reserve moved further than seedheads in patches inside the Reserve both toward and away from the patches. The initial maximum distance that any seedhead moved away from a patch was 1075 cm outside the Reserve compared with 22 cm inside. Likewise, the maximum distance that any seedhead moved toward a patch was 450 cm outside the Reserve and 15 cm inside. Final maximum dispersal distances away from the patch were 1400 cm outside the Reserve, compared with 109 cm from a patch inside the Reserve. Maximum dispersal distances toward the patch was 1200 cm in a patch outside the Reserve and 41 cm in a patch which was inside the Reserve.

Figure 5.5: Difference between the number of seedheads moving toward the patch compared with away from it for 9 months after deployment (final). Values above 0 indicate a tendency for seedheads within a release site to move toward the patch, and vice versa. Boxes show 25th, 75th and 50th percentiles and whiskers extend to maximum and minimum values.



5.3.3 Seedhead dispersal on animal tracks

Seedhead recovery rates were high with 95.8% and 88.15% of seedheads recovered from a total of 3480 seedheads deployed after 3 and 9 ½ months respectively. As with the first experiment, many of the seedheads which were lost were in sandy areas. Pairing between the average distance moved per quadrat for each on and off track pair was not effective for either the initial (Pearson Correlation, r=0.04506, n=61, P=0.3651) or final reading (Pearson Correlation, r=0.2078, n=59, P=0.0572). Due to the low effectiveness of pairing, subsequent analyses treated release site pairs as independent.

Distance

Seedheads moved further when released on tracks than off tracks both inside and outside the Reserve in terms of the average distance moved per quadrat and the maximum distance moved per quadrat (ANOVA, $P\leq0.0001$, df=1 in both cases; Table

5.5 a & b; Figure 5.6). Seedheads moved further when released outside the Reserve for the duration of the experiment (ANOVA, $P \leq 0.001$, df=1 in both cases; Table 5.5 a & b). There was no significant effect of patch nested within grazing pressure on the maximum distance moved or the average distance moved per quadrat at any time (ANOVA, $P > 0.05$, df=6; Table 5.5 a & b). More seedheads moved from each quadrat on the tracks outside the Reserve than in any other position (ANOVA, $P < 0.05$ in all cases, Table 5.5 c). Instead of seedheads becoming lodged rapidly as they did in the previous experiment, seedhead dispersal continued between readings.

Seedheads released on tracks in patches outside the Reserve moved further than those in any other position (Tukey, $P < 0.05$, Figure 5.6). Seedheads released off the tracks in patches outside the Reserve moved the same mean distance as seedheads released on the tracks in patches inside the Reserve. Dispersal distances were smallest for seedheads released off the tracks inside the Reserve.

Figure 5.6: Average distance seedheads moved for the on and off track positions inside and outside the Reserve for the track dispersal experiment. Mean and SEMs for movement $9^1/_2$ months after deployment (final). Different letters denote significant differences (Tukey, $P < 0.05$, on rank transformed data).

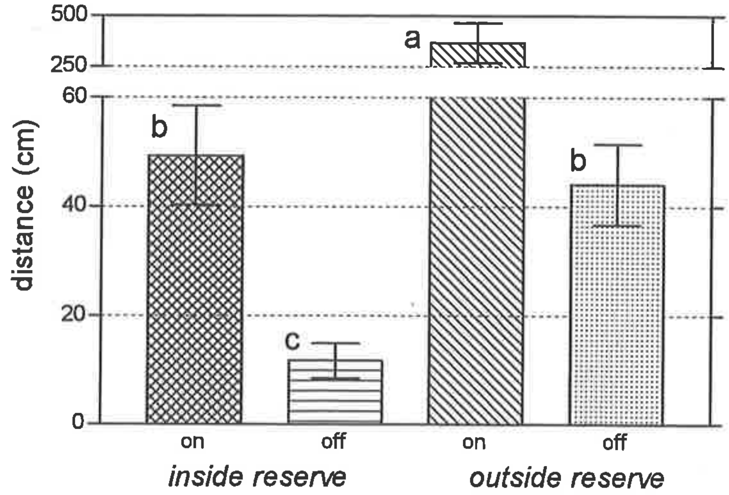


Table 5.5: Mixed model nested ANOVA of the track dispersal experiment for a) the average distance seedheads moved per quadrat (rank transformed) b) the maximum distance a seedhead moved per quadrat (ln(distance+10) transformed) and c) the number of seedheads moving (logit transformed) for data collected 3 months after deployment (initial) and 9 ½ months after deployment (final).

a)

		initial			final		
source	df	MS	F	*P*≤	MS	F	*P*≤
model	8	11363.1	21.4929	0.0001	10836.8	23.5363	0.0001
grazing pressure	1	31387	103.124	0.0001	31917.7	91.0543	0.0001
patch[grazing pressure]	6	294.356	0.5568	0.7638	345.93	0.7513	0.6097
on/off tracks	1	57304.8	108.390	0.0001	49753.6	108.059	0.0001
residual	114	528.7			460.4		

b)

		initial			final		
source	df	MS	F	*P*≤	MS	F	*P*≤
model	8	17.581	14.2237	0.0001	10.0822	12.5031	0.0001
grazing pressure	1	52.811	84.0035	0.0001	31.9081	58.7090	0.0001
patch[grazing pressure]	6	0.6016	0.4867	0.8171	0.53248	0.6603	0.6818
on/off tracks	1	82.3356	66.6127	0.0001	40.6041	50.3538	0.0001
residual	114	1.236			0.8064		

c)

		initial			final		
source	df	MS	F	*P*≤	MS	F	*P*≤
model	8	24.6551	20.3792	0.0001	193.8429	22.5875	0.0001
grazing pressure	1	58.2821	25.2262	0.0021	48.4461	30.0462	0.0013
patch[grazing pressure]	6	2.3621	1.9525	0.0782	1.64314	1.8704	0.0923
on/off tracks	1	122.763	101.4725	0.0001	94.3744	107.4279	0.0001
residual	115	1.2098			0.8785		

Direction

Seedheads moved in the same direction irrespective of being deployed on or off the track for the initial and the final readings (ANOVA, initial: *P*=0.1386, final: *P*=0.2026, df=6 in both cases; Table 5.6). Likewise, grazing pressure did not affect the direction that seedheads moved (ANOVA, initial: *P*=0.7645, final: *P*=0.8216, df=1; Table 5.6). Although there was no difference in the direction that seedheads moved initially for patches within each grazing pressure (ANOVA, *P*=0.1183, df=6; Table 5.6) there was a significant difference between the direction seedheads moved after 9 ½ months

(ANOVA, final reading, P=0.0009, df=6, Table 5.6). More seedheads moved toward the patches in some patches outside the Reserve (Tukey, P<0.05).

Table 5.6: ANOVA on rank transformed differences of the proportion of seedheads moving toward compared with away from patches for the track dispersal experiment, 3 months after deployment (initial) and 9 ½ months (final) after deployment.

		initial			final		
source	df	MS	F	$P\leq$	MS	F	$P\leq$
model	8	850.986	1.6141	0.1351	1427.22	3.5130	0.0018
grazing pressure	1	89.04	0.0972	0.7654	94.7267	0.0554	0.8216
patch[grazing pressure]	6	929.476	1.7629	0.1183	1772.71	4.3634	0.0009
on/off tracks	1	1181.25	2.2405	0.1386	672.321	1.6549	0.2026
residual	75	527.228			406.27		

Seedheads moved in a particular direction depending on the patch and whether seedheads were deployed on or off the tracks (ie mean (number toward-number away)=0). Initially, one outside patch (Patch 3, on tracks) had most seedheads moving toward it (t-test, t=2.850, P=0.036, n=9), while Patch 7 (on tracks) had more seedheads moving away from it (t-test, t=-3.219, P=0.023, n=9). Patch 3 (on tracks) also had more seedheads moving toward it after 9 ½ months (t-test, t=2.638, P=0.046, n=9).

Seedheads deployed off the tracks inside the Reserve did not move predominantly in any direction (Figure 5.7, median=0). In contrast, more seedheads moved away from the patch when released off the tracks outside the Reserve (median horizontal bar > 0). More seedheads moved toward the patch when deployed in the on track position both inside and outside the Reserve. The logit differences were highly variable for both on and off track positions within each grazing pressure. This indicates that seedheads moved predominantly either toward or away from the patch from most of the release sites.

Maximum dispersal distances of seedheads were recorded moving toward the patch (maximum 3800 cm) compared with away (maximum 1900 cm) (Figure 5.8). There was negligible movement inside the Reserve (maximum 664 cm) compared with outside the Reserve.

Figure 5.7: Scattergram of the difference in the logit number of seedheads moving toward and away from a patch for on and off track positions both inside and outside the Reserve. Values > 0 have more seedheads moving toward the patch and conversely for values below 0. Horizontal bars indicate the median values.

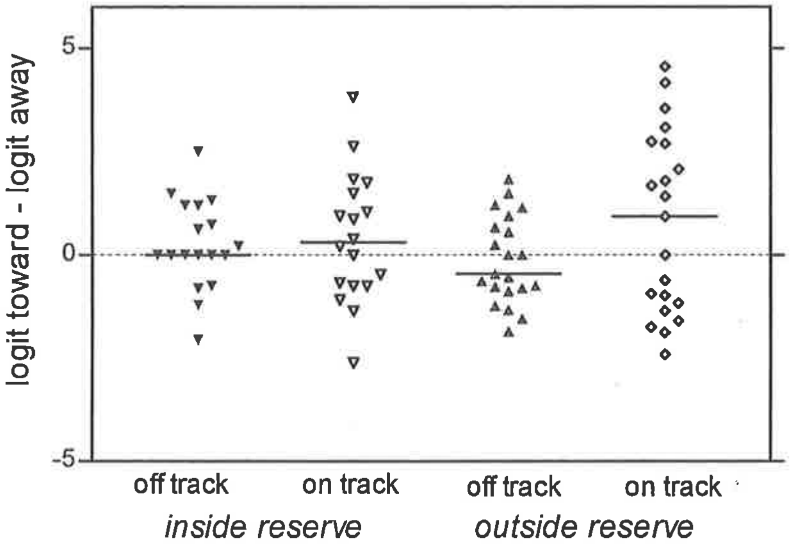
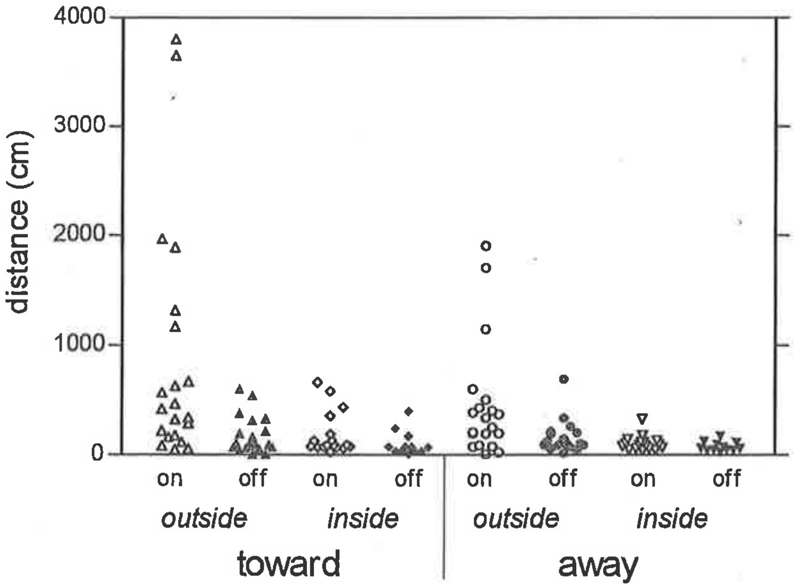


Figure 5.8: Scattergram of the maximum distances moved per quadrat either toward or away from patches inside and outside the Reserve in the on and off track positions. Values are movement recorded 9 ½ months after deployment (final).



5.3.4 Germination of seeds from animal dung

There was a lower abundance of seedlings emerging from kangaroo and sheep dung than from rabbit dung (Kruskal-Wallis, χ^2=13.87, P=0.0031, df=3; Tukey, P<0.05 on ranked data). Total seedling emergence of all species was low with the mean values per pot ranging from 0.3 (kangaroo) - 3 (emu). No *Erodiophyllum elderi* seedlings emerged from any type of dung.

5.4 DISCUSSION

Erodiophyllum elderi seedhead movement was generally limited to within patch, short distance dispersal over a period of nine months. Limited dispersal away from patches was aided by animals trampling and kicking the seedheads. Both grazing pressure and rainfall influence seedhead dispersal patterns. I suggest that the indirect effect of grazing pressure through the reduction of standing biomass is similar to the effect of drought in terms of their effects on the distance and direction that seedheads move. Seedhead dispersal between patches may occur during extremely rare heavy rainfall events allowing spatial averaging between local populations on that time scale, although other mechanisms are needed for within patch persistence on shorter time scales.

E. elderi seedheads do not possess characters that promote long distance dispersal. Seedheads rapidly became lodged in depressions or caught in seed traps such as vegetation or debris on the ground. In addition, bracts effectively anchor seedheads to the ground when they are open, unless there is sufficient sheet water flow (personal observation). Similarly, dispersal for seed capsules of the True Rose of Jericho (*Antastica hierochuntia*) depends on the quantity of rainfall. *Antastica hierochuntia* seeds are anchored to the ground immediately after they are dislodged from the maternal plant (Friedman and Stein 1980) and only during sufficiently large rainfall events are carried downstream.

Two different dispersal agents resulted in variable *E. elderi* seedhead dispersal patterns for both the distance moved and direction. Sheet water flow resulted in seedhead dispersal directed downhill and is often a major dispersal agent for arid plant seeds

(Friedman and Stein 1980; Gutterman 1994; Gutterman and Ginott 1994). As a consequence of sheet water flow resulting in dispersal to low-lying areas such as runnels and creek beds (Friedman and Stein 1980), seeds are likely to disperse to areas with relatively high water availability (eg. Friedman and Stein 1980). Movement of *E. elderi* seedheads towards the low lying area of a patch is therefore likely to be beneficial for subsequent seed germination and seedling establishment. However, because seedheads accumulate in areas within the patches and beneath parent plants, there is potential for negative seedling-seedling interaction due to the large densities of potentially competing seedlings. Seed accumulation may influence seed germination behaviour (Inouye 1980), or increase density-dependent interactions between seedlings (Inouye *et al.* 1980; Schupp 1995). The effect of large seed densities on seedling emergence, growth and survival is examined in Chapter 7. The other dispersal agent in this experiment was the trampling effects of animals, principally sheep, which resulted in a scattered pattern of seedheads around the release site and movement away from the patch. Dispersal through seedhead trampling may be important for inter-patch dispersal and patch expansion.

Patches in areas of high grazing pressure had large seedhead dispersal distances which were due to both the direct and indirect effects of grazing. However, during and after a significant rainfall event, animal tracks acted as creeks, channelling seedheads and other debris downhill toward the lowest point within a patch. In contrast, dispersal during the same rainfall event inside the Reserve was limited. Fallen branches trap wind blown and water washed material (Friedel *et al.* 1990; Ludwig *et al.* 1994) and therefore it is not surprising that dispersal was limited inside the Reserve where the vegetation is dense (Watkinson 1978). Both increased soil compaction through trampling (Stafford-Smith and Pickup 1990; Ludwig *et al.* 1994), and the reduction in standing biomass through grazing increases run-off and erosion (Stafford-Smith and Pickup 1990). These things result in lower nutrient levels in heavily grazed areas (Tongway and Ludwig 1994) which results in reduced growth of vegetation in these areas.

Although dispersal through trampling affected the occurrence and distance of seedhead dispersal, dispersal for the *E. elderi* seedhead did not appear to have any specific adaptation for animal dispersal. Different characteristics of a seed can promote dispersal via carrier animals (Gutterman 1994) through sticking to the fur of animals or ingestion. In particular, because seedhead dispersal was low inside the Reserve where kangaroos were present but sheep were not, adaptations for animal dispersal seem unlikely. Because there was no emergence of *E. elderi* seedlings in any type of egesta collected from within the patches, ingestion of seeds or seedheads is unlikely to contribute to dispersal.

Seedhead dispersal away from patches and into another patch can only occur via mechanisms which result in movement up the slope of patch edges. Maximum dispersal distances away from patches over 9 ½ months was 19 m, while the maximum movement toward a patch was 38 m. Dispersal over decades, if the seedheads persist for that long, is therefore only likely to occur between patches separated by small distances (less than a few hundred metres) unless other processes not measured in these experiments affect dispersal. *Erodiophyllum elderi* patches are likely to remain unconnected either by the trampling effects of sheep or by the redistribution of seedheads through moderate rainfall, as recorded during my experiments. Furthermore, seedhead dispersal away from patches will be inhibited by sand dunes bordering *E. elderi* patches because seedheads get buried in sand.

Seedhead dispersal appears to depend on both the rainfall experienced and the amount of standing biomass and soil stability in the area. The standing biomass within patches depends on rainfall over the preceding few years, the current grazing pressure and any historical impact from grazing pressure. The preferential grazing of sheep in islands of productivity (Friedel *et al.* 1990) often leads to a decrease in vegetative cover (Tongway and Ludwig 1994). In these patches, vegetation and dead material are unlikely to build up to the same extent as lightly grazed areas and dispersal distances will therefore be greater than in the lightly grazed areas. Movement of seedheads through sheet water flow combined with the redistribution of seedheads through animal movement is likely to result in the expansion and contraction of the seedhead distribution over time. The distribution of seedheads will influence the distribution of *E. elderi*. The importance of wind and water transportation processes in redistributing water, litter and sediments within a landscape, particularly in areas with uneven topography (Ludwig *et al.* 1994) are well known. The effects of water redistribution varies dramatically with the quantity and intensity of individual rainfall events (Ludwig *et al.* 1994). As it is not possible to examine the effects of all rainfall events during this study I have developed a theoretical framework for seedhead distribution contraction and expansion. This framework is based on the quantity of rainfall and the state of the patch, in terms of standing biomass as a result of either drought conditions or grazing effects.

A theoretical framework for patch expansion and contraction

In this framework there are three states that *E. elderi* patches can occupy according to their standing vegetation and grazing pressure. In this framework I use "patch" to refer to the current seedhead distribution, because seed supply seems to be one of the main factors limiting *E. elderi* distribution (chapter 2). The three patch states are 1) lush vegetation, low grazing pressure, 2) low vegetation, heavy grazing pressure, and 3) low vegetation, low grazing pressure. Lush vegetation is the result of either low grazing pressure or occurs after several years of high rainfall. Low vegetation may be due to either continued drought or recent heavy grazing. Seedhead dispersal patterns depend on both the state of the patch and the rainfall experienced.

Small rainfall events (up to 20 mm in a day or over several days) occur frequently and can enhance seed germination (Loria and Noy-Meir 1979-1980) and seedling growth due to the increased water in run-on areas. Seedheads are unlikely to move far (<50 cm) during such rainfall events, perhaps moving to small depressions in the ground or beneath adult plants. This is partly because rainfall opens seedhead bracts which anchor seedheads to the ground inhibiting further seedhead dispersal. Hence, small rainfall events are only likely to influence small scale, within patch vegetation patterns and are unlikely to result in significant expansion or contraction of patches in the two classifications with low grazing pressure listed above. In heavily grazed areas however, seedhead redistribution through seedhead trampling may result in a significant patch expansion.

Sufficiently large rainfall events (20 - 80 mm occurring in a day) occur less frequently and these events can move seedheads up to 30 m. These rainfall events are unlikely to result in movement of seedheads between patches, or indeed much movement away from patches. In patches with lush vegetation, there is plenty of seed trapping material and seedheads will either move short distances or not move at all. In these situations, the *E. elderi* patch can only have minimal expansion, depending on animal movement. Alternatively, if such rainfall occurs in patches with low vegetation, it is likely to redistribute seedheads dramatically, moving many seedheads from the edge of the patch towards the lower central region. The advantage of seedhead dispersal directed downhill is that it transports seeds away from the extremities of the patch to a more suitable area for subsequent germination and growth (eg. higher water availability, Jericho (Kadmon and Shmida 1990). In areas with heavy grazing, seedheads will typically move toward patches through sheet water flow, although some seedheads may move a considerable distance away from the patch through trampling processes.

Finally, the structure of the Australian arid landscape can be changed with extremely heavy rainfall events occurring over several days (Friedel 1991). Deluges of rain (more than 80mm over a few hours) may disperse seedheads between patches irrespective of the patch state considered. However, these large rainfall events are rare and may only occur every couple of centuries. One such deluge at Koonamore was recorded in 1939 when a rainfall event of 140 mm over a period of two days caused massive flooding. Although dispersal during these rainfall events will still be controlled by water, dispersal between patches may occur when excess water runs out of the patch into another, transporting seeds and other debris long distances (Ludwig *et al.* 1994). Seeds may be able to move between patches during such rainfall events and may also colonise new areas. Insufficient data has been collected to predict the frequency of these rare events and their effect on dispersal is hypothetical at this stage. However, interactions between patches are possible over time scales of several centuries and may be important for the long term persistence of the *E. elderi*. In addition, germination and successful growth are likely to occur after such an event which may result in successful *E. elderi* establishment after long distance dispersal. This type of rainfall event may result in the expansion of patches and may enable spatial averaging between patches, akin to the theoretical prediction from metapopulation models.

There is no guarantee that long distance dispersal will result in suitable placement of *Erodiophyllum elderi* seedheads and therefore it is less risky for *E. elderi* seedheads to have limited dispersal most of the time. Essentially, *E. elderi* seedheads have limited dispersal during typical rainfall events which enable *E. elderi* seedheads to remain in favourable areas, and long distance dispersal during extraordinary rainfall events. The effects of grazing on seedhead dispersal are confounding as seedheads can move toward a patch and also move away from a patch. The patterns of movement through indirect and direct effects of grazing depend on the grazing pressure within a patch, the degree of patch degradation and the quantity of rainfall. Despite the fact that species with a patchy distribution without the ability to disperse between patches are doomed to certain extinction (Levin *et al.* 1984) many arid plant seeds, including *E. elderi*, possess characters which inhibit long distance dispersal (Ellner and Shmida 1981, Jurado *et al.* 1991). Therefore, short-lived arid land species with limited dispersal need a within patch persistence strategy such as a long-lived seed bank. Nevertheless, irregular deluges of rain have the potential to redistribute many seeds, particularly for species with above ground seed banks. The redistribution of seeds during large rainfall events may have important consequences on species distribution and persistence.

6. The ecological and evolutionary significance of woody seed holding structures.

6.1 INTRODUCTION

Seed banks are important for the persistence of ephemeral species as they enable their survival during periods of unfavourable conditions (Inouye 1980; Gutterman 1994). Seed set and subsequent input into the seed bank is often driven by rainfall for short-lived desert species (Kemp 1989) and varies widely with total failure in some years (Cohen 1966; Pake and Venable 1996). Seeds display a range of dormancy mechanisms to ensure the survival of some seeds in the seed bank in case post-germination conditions are unfavourable (Ellner 1985a). Although seed dormancy in desert ephemerals is thought to be a bet-hedging adaptation to environmental uncertainty (Philippi 1993a), competition without uncertainty may also favour dormancy (Leon 1985) although Ellner (1987) questions the conclusions from León's model. In either case, the main tenet is that seed germination is spread through time to escape unfavourable conditions.

Some species impose dormancy by surrounding seeds with maternal tissue rather than with inherent dormancy of the seed. While in maternal tissue, seed behaviour of these species is controlled until germination (Westoby 1981) and seeds can be protected from environmental fluctuations and predators (eg. *Asteriscus pygmaeus*, Gutterman and Ginott 1994; *Anastatica hierochuntica*, Friedman *et al.* 1978). Seeds generally germinate readily once released from maternal structures, although, in the case of multi-seeded fruits, this may depend on the position of the seed in the fruiting structure (Gutterman 1972; Gutterman 1994; Gutterman and Ginott 1994). The range in timing of seed germination from within a fruiting structure is in agreement with Westoby (1981) and has the effect of reducing competitive interactions between sibling seedlings, hence spreading the risk of germination through time.

Breaking dormancy in an unpredictable environment is risky for seeds as conditions may not be suitable for post-emergence success. However, remaining dormant in the soil seed bank is also risky as seeds can die from predation, infection and age related reduction in viability (Inouye 1980; Ellner 1985 a & b). Therefore a trade-off exists between breaking dormancy with possible mortality due to unfavourable post-emergence conditions, and remaining in the seed bank awaiting more favourable conditions with the risk of mortality while waiting. In an unpredictable environment the question remains as to what proportion of seeds should remain in the seed bank, and what proportion should germinate? Ultimately, the best strategy is to spread the risk so that one or several post-emergence failures are not decisively harmful.

Several theoretical models were developed to explore the trade-off between germination and dormancy for annual species in randomly varying environments (eg. Cohen 1966; 1968; Ellner 1985 a & b). Cohen's models predict that the optimal germination fraction is an increasing function of both the frequency of good years and the expected yield in those good years (Cohen 1966; 1968). If there is a high probability of total reproductive failure due to unfavourable conditions, seed yield needs to be high when successful, ungerminated seeds need to survive many generations in the soil and the yearly germination fraction needs to be low (Cohen 1966). Large variability in seed yield is the main environmental factor contributing to a low optimal germination fraction (Cohen 1968).

Ellner (1985 a & b) extends Cohen's models by including density-dependent effects on seed yield and incorporating a germination response to specific cues which are correlated with favourable upcoming environmental conditions. Ellner (1985a) argues that if seeds germinate in response to a cue but have no information of future conditions, then the germination fraction should be constant over time. Also, if seed survival rate is high in the seed bank, the optimal germination fraction depends only on the variability of the yield and seed survivorship, with an increase in environmental variability favouring a lower optimal germination fraction (Ellner 1985b). In support of this, Philippi and Seger (1989) found that the fraction of *Lepidium lasiocarpum* seeds germinating from three sites was rank-correlated with mean rainfall. However, Ellner and Cohen generally assume a constant germination fraction across years, with no consideration of any seed bank age structure (Philippi 1993a). The assumption of a constant 'optimal' germination fraction is a limitation of these models (Ellner 1985a), and, in particular, may not be relevant for synaptospermic species (*i.e.* species which have more than two seeds held in a dispersal unit (Gutterman 1994)).

Seed germination behaviour varies considerably between years depending on environmental cues in a range of habitats (Venable 1989; Kalisz 1991; Philippi 1993b; Pake and Venable 1996). The need for a persistent seed bank for opportunistic arid species is clear because reproduction, growth and survival of many plants is dependent on highly variable rainfall and is often unsuccessful. Seed banks are therefore likely to be highly age structured to ensure a persistent seed bank over a period of years. Hence, questions regarding seed release and germination strategies need to address the issue of seed bank age structure.

In this chapter I explore seed release from *Erodiophyllum elderi* seedheads with laboratory experiments, field experiments and computer modelling. Up to 130 *E. elderi* seeds are held in the woody fruiting capitula which are 2 - 2.5 cm long (Black 1986), referred to as seedheads (Figure 6.1). In the first half of this chapter I investigate the role that seedheads have on seed release. Specifically, I ask: Does the seedhead regulate seed release patterns? and how are seeds released from the seedheads? How does seedhead age structure affect seed release, seed viability and seed germination? Do seeds have any inherent dormancy, or is dormancy regulated by the seedhead? What effect does precipitation or soaking in water have on seed release patterns?

In the second part of this chapter, I construct an Evolutionarily Stable Strategy (ESS) model to examine a range of release strategies for seeds from *E. elderi* seedheads and compare the results with constant germination fraction models (Cohen 1966; 1968; Ellner 1985 a & b). This model characterises germination behaviours that may be evolutionarily stable in the sense that corresponding genotypes successfully resist "invasion" by rare mutants with a different behaviour (Ellner 1985a). Specifically I ask: Are models of annual seed banks relevant to the seed release patterns from *E. elderi* seedheads? What is the optimal release curve of seeds from seedheads in terms of an ESS strategy, if such a strategy exists?

6.2 METHODS AND ANALYSES - LABORATORY AND FIELD EXPERIMENTS

6.2.1 Seedhead stage class description and development

Seedheads were placed into six broad stage classes relating to seedhead age, although their precise age was unknown (Plate 6.1). The stages were defined on the basis of the following features with additional notes in brackets:

stage 1) ray florets present, dull green, (still on plant);
stage 2a) deep brown, ray florets present, bracts slightly open, (still on plant);
stage 2b) ray florets absent, deep brown, bracts slightly open, (generally still on the plant although they may occasionally be found on the ground);
stage 3) ray florets absent, light brown, bracts closed, (on the ground);
stage 4a) seedhead beginning to degrade, light brown, (always on the ground, often with particles of soil lodged between bracts);
stage 4b) seedhead in state of degradation with many bracts broken off, light brown (always on the ground, often with hole through the centre of seedhead).

Seedheads observed in the field as developing buds and flowers in November 1993 were monitored for development through the stages until October 1998. After a few months they had developed into stage 2a seedheads. I collected several hundred in September 1995 and placed them in an area of 1.5 m diameter, near Bindy-i Research Centre (Figure 2.4, page 26) to monitor seedhead development. I also collected several hundred seedheads from stages 2b, 3, 4a and 4b in June 1996 and monitored their development until September 1998.

6.2.2 Seedhead weight, seed abundance and seed viability

To determine whether seedhead weight varied between stages indicating either seed loss or seedhead degradation I weighed 25 seedheads from each stage. Seedhead weights were analysed with a one-way ANOVA after data were natural logarithmically transformed due to heteroscedasticity. Differences between stages were examined with Tukey's HSD comparisons.

To determine whether more seeds had been released from the older seedhead stages, I counted the abundance of seeds remaining in seedheads and recorded the number of places from which seeds had been released. The number of seeds in each seedhead were counted for ten seedheads from each stage. Viable seed abundances for each seedhead stage were analysed with a one-way ANOVA and subsequent Tukey's HSD comparisons.

To determine whether seed germination rates and viability of seeds differ between seedhead stages, I removed seeds from seedheads and allowed them to germinate. Five seedheads from each of the seedhead stages were collected on 11-Sep-1995. Seeds were removed by soaking the seedheads in water for an hour and prying the seeds out carefully with tweezers to ensure minimal damage to the seed. Seeds were placed in petri dishes lined with filter paper. Distilled water was then added. Seed emergence at room temperature was monitored for seven days. Water was replaced daily and emerged seeds were removed from the dishes. Due to infection of seeds, the germination trials had to be abandoned after one week. Within this time however, most seeds had germinated. Seeds which did not emerge in that time were tested for viability by the 'squeeze' method and seeds which were juicy, oily or fleshy when squeezed were deemed viable. This technique was used for testing viability instead of testing with tetrazolium chloride because of the difficulty in manipulating the small seeds and the small size of the embryo. The cumulative germination of seeds from each stage was analysed through time with a repeated measures MANOVA.

Plate 6.1: Photograph showing each of the seedhead stages used in the experiments.

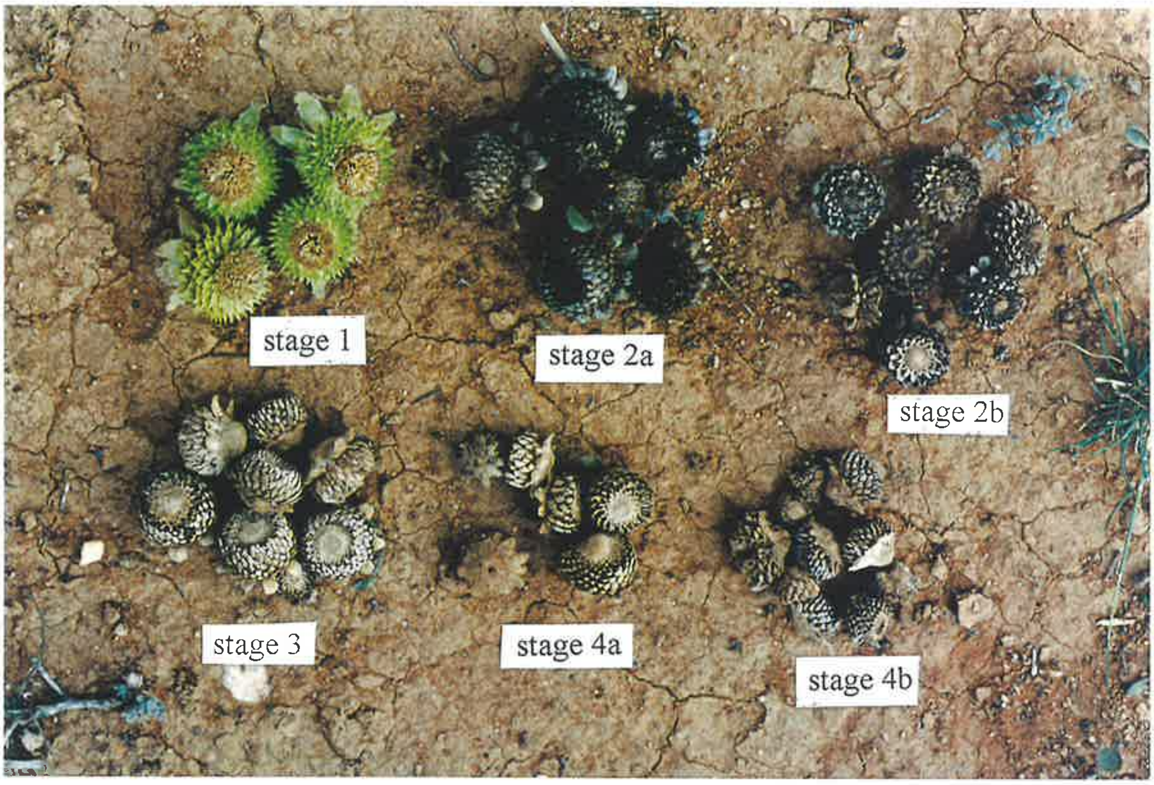
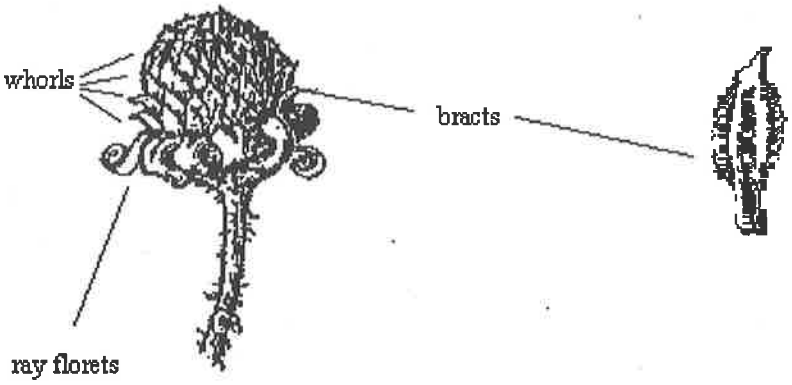


Plate 6.2: Evidence of termite activity in seedheads and termite. Termites tend to eat the softer centre of seedheads.

6.2.3 Position of seeds in seedheads

To examine where seeds had been released from the seedheads, and whether this varies between seedhead stages, the position of seeds within seedheads was recorded. Seeds in six seedheads from stages 2b, 3, 4a and 4b were examined to determine where seeds had been released from seedheads. The number of bracts on each whorl, the number of seeds in each whorl and the number of whorls in each seedhead were recorded (Figure 6.1). In the previous section I noticed that seedheads from stages 1 and 2a had rarely released any seeds and were therefore excluded from this examination.

Figure 6.1: *Erodiophyllum elderi* seedhead showing whorls going from the top to the bottom of the seedhead, with the bracts along each whorl, and the ray florets at the base of the seedhead. Included is an enlarged view of a bract. Diagram adapted from Black (1986). Seedhead width and height ranges up to 2.5 cm.



Due to the variation in seedhead size, the number of whorls and the number of bracts, seed position in the seedheads were analysed as proportions present in the top whorl (top), one whorl half way down (middle), and the basal whorl (base). The proportion of seeds remaining in the whorls (*ie* number of seeds per whorl / number of bracts per whorl) were analysed with a two-way ANOVA with stage and position as factors.

6.2.4 Seed release

6.2.4.1 In situ seed release

To determine whether seed release varied between seedhead stages, *in situ* seed release was monitored over a month when rainfall was expected. Seedheads were placed in a series of trays divided into eight separate compartments, 11.5 x 6.5 cm, each 6 cm deep, in September 1998. Trays were lined with fine mesh nylon cloth of gap size 0.5 mm which allows water through readily but not seeds. Sixteen replicate seedheads from each of seedhead stages 2b, 3, 4a and 4b were randomly assigned to individual compartments. Trays were labelled and positioned on a frame 15 cm above the ground to ensure that rain water drained through the trays, preventing water from pooling. A rainfall gauge was positioned near the trays. Rainfall, cloud cover, seed release and whether the bracts were fully, ½ or ¼ open or fully closed were recorded every several hours for 30 days. This study was conducted in Adelaide rather than at Koonamore to allow regular monitoring of seed release and bract opening.

Cumulative seed release was compared between seedhead stages to determine whether any particular stage released more seeds over the course of the experiment. The cumulative number of seeds released from seedheads in stage classes 2b, 3, 4a and 4b were compared with a Kruskal-Wallis non-parametric test. MANOVAs on cumulative seed release values were rendered inappropriate because seed release values were low.

Daily seed release values were correlated with rainfall over the course of the experiment to determine whether the number of seeds released depended on the occurrence and quantity of rainfall. The total abundance of seeds released from each stage class for each day were correlated with daily rainfall using a Spearman rank correlation. However, caution should be applied to the interpretation of the results because the seed release values were not strictly independent due to the repeated readings of the same seedheads through time.

6.2.4.2 Seed release from soaking seedheads

To determine whether the number of seeds released from seedheads was related to soaking time, seed release was monitored from seedheads soaking in water. Fifty seedheads from each of seedhead stages 2b, 3, 4a and 4b were placed in individual 70 ml vials containing 50 ml of water and left soaking. After ½, 1, 5, 24 and 48 hours, ten seedheads from each stage class were removed. The number of seeds released from each seedhead was recorded. The number of seeds released by stage class and soaking time were analysed with separate Kruskal-Wallis non-parametric tests.

6.2.4.3 Other factors which may influence seed release and survival

When collecting seedheads for this experiment, and others in this thesis, I often found termites beneath, and in, seedheads. Although it is unclear what effect, if any, termites have on seeds within the seedheads, it appears that termites are responsible for boring holes through the centre of the seedhead (Plate 6.2, page 126). Evidence of termite activity in seedheads was monitored in fifteen 1x1 m quadrats on 30-Aug-1996 within each patch in the permanent plots described in Chapter 3. The proportion of seedheads with evidence of termite activity was analysed with a Kruskal-Wallis test and Dunn's multiple comparison test.

6.3 RESULTS - LABORATORY AND FIELD EXPERIMENTS

6.3.1 Seedhead stage class development

After 3 ½ years, less than 10% of the stage 2a seedheads had developed into stage 2b seedheads, while after five years, 80% of the stage 2a seedheads had become stage 2b seedheads with the loss of ray florets. In general seedheads from stages 2b, 3, 4a and 4b had not changed between stages after two years and four months in the field. During this time however, ≈15% of stage 4a seedheads had progressed to stage 4b seedheads with considerable degradation in some seedheads.

6.3.2 Seedhead weight, seed abundance and seed viability

Seedheads from stage class 4b weighed less than seedheads from all other stages (one-way ANOVA on natural logarithmic transformed data, $P<0.0001$, F=21.96, n=5; Tukey, $P<0.01$; Figure 6.2 a). Stage 4a seedheads weighed less than stage 3 seedheads but not stage 2a or 2b. Stage 4a and 4b seedhead weights were less variable than all other stage seedheads.

Similarly, the number of viable seeds in stage 4b seedheads were lower than all other stages (one-way ANOVA, $P<0.0001$, F=15.67, n=5; Tukey $P<0.001$; Figure 6.2 b). There were no significant difference in the abundance of viable seeds present in seedheads from stages 2a, 2b, 3 and 4a.

50% of all seeds removed from seedheads germinated within 3 - 4 days of the addition of water in petri dishes (Figure 6.3). There were no significant differences between stages for the cumulative germination throughout the week (MANOVA, stage: F=0.9129, *P*=0.4568; Table 6.1). As the week progressed more seeds germinated (MANOVA, time: F=40.9163, *P*<0.00001; Table 6.1; Figure 6.3). The significant interaction between stage and time shows that seeds from different seedhead stages germinate at different times (MANOVA, time*stage: F=2.0359, *P*=0.0296; Table 6.1; Figure 6.3). This was mainly due to seeds from stage 2a seedheads germinating after the addition of water on day 1, whereas there was little germination of seeds from seedheads in other stage classes before day 2.

Table 6.1: Repeated measures MANOVA on cumulative germination of seeds removed from seedheads from stage classes 2b, 3, 4a and 4b.

Test	Pillai's Trace	Exact F	$\mathrm{df}_{\mathrm{num}}$	$\mathrm{df}_{\mathrm{den}}$	Prob>F
all between interactions					
intercept	0.9588258	372.5924	1	16	0.0000
stage	0.1461517	0.9129	3	16	0.4568
all within interactions					
time	0.9662634	40.9163	7	10	0.0000
time*stage	1.6286391	2.0359	21	36	0.0296

Figure 6.2: a) seedhead weight and b) number of viable seeds for each of the seedhead stages. Boxes show 25th, 50th and 75th percentiles and whiskers extend to maximum and minimum values. Different letters denote significant differences (Tukey, *P*<0.05 for a) natural logarithm transformed data, and b) raw data).

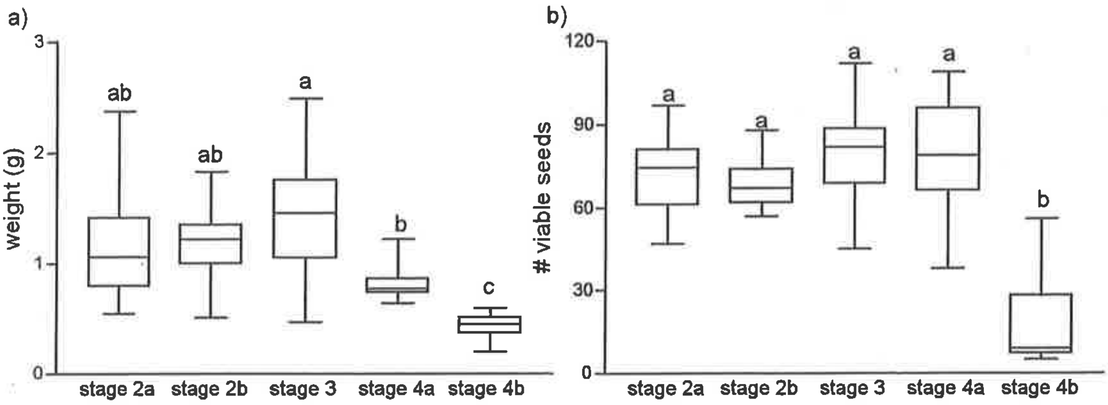
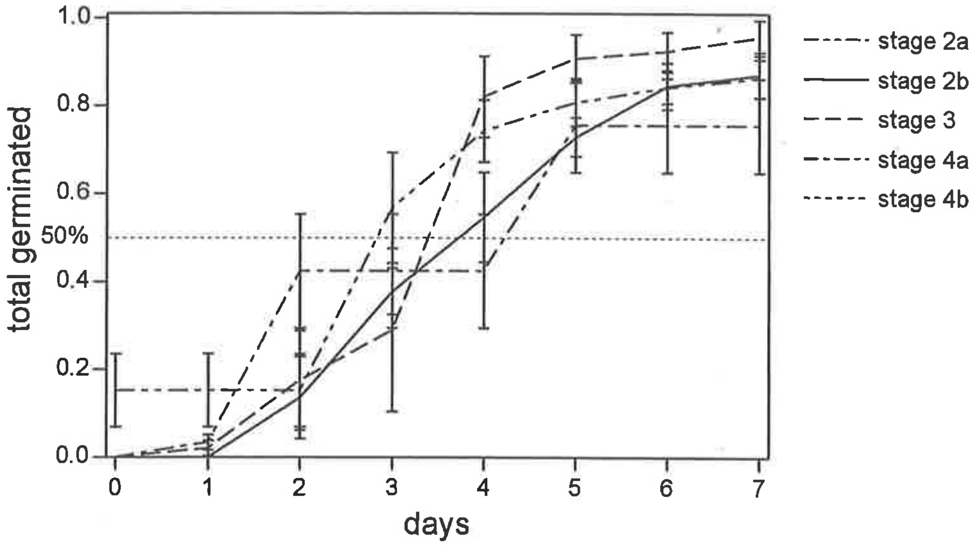


Figure 6.3: Cumulative germination of seeds from each of the seedhead stages over one week. Values plotted are mean ± SEM based on five seedheads from each stage.



86% of the seeds removed from the seedheads germinated within one week after the addition of water. Five out of the twenty seedheads examined had 100% germination within the first week, and half of the seedheads examined had more than 90% germination within the first week. Ninety eight percent of seeds extracted from seedheads and placed on the germination dishes were viable. Seeds from stage 1 seedheads did not germinate despite being viable according to the squeeze test. In all cases, seeds removed from stage 1 seedheads became rapidly infected.

6.3.3 Position of seeds in seedheads

There were fewer seeds present at the top of the seedheads than in the middle and the base for all seedhead stages (ANOVA, position: *P*<0.0001, F=24.04, df=2; Figure 6.4, Table 6.2). There were fewer seeds in stage 4b seedheads than in any other seedhead stage (ANOVA, stage: *P*<0.0001, F=25.85, df=3; Figure 6.4, Table 6.2). In most cases, 100% of seeds were present in the middle and base of stage 2b, 3 and 4a seedheads. There were virtually no seeds present at the top of stage 4b seedheads (average 2% present). Seeds are released from the top of the seedhead first, with subsequent release occurring from the top whorl down to the basal whorl. Not all seeds within a whorl are released simultaneously.

Figure 6.4: The proportion of seeds remaining in stage 2b, 3, 4a and 4b seedheads at the top of the seedhead, the middle and the base. Values plotted are mean ± SD based on six seedheads per stage.

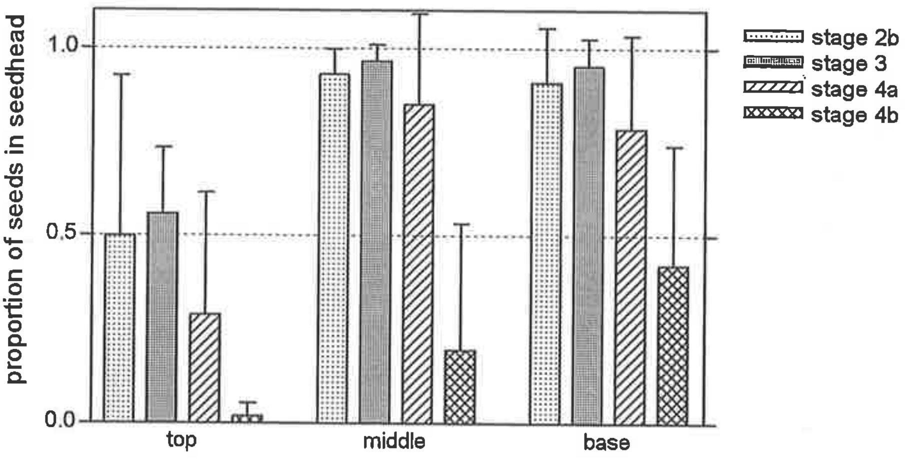


Table 6.2: Two-way ANOVA results for the proportion of seeds in seedhead stages 2b, 3, 4a and 4b according to position within the seedhead (top, middle and base). N=6.

source	df	MS	F	$P\leq$
stage class	3	1.529	25.85	0.0001
position	2	1.422	24.04	0.0001
interaction	6	0.05414	0.9152	0.4897
residual	66	0.05916		

6.3.4 Seed release

6.3.4.1 In situ seed release

Unfortunately, the trays holding the seedheads were knocked over during the course of the experiment. Although I salvaged the trays and the seedheads, this event had a significant impact on seed release values for that day (Figure 6.5). As it had rained prior to this happening, seedhead bracts were open, and the knocking of the trays enabled seeds to be released from seedheads from all stages. The following analyses were performed including and excluding this days data.

More seeds were released from stage 4b seedheads than stage 2b seedheads over the course of the experiment (Kruskal-Wallis, χ^2=10.95, *P*=0.0120; Dunn's, *P*<0.05; Figure 6.6; Table 6.3). There was no difference between the cumulative release of seeds from seedheads in either stage 3 or 4a and stage 2b or 4b. Including the seeds which were released when the trays were upturned did not affect this result (Kruskal-Wallis, χ^2=11.26, *P*=0.0104; Dunn's, *P*<0.05). More seeds were released during the course of the experiment from stage 4b seedheads than seedheads from other stages (Table 6.3) and there were correspondingly more stage 4b seedheads that released seeds both including and excluding the data on the day that the trays turned over.

Figure 6.5: Daily rainfall and number of seeds released over a period of 30 days. Seed release values are combined stage class totals. Trays were upturned on day 4 which corresponded to an unprecedented seed release.

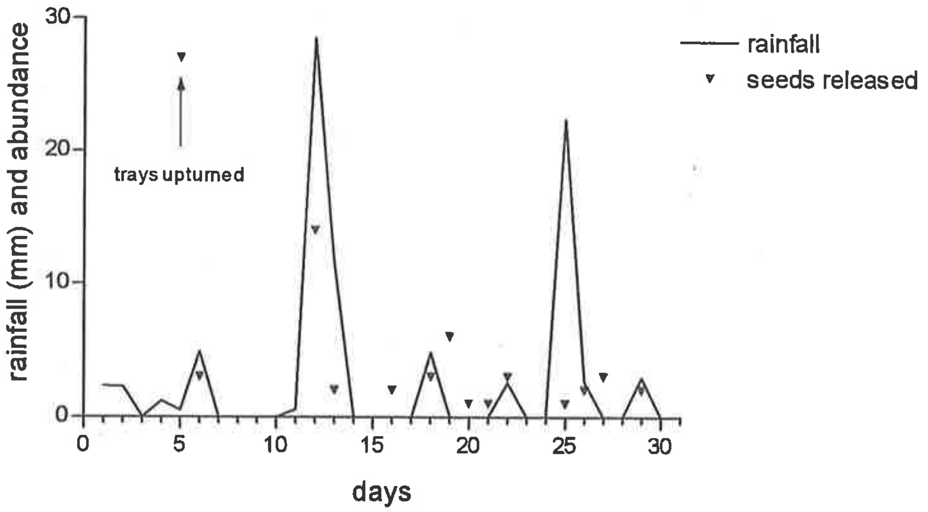


Table 6.3: Cumulative totals of seedheads releasing seeds for the duration of the seed release experiment and the total number of seeds released according to seedhead stage. Values exclude or include the data from when the trays upturned as indicated.

		stage 2b	stage 3	stage 4a	stage 4b
number of seedheads releasing seeds	excluding	2	6	6	11
	including	5	8	11	14
number of seeds released	excluding	3	7	11	22
	including	9	13	20	28

Most seeds were released within a few days after rainfall had occurred (Figure 6.5), although there were seeds released occasionally from stage 4a and 4b seedheads on days without rain. The abundance of seeds released was not significantly correlated with rainfall for any stage class or for the combined total release when all null rainfall and release values were excluded (Table 6.4). However, there were only three rainfall events over 5 mm, with nine below 5 mm, and the lack of correlation may simply reflect rainfall values which were insufficient for seed release. On all occasions when rainfall exceeded 5 mm, seeds were released, and the highest rainfall event (28.5 mm) corresponded with the largest number of seeds released in a day (number of seeds released = 14). Rainfall was not correlated with time during the course of the experiment.

Figure 6.6: Abundance of seeds released from each stage seedhead for the duration of the seed release experiment for a) all data included, and b) excluding data from when the trays turned over. Different letters denote significant differences (Dunn's test, *P*<0.05). Boxes show 25th, 50th and 75th percentiles and whiskers extend to maximum and minimum values

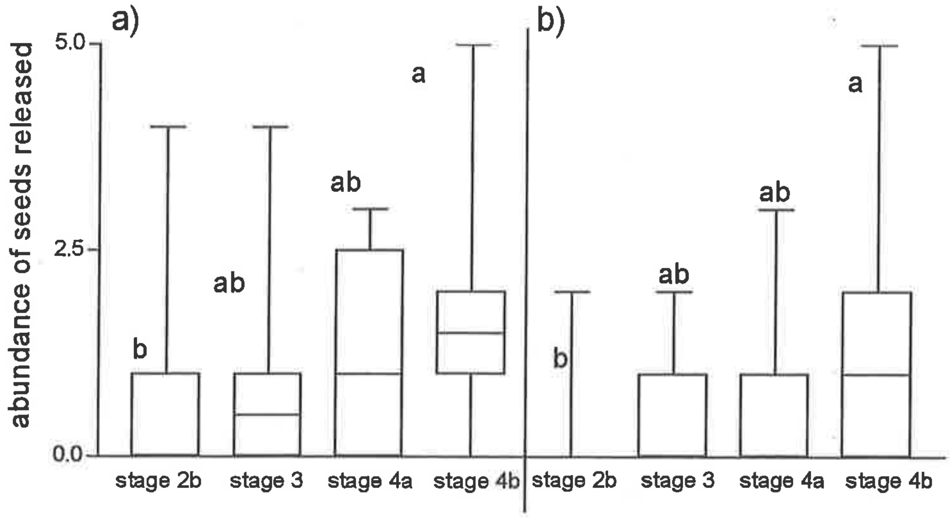


Table 6.4: Correlation between the daily abundance of seeds released from seedheads and rainfall for each stage and the combined totals.

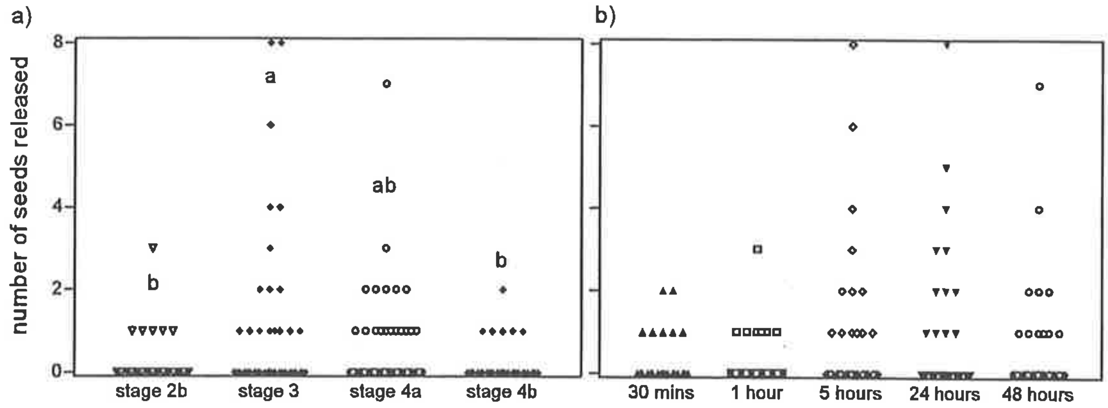
	Combined	stage 2b	stage 3	stage 4a	stage 4b
Spearman r	0.3372	0.4392	0.01513	0.1751	0.09990
$P \leq$	0.1580	0.1333	0.9573	0.5167	0.7128
number of XY pairs	19	13	15	16	16

6.3.4.2 Seed release from soaking seedheads

There was a low rate (0.9%) of seeds released from seedheads irrespective of soaking time (Figure 6.7). Only 111 seeds were released out of the estimated 12 077 seeds held in the seedheads (based on average number of seeds in the various seedhead stages from section 6.3.1). There was no effect of the length of time seedheads were left soaking in water on the abundance of seeds released from seedheads (Kruskal-Wallis, χ^2=5.01, n=5, *P*=0.2858). Overall, significantly more seeds were released from stage 3 seedheads than 2b and 4b seedheads (Kruskal-Wallis, χ^2=21.60, n=4, *P*≤0.0001; Dunn's *P*<0.05).

Additionally, seedheads floated in vials for at least 24 hours before sinking. After 24 hours seedheads either reached some density and sank or they no longer had air between the bracts to keep them floating. Seedheads also floated for some time in large bodies of water in the field although no specific length of time was measured.

Figure 6.7: Seed release for a) different stage seedheads, and b) soaking in water vials for different lengths of time. Values include all 10 replicates for each stage/time combination. Different letters denote significant differences (Dunn's test, *P*<0.05).

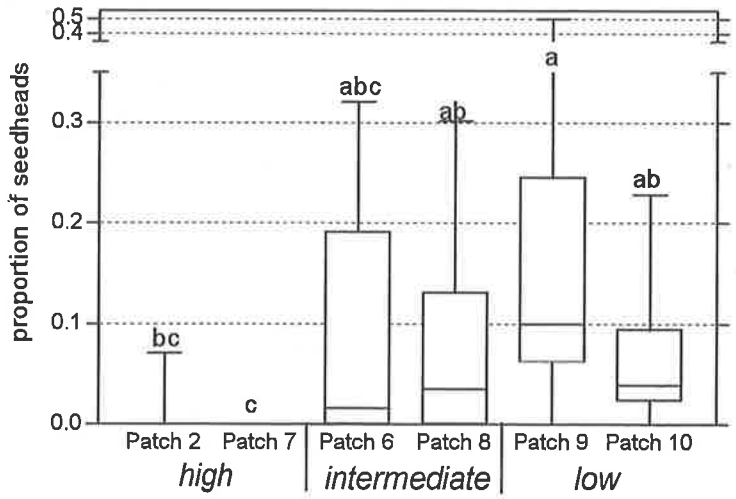


6.3.4.3 Other factors which may influence seed release and survival

Evidence of termite activity in seedheads was widespread throughout most of the *E. elderi* patches examined, although it was more common in patches with low grazing pressure (Figure 6.8). A greater proportion of seedheads had termite activity in Patch 9 compared with Patch 2 and Patch 7 (Kruskal-Wallis, $\chi^2=33.42$, n=6, $P<0.0001$; Dunn's, $P<0.05$). The most heavily grazed patch (Patch 7) had the lowest proportion of seedheads with evidence of termite activity. The highest median value of seedheads with evidence of termite activity was 10%. This was recorded inside the reserve in Patch 9. The maximum proportion of seedheads with termite activity in any quadrat was 50% which was also in Patch 9.

In addition to the termite activity in the seedheads, I saw seeds on the ground and ants carrying *E. elderi* seeds on several occasions after heavy rain. I also observed *E. elderi* seedlings sprouting around the opening of ant mounds.

Figure 6.8: Proportion of seedheads with evidence of termite activity within each of the patches in high, intermediate and low grazing pressures. Different letters denote significant differences (Dunn's, $P<0.05$). Boxes show 25th, 50th and 75th percentiles and whiskers extend to maximum and minimum values.



6.4 SEED RELEASE MODEL

In this section, I adapt and extend Cohen's (1966; 1968) and Ellner's (1985 a & b) models of seed germination strategies for annual plants. These models are modified to represent seed release from *Erodiophyllum elderi* seedheads. In Cohen and Ellner's models there is an 'optimal' seed germination fraction each year. I investigate alternative seed release strategies from *E. elderi* seedheads, as seed release from woody maternal structures is most likely not a constant fraction every year. I consider the situation where seeds are released from seedheads according to defined release curves over a fixed period of time.

6.4.1 Population transition matrix

I construct a matrix model which incorporates stochastic reproductive output of seedlings (equation 6.1). Instead of modelling individual seedheads, I model seeds which are released from a stage structured seed population to simulate seeds being released from actual seedheads. Each year a proportion (q_i) of seeds germinate from seeds in class *i*, simulating release from a seedhead in stage *i*. These seedlings produce F_i new seeds, where F_i is a random variable drawn from a log normal distribution. These seedlings produce stage 1 seeds which, in turn, can germinate and reproduce the following year.

The non-zero entries of the seed population transition matrix are:

$$\begin{bmatrix} F_1q_1 & F_2q_2 & F_3q_3 & \cdots & F_{m-1}q_{m-1} & F_m(q_m) \\ (1-q_1)(1-d_1) & & & & & \\ & (1-q_2)(1-d_2) & & & & \\ & & (1-q_3)(1-d_3) & & & \\ & & & \ddots & & \\ & & & & (1-q_{m-1})(1-d_{m-1}) & (1-q_m)(1-d_m) \end{bmatrix} \tag{6.1}$$

where F_i is the reproductive output per seedling from seed stage *i*, q_i is the proportion of seeds which are released and germinate from seed stage *i*, *m* is the maximum number of stage classes possible, and d_i is the proportion of seeds that die in the seedhead in the transition from stage *i* to stage *i*+1. This model allows seeds to be released following a variety of release curves determined by the *q* terms. For this model I set m=11, and the q values are determined by the release curves in Figure 6.10 which are discussed in detail in section 6.4.2. Instead of all seeds being released by the seedhead at the final time step, q_m is arbitrarily set to 0.5. This simplifies the analysis by preventing population extinction in the model. For all release curves, I assume 95% of seeds out of a total of 100 initial seeds are released within ten time steps.

The matrix element (m, m) allows some survival of seeds in the last stage. Therefore, this last stage consists of seeds of age m and higher. The assumptions of zero reproduction during drought years allow the possibility of indeterminately long periods with no reproduction. Hence, without the additional possibility of persistence of some seeds for indeterminate periods of time, extinction would be inevitable in all of the scenarios considered below. Although under some circumstances such extinction might be realistic, the standard methods of analysis based on long-term low density growth rates would fail. The inclusion of some probability of surviving another year avoids this problem.

I set $d_1=d_2=d_3=\ldots=d_m=d$ because seed viability tests in section 6.3.2 showed no difference between the number of seeds which were not viable in seedheads of different ages. Although there were very few seeds which were not viable (<2%) in the seedheads, suggesting a low value for d, I examine the effect of both high and low death rates of seeds (d = 0.001 and 0.1).

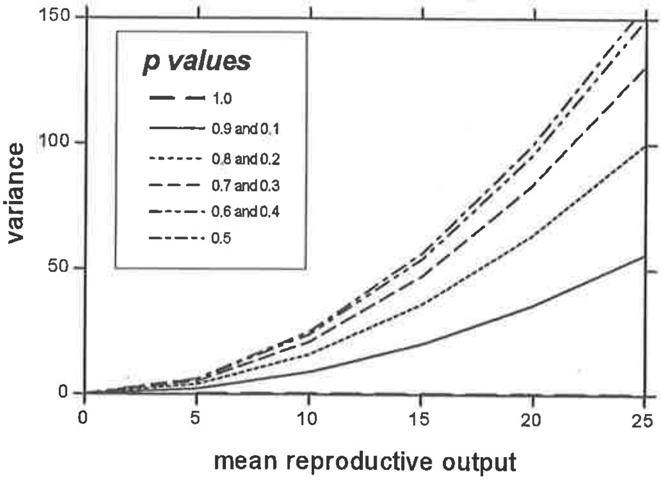
I also set $F_1=F_2=F_3=\ldots=F_{\mathrm{m}}=F$ because there is currently no biological evidence to suggest that the reproductive output differs for seeds from different stage classes. Reproduction (F) is the per individual contribution to the seed bank from seeds which have been released from the seedhead and germinated. The probability of a year with some reproduction is p and represents years with sufficient rainfall for reproduction. During those years, I assume that F is a random variable, $G(\mu,\sigma^2)$, drawn from a log normal distribution, where μ and σ^2 are the mean and variance of the log of $G(\mu,\sigma^2)$. Formally, the reproductive output (F) is given by:

$$F(\mu_F,\sigma^2{}_F)=\begin{cases} G(\mu,\sigma^2) & \text{with probability } p, \\ 0 & \text{with probability } (1-p). \end{cases} \tag{6.2}$$

where $G(\mu, \sigma^2)$ is a random variable drawn from a log normal distribution with a mean reproductive rate μ, σ^2 is the variance of the reproductive rate, and p is the probability of a reproductively successful year.

Reproduction is assumed to depend directly on rainfall which is log normally distributed for Koonamore, as is common in many arid areas. Total reproductive failure occurs with probability $(1-p)$ which represents years with insufficient rainfall for successful establishment, growth and reproduction, although seeds are still released during these years. Seeds which are released during these years either die or do not attain sufficient growth to reach maturity. To maintain a constant mean (μ_F) and variance (σ^2_F) for the reproductive output while including the p term requires a minimum variance of the log normally distributed function (Figure 6.9).

Figure 6.9: Relationship between the minimum mean (μ) and variance (σ^2) required in the log normal distribution to maintain a constant overall mean (μ_F) reproductive output, F when the probability of a good year (p) is included.



6.4.2 Fixed seed release curves

Seedheads are assumed to survive for at least ten time steps and, in this period, seeds are released from the seedhead according to fixed release curves. Although seed release is fixed in this model, it is not an 'optimal' fraction. Rather, seed release is either rapid in the first few years or very slow in the first few years (Figure 6.10). Seed release curves follow the form of equation 6.3:

$$y = k\left(1 - \left(\tfrac{t}{T}\right)^{\theta}\right), \tag{6.3}$$

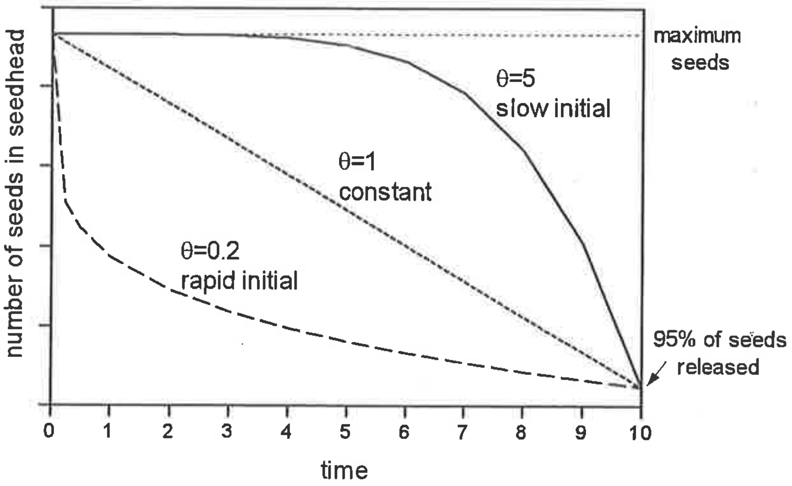
where y is the number of seeds in a seedhead at time t, k is the initial number of seeds in a seedhead, T is the number of time steps until some proportion of the seeds have been released and θ is a variable which determines the shape of the release curve. The biological interpretation of the different θ values in Figure 6.10 are:

$\theta = 0.2$, rapid initial: seeds are released from the seedheads rapidly, with most seeds released within the first 1 - 2 years while very few seeds remain in the seedhead towards the end of the seedheads life,

$\theta = 1$, constant amount: a constant number of seeds are released at each time step. This could represent the release of one row of seeds each time step,

$\theta = 5$, slow initial: very few seeds are released in the first few years, followed by an increasing rate of seed release as the seedhead ages. This represents the occasional release of a few seeds followed by the release of large numbers of seeds as the seedhead breaks apart.

Figure 6.10: Fixed seed release curves for 95% seed release from seedheads over a ten year period. The shape of the release curves depends on the parameter θ.



In this model I assume that seed release is followed by immediate germination and seedlings either grow to maturity or not, depending on environmental conditions *(p)*.

The assumption of seed germination immediately after release from the seedhead is based on results in section 6.3.2 which show rapid seed germination with the addition of water once after release. Although results from section 6.3.4.1 indicate that seed release is driven to some extent by individual rainfall events, I model cumulative release over a particular time step (eg. 1 year). It is reasonable to assume that some seeds will be released each year irrespective of whether they reach maturity because of the continued emergence of seedlings (Chapter 3) during years with low rainfall. In addition, the soil seed bank was virtually non-existent (Chapter 2) and most likely exists only after seeds have been released from seedheads during precipitation.

6.4.3 Density-independent case:

To determine which strategies should arise by natural selection, we seek a measure of the long term fitness of a strategy. The standard procedure is to use the geometric mean fitness in the case where the life-history model can be defined by a simple difference equation (Cohen 1966; Venable 1989). In this case, where the model is defined by a matrix equation, the corresponding quantity is the long-term growth, which is equal to:

$$\lim_{T\to\infty}\frac{(\ln N(T)-\ln N(0))}{T}$$

(Tuljapurkar and Orzack 1980). This quantity exists and is a constant for a wide range of models defined by matrix equations (Tuljapurkar and Orzack 1980; Heyde 1985). For estimation by simulation only, finite times are used, but the expected value of

$$\frac{\ln N(T+t)-\ln N(t)}{T}$$

for large t is a good approximation to the limit. This mean value was estimated by the procedure below.

To examine which seed release strategy has the highest fitness, the long term growth rate (*ltgr)* were compared for several θ values under a variety of parameter combinations. The strategy with the highest *ltgr* is assumed to be the outcome that would result from natural selection, which I will refer to as the "winning" strategy.

Long term average growth rates below zero represent populations which are declining and parameter combinations which do not allow persistence. In all cases, the *ltgr* was based on 1000 time steps for each simulation. The average *ltgr* and the associated standard deviation were calculated from 100 simulations of each parameter combination.

The probability of a successful year *(p)* was set to be 0.3 or 0.7, to examine the effect that the proportion of years with successful reproduction has on the best seed release strategy. I also examined the effect of increasing the death rate of seeds held in the seedheads (d) from 0.001 to 0.1. The effect of a high and low reproductive output and high and low variances were examined with $\mu_F = 2$, $\sigma_F{}^2 = 4$ and 8 and $\mu_F = 5$, $\sigma_F{}^2 = 10$ and 20. The mean and variance of the reproductive output was held constant including the p term.

6.4.4 Density-dependent reproductive output:

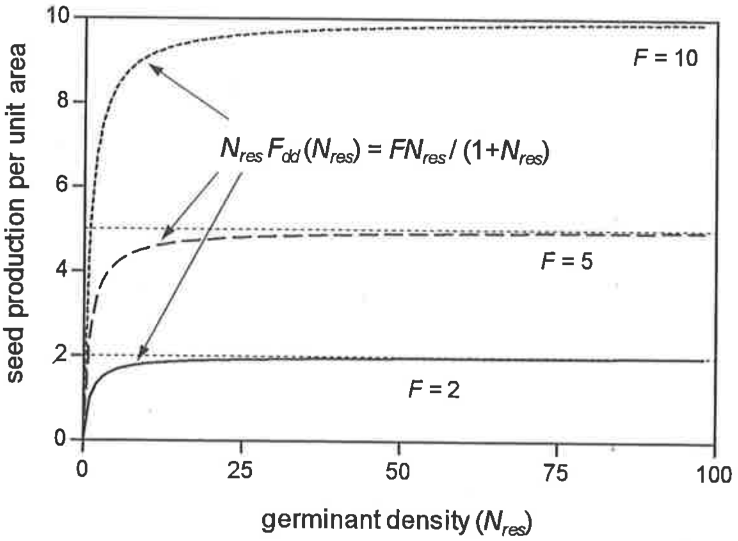
To determine whether density-dependence changes the fitness of the θ seed release curves, density-dependent effects were incorporated into the model. To incorporate density-dependent effects on the reproductive output of seedlings, an Evolutionarily Stable Strategy (ESS) analysis is used because optimisation models are not appropriate for density-dependent models (Philippi 1993a). To do this, a small number of seedheads with a particular release strategy (invader type) are introduced into a resident population of seedheads with a different release strategy and invasability examined. If the invader has a population growth rate > 0, it can invade the resident strategy. An ESS occurs, if one exists, when an invader strategy can invade all resident strategies but can not be invaded itself.

Density dependent effects on the reproductive output are incorporated into the model by modifying the reproductive output of seedlings as a function of density. The density-dependent reproductive output (F_{dd}) for both the invader and the resident populations are a function of the number of resident strategy seedlings present, N_{res} (equation 6.4). The reproductive output of both the invader and resident types are calculated considering the density-dependent effects from the resident seedling density only. This is because the invader population is small and assumed to exert negligible effects on both the residents and the invaders. The density-dependent reproductive output for the resident and invader populations are given by:

$$F_{dd} = \frac{F}{\left(C + N_{res}\right)}, \tag{6.4}$$

where F is the density-independent reproductive output (also the maximum reproductive output per unit area), N_{res} is the number of resident strategy seedlings present and C is a positive constant, in this case set to 1. This follows the formulation of density-dependence in Ellner (1985b) and is illustrated graphically in Figure 6.11. Density dependence is assumed to affect the reproductive output of seedlings rather than their mortality.

Figure 6.11: Total seed production per unit area with density-dependent effects for a range of F values.



The density-dependent reproductive output F_{dd} has a lower mean and variance compared with a particular density-independent reproductive output, F. However, as N_{res} varies, the reduction in the mean reproductive rate for a given distribution of F is state dependent. Consequently, direct comparisons between the density-independent and density-dependent simulations for reproductive output with a given μ_F and $\sigma_F{}^2$ are misleading.

To determine invasability of the seed release strategies, the average long term population growth rates (*ltgr*) are calculated for each invader- resident θ combination.

A particular θ strategy is said to "invade" the resident population if the *ltgr* is greater than 0. The *ltgr* and the associated standard deviations were calculated from 50 simulations for each parameter combination and tested for a significant difference from 0. In all cases, the *ltgr* for both the invader and resident populations was calculated from the last 500 of 1000 time steps for each simulation. This allows the distribution of seeds to reach a steady state according to stage class, and removes the effect of transients.

The probability of a successful year (*p*) was set at 0.3 and 0.7 to examine the effect of reducing the proportion of years with successful reproduction on the best seed release strategy. I also examined the effect of increasing the death rate of seeds held in seedheads (*d*) from 0.001 to 0.1. The effect of high and low reproductive output and high and low variances were examined with $\mu_F = 2$, $\sigma_F{}^2 = 4$ and 8 and $\mu_F = 5$, $\sigma_F{}^2 =$ 10 and 20.

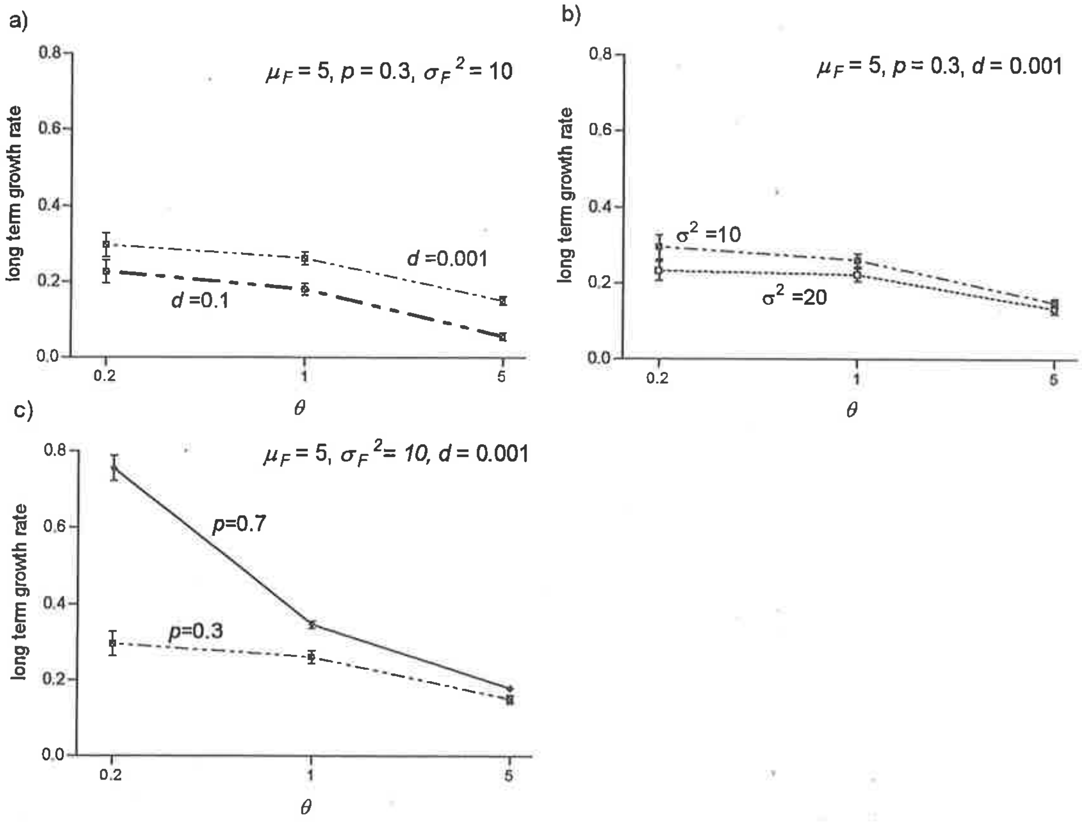
The simulation model was written in GAUSS v 3.0 (Aptech 1992).

6.5 RESULTS - SEED RELEASE MODEL

6.5.1.1 Density-independent case:

Increasing the death rate of seeds stored in the seedhead and increasing the variance of the reproductive output lowered the *ltgr* for all θ values (Figure 6.12 a & b). However, the effect of increasing the variance of the reproductive output was smaller with large theta ($\theta = 5$) compared with small theta ($\theta = 0.2$). Lowering the probability of reproductively successful years (*p)* had the biggest effect on the rapid initial release strategy ($\theta = 0.2$) compared with either the constant release or slow initial release strategies (Figure 6.12 b). A decrease in the probability of a reproductively successful year ($p = 0.7$ to 0.3) lowered the *ltgr* for all θ curves (Figure 6.12 c), although the magnitude of change was larger with smaller θ. When *p* was high (0.7), the winning θ strategy (*i.e.* highest *ltgr*) was the rapid initial release ($\theta = 0.2$). However, as *p* was lowered to 0.3, the constant release strategy ($\theta = 1$) became the winning strategy. The slow initial release of seeds ($\theta = 5$) was not the winning seed release strategy under any of the parameter combinations examined.

Figure 6.12: Effect of increasing a) seed death rate of seeds held in the seedhead, b) the variance of reproductive output and c) the probability of a successfully reproductive year on the long term growth rates for the different seed release curves.



6.5.1.2 Density-dependent case:

There are often co-existing strategies rather than a clear ESS for the three θ values examined (Table 6.5). For an ESS strategy to exist for a particular θ strategy, a series of ticks need to be present in the corresponding column of Table 6.5, while a series of crosses need to be found in the corresponding row. Under certain parameter combinations, some strategies were able to invade other strategies but could not be invaded themselves. When the seed death rate was low (Table 6.5 1a & 2a), the slow initial release strategy ($\theta = 5$) could invade the fast initial release strategy ($\theta = 0.2$), but could not be invaded by the fast initial release strategy. However, with high seed death rates (Table 6.5 1b & 2b), both the constant release ($\theta = 1$) and the rapid initial release ($\theta = 0.2$) strategies could invade the slow initial release strategy (θ= 5), while $\theta = 5$ could not invade either strategy.

When the probability of a successful year was high ($p = 0.7$), both the slow initial release and the constant release strategies could co-exist irrespective of the variance in the reproductive output or the seed death rate. Under the same conditions ($p = 0.7$) neither the constant release ($\theta = 1$) nor the rapid initial release ($\theta = 0.2$) strategies could be invaded. However, if conditions are less favourable ($p = 0.3$), then the ESS is either to release a constant fraction ($\theta = 1$) or hold onto seeds until much later ($\theta = 5$). Likewise, if there is a high seed death rate, ($d = 0.1$), then the ESS is to release seeds rapidly during the first few years. However, there is no advantage in releasing seeds quickly if there is a low death rate of seeds in the seedhead ($d = 0.001$).

The results from the first half of this chapter suggests that the seed release curve most likely to occur for seeds from *Erodiophyllum elderi* seedheads is a slow initial release while there are many seeds present in the seedhead, followed by a rapid release once the seedhead begins to degrade (*i.e.* $\theta = 5$). The slow initial release strategy ($\theta = 5$) is only better than rapid initial release ($\theta = 0.2$) when there is a low seed death rate. The slow initial release strategy did not perform better than the constant release rate ($\theta = 1$) under any of the conditions examined, although the strategies were able to co-exist when the probability of successful reproduction was high ($p = 0.7$) and the seed death rate was low ($d = 0.1$).

Table 6.5: Invasability of θ strategies for mean reproductive output $\mu_F = 5$ for 1) $\sigma_F^2 = 5.5$, and 2) $\sigma_F^2 = 25$ each with a) low death rate of seeds held within the seedheads (d= 0.001) and b) high seed death rate (d= 0.1). ✓ indicates that the invader strategy has growth rate > 0, × indicates that the growth rate is < 0, and – indicates that the growth rate of the invader is not significantly different to 0. The conditions under which invasion or non invasion occur are listed. For an ESS strategy to exist for a particular θ, a series of ticks need to be present in the θ column and a series of crosses need to be found in the corresponding row.

1) $\sigma_F^2 = 5.5$

a) low seed death rate

res θ	invader θ 0.2	1	5
0.2		✓	✓
1	✓		–: p=0.7 ×: p=0.3
5	–	✓	

b) high seed death rate

res θ	invader θ 0.2	1	5
0.2		✓	×
1	×: p=0.3		×
5	✓	✓	

2) $\sigma_F^2 = 25$

a) low seed death rate

res θ	invader θ 0.2	1	5
0.2		✓	✓
1	✓		–: p=0.7 ×: p=0.3
5	–	✓	

b) high seed death rate

res θ	invader θ 0.2	1	5
0.2		✓	×
1	✓		×
5	×: p=0.3	✓	

6.6 DISCUSSION

Through the elaborate mechanisms of seed dormancy and seed release from hard woody seedheads, *Erodiophyllum elderi* maintains a long lived seed bank. The slow degradation of seedheads observed in the field, and the associated slow release of seeds from seedheads, spreads the risk of germination through time. Despite the stage structured nature of the *E. elderi* seed bank, simple models for annual species with constant germination fractions seem to predict many aspects of this species (Cohen 1966: 1968; Ellner 1985 a & b). However, from field experiments, the seed release curve from *E. elderi* seedheads is most likely a slow initial release followed by a rapid release as the seedhead degrades. However, according to the seed release model, this shape curve is only likely to occur if the death rate of seeds held in the seedhead is low and the probability of successful years is high. Dormancy strategies can reduce massive seed consumption from predators by storage in maternal tissue (Inouye 1980; Kamenetsky and Gutterman 1994) and can reduce sibling-sibling competition between seedlings (Inouye 1980; Venable 1989; Gutterman 1994; Murray 1998). The relative importance of each of these factors in driving the evolution of the *E. elderi* seedhead is unknown. Additionally, maintaining a long term seed bank is important because reproductive variance is high with many years with no input into the seed bank (discussed in Chapters 3 and 4).

Seeds are held in *E. elderi* seedheads by hard, spiny bracts which open when wet, and close once the seedhead dries out. The repeated opening and closing of these bracts allows the slow release of seeds over a period of many years, in a manner similar to *Astericus hierochuntis*, a desert annual which inhabits low lying areas in Israel (Gutterman and Ginott 1994). Although *E. elderi* bracts open with a small amount of water (< 1 mm rainfall in the field, and sometimes with morning dew, personal observation) this does not necessarily result in seed release. Irrespective of stage class, studies of seeds within seedheads shows that seed release occurs from the top of the seedhead first, followed by seed release from the middle and then the base of the seedhead. The lower weight of degraded seedheads and the lower numbers of seeds present suggest that most seeds are released once, or as, the seedhead begins to break down.

Erodiophyllum elderi seedhead degradation may take many years to occur and this degradation appears to determine, to a large extent, the number of seeds which are released at any given time. Through time, bracts are broken off by particulate material (mainly sand) being lodged between the bracts. Field studies show that while bracts are present, seeds are generally released from the seedhead during rainfall events. The association of seed release with conditions suitable for germination reduces the chance of seed loss between phases. As seedheads degrade, bracts are lost and seeds are released from seedheads up to several days after rain. Consequently, seed release mechanisms vary, depending on the age of the seedhead. One advantage of different release mechanisms for capsules of different ages from the same plant is that not all seeds are released simultaneously (Gutterman *et al.* 1967).

Although open bracts are necessary for seed release, the absorption of water into the seedhead during precipitation may also reduce seed release. As the seedhead absorbs water, the bracts open and pressure is applied to the neighbouring seeds, making it difficult for them to be released. This may explain why very few seeds are released from the youngest seedhead stages, as maximum pressure is applied to all seeds within the seedhead. Once some seeds are released the pressure applied to the neighbouring seeds is reduced and it becomes easier for seeds to be released. Other synaptospermic species release seeds readily with the onset of rain (Gutterman 1972). For some species, seed release mechanisms can be explosive and, with the onset of rain, seeds shoot out from the seed holding structures on the plant (Friedman *et al.* 1978; Friedman and Stein 1980). I found no evidence of explosive seed release from *E. elderi* seedheads despite some dependence on rainfall for seed release.

There is no fixed age for transition between the visibly distinct seedhead stages because seedhead development will depend partly on experience, such as rolling around on the ground, and not just chronological age. Unfortunately, seedhead dynamics are too slow to follow cohorts of seedheads to determine the actual age of seedheads within the scope of this study. However, I estimate degraded seedheads to be at least 15 - 25 years old and this is currently being investigated in the field. When seedheads were soaked in water, more seeds were released from stage 3 seedheads than from seedheads in other stages. This is probably because of two reasons: firstly, stage 3 seedheads have more seeds available to be released than either stage 4a or 4b seedheads, and secondly, seeds are more likely to be released from stage 3 seedheads than the earlier stages due to the degree of degradation. However, as I did not examine the establishment and reproductive output of seedlings released from different stage classes, the consequence of different seed release rates from different seedhead stages on the population dynamics of *E. elderi* remains unknown.

Rainfall is the primary factor enabling seed release from *E. elderi* seedheads. What remains unclear is the number of seeds which will be released for any given rainfall event, and how much rainfall is needed for seed release to occur? There were very few seeds released when seedheads were soaked in water for up to 48 hours, which suggests that the length of time water remains after a rainfall event is unlikely to further increase the number of seeds released. Therefore, more seeds are unlikely to be released with an increased amount of rainfall above some particular value, even if pooling in the field occurs. If such an upper threshold on seed release with increasing rainfall exists, then it may reflect that future environmental conditions are unpredictable. Ellner (1985b) suggests that if future environmental conditions are unpredictable, the best strategy is some 'optimal' fraction rather than germination correlated with environmental conditions.

Dormancy is imposed on *E. elderi* seeds by the physical constraint of being held in the seedhead and, once removed, seeds germinate readily with the addition of water. The rapid germination of seeds when released from within a single seedhead appears to be superficially in contrast with Westoby (1981), who suggests that seeds dispersed in a fruiting structure should have a diversity of germination behaviours. Although *E. elderi* seeds lack inherent dormancy, the slow release of seeds from the seedhead creates temporally diverse germination behaviours, as predicted by Westoby (1981). In contrast to *E. elderi*, seeds from many desert ephemerals show highly sophisticated dormancy breaking requirements (Went 1949; Gutterman 1994). Environmental fluctuations experienced by the soil seed bank are likely to be moderated for seeds stored in maternal structures. This reduction in environmental variation may delay germination and extend the viability of seeds.

By being held in a multi-seeded structure, *E. elderi* seeds have some advantages akin to a large seeded species. Although *E. elderi* seeds had high viability (98%) which is typical of large seeded species, individual seeds do not have the high reproductive success characteristic of large seeded species (Silvertown 1989; Pake and Venable 1996). *E. elderi* has a large viable seed bank with low germination rates, which buffers the population against highly variable per capita reproductive success (Pake and Venable 1996). High seed viability is predicted when conditions support a low seed germination proportion (Cohen 1968). Similarly, the ESS model developed here shows that the most realistic strategy for *E. elderi* seeds (slow initial release followed by rapid release when the seedhead begins to degrade) is only possible when the death rate of seeds stored in the seedhead is low. Through high seed viability by storage in the seedhead, this seed release curve is possible for this species. Large seed banks are also important in reducing the chance of seed predation through predator satiation in ecosystems where predators are prominent (Louda 1989).

Termites and ants may influence seed release and post-release mortality which highlights further benefits of the seedhead. Termites can affect both soil properties and the ephemeral flora in arid communities (Watson and Gay 1970), particularly during drought conditions (Watson *et al.* 1973). The effect of termites on seed release and the survival of *E. elderi* seeds is unclear, although they appear to assist in breaking down seedheads. If termites hasten seed release, seed loss may increase due to seed release at a time when germination requirements are not necessarily met. Although termites consume a large fraction of dead organic matter (Whitford *et al.* 1992) they are unlikely to be seed predators. In contrast, ants may be important predators or dispersers of *E. elderi* seeds. This is not surprising as many Australian arid species have seeds which are heavily preyed upon by ants, and many have adaptations to assist in ant dispersal (Davidson and Morton 1981). My observations of *E. elderi* seedlings growing on ant mounds suggests that ants may contribute to post-release dispersal, although this clearly needs further investigation. The protection of seeds in the *E. elderi* seedhead may reduce the negative effects of ant predation. Indeed, Kamenetsky (1994) suggests one advantage of a multi-seeded structure is the protection afforded to the seeds against seed predation. In addition, the selective forces favouring predator avoidance can be intense (Ellner and Shmida 1981). The effect of ant predation on seed release strategies could (and should) be incorporated into an extension of the ESS model developed in this chapter.

Although prolonged dormancy for *E. elderi* seeds is regulated by maternal tissue, while inherent dormancy is controlled by embryonic tissue (Westoby 1981), the ecological effect is the same. In both cases a persistent seed bank capable of germinating immediately under favourable conditions exists, while many seeds are viable but incapable of immediate germination (Philippi 1993b). The *E. elderi* seedhead spreads the risk of germination through time by imposing long term dormancy within the seedhead with a similar result to the intricate dormancy breaking requirements for soil seed banks of many desert ephemerals. However, for prolonged dormancy to be effective, seeds must be highly viable, as observed for seeds stored in the *E. elderi* seedhead. Cohen (1968) suggests that the evolution of long term viability and prolonged dormancy takes place simultaneously by an identical mechanism. In the case of *E. elderi*, both high viability and prolonged dormancy are achieved with the seedhead. The evolutionary development of the seedhead was therefore likely to be an adaptation to a fluctuating environment. Additionally, spreading the risk of germination through time ensures a long term seed bank and may reduce sibling-sibling competitive interactions by creating a temporal distribution in seed germination (Venable 1989; Gutterman 1994).

7. Seedling establishment

7.1 INTRODUCTION

Seedling germination and establishment can be enhanced in arid environments by a variety of mechanisms modifying an otherwise unsuitable environment. These mechanisms include resource accumulation, amelioration of the environment and directed seed dispersal to suitable sites. However, there are often conflicting results about the importance and the effect of any particular mechanism (eg. leaf litter effects Facelli and Pickett 1991). For example, germination is sometimes enhanced by the presence of leaf litter (Fowler 1986) even though the survival of *Senecio* seedlings decreased when they were growing beneath dead individuals of the grass *Poa annua* (Bergelson 1990). The importance of different mechanisms may also change throughout the life span of a plant. For example, the presence of adult shrubs can promote seedling germination (Osborn *et al.* 1932) but may affect seedlings adversely through competition (Friedman and Orshan 1975; Friedman *et al.* 1977; Aguiar *et al.* 1992; Telfer 1998). Many processes during the early stages of a plant's life are fundamental to future seedling success. Dispersal is one of the most important of these mechanisms as the location of seeds has a dramatic effect on germination patterns and, to a large extent, determines future inter- and intra-specific interactions.

Dispersal processes often result in a highly variable seed bank distribution for many desert communities (Kemp 1989; Gutterman 1994). In some cases, seeds are dispersed to sites suitable for germination (Kemp 1989) while in others they are not (Venable and Lawlor 1980). Seed bank patchiness can be amplified through directed dispersal (Howe and Smallwood 1982) resulting in seed deposition beneath a parent or into specific microsites or seed caches (Kemp 1989). Sheet water flow is an important dispersal factor in desert systems and redistributes seeds and other debris (Kemp 1989). Dispersal patterns are modified by seed traps including parent plants (Aguiar *et al.* 1992), bits of wood and other material. One consequence of seed accumulation is subsequently large seedling densities once germination has occurred. For example, seeds may accumulate in depressions in the ground where there is increased water availability which promotes germination (Friedman *et al.* 1977; Friedman and Stein 1980).

If many seeds germinate in areas with large seed abundances, the promotion of germination may be offset by negative density-dependent effects due to higher seedling abundances (Bergelson 1990). Therefore, the accumulation of seeds in particular areas may result in a conflict between site suitability for seed and seedling requirements (Schupp 1995). Ensuing negative seedling-seedling interactions can result in a reduction in reproductive output or increased seedling mortality (Inouye 1980; Inouye *et al.* 1980; Gurevitch 1986). To avoid this negative effect, high seedling densities for some desert annuals inhibit subsequent seed germination (Inouye 1980). However, in desert communities, where resources are scarce, the negative interactions between seedlings in these areas of high seedling density may still be less detrimental than the alternative environment away from the area.

As well as the potential density-dependent effects between sibling seedlings, the accumulation of seeds in the vicinity of parent plants may result in competitive effects between parents and their offspring. For example, in the Patagonian steppe, root competition with established plants was greater than the aerial protection afforded by the shrubs (Aguiar *et al.* 1992). Although the importance of competitive interactions has frequently been questioned (Went 1949; Fowler 1986; Hastings 1987), the role of biotic interactions in determining the structure of desert plant communities is well known (Fonteyn and Mahall 1981; Schoener 1983). In contrast, facilitative effects are less well known (Callaway and Walker 1997) although protection from herbivory (Osborn *et al.* 1932) and leaf litter effects (Fowler 1986) have been studied. The balance between the benefits for seedling germination and costs due to future interactions swings precariously. There are complex combinations of competitive and facilitative interactions occurring in many communities (Callaway and Walker 1997).

The observed pattern of seedlings is the result of interactions during dispersal, germination and establishment processes (Kemp 1989). The placement of seeds and the effect of a wide range of factors on seedling establishment and survival are therefore important for the final reproductive output of plants. There appear to be no generalised effects of the importance of factors which affect seedling germination, growth and establishment across communities. Through studying aspects of a plant's initial stages, the relative importance of each of these processes may be understood (Bengtsson *et al.* 1994; Briones *et al.* 1996).

The accumulation of *Erodiophyllum elderi* seedheads may result in high seedling densities after germination events. In some cases, seedheads accumulate beneath adult plants and, in others, seedheads are part of the debris accumulating in areas through sheet water flow. After mature plants die, the leaf litter which remains on the ground for several years may influence germination and establishment of seedlings. Seed accumulation may result in potential seed-seedling site conflicts, the effects of which are confounded by potential facilitative effects from *E. elderi* plant leaf litter or nutrient accumulation beneath the plants.

In this chapter I examine the effects of seed distribution in relation to subsequent germination, establishment and growth of *E. elderi* seedlings. Specifically, I ask: Do large densities of seedlings inhibit further germination? Are seedlings and seedhead abundances higher in drift material redistributed by sheet water flow? To what extent do seedheads accumulate beneath mature *E. elderi*? Is this pattern similar for seedling germination patterns? Is there a seed-seedling site conflict? Do *E. elderi* modify the area beneath them creating a micro-environment? Do seedlings experience density-dependent effects? and, are these modified by the presence of *E. elderi* leaf litter?

7.2 METHODS AND ANALYSES

7.2.1 Effect of seedhead density on seedling germination and survival

7.2.1.1 Seedhead and seedling survey

To determine whether high seedling densities inhibit further germination in the field, I examine whether seedling and seedhead abundance relationships are linear. I also examine how grazing pressure affects this relationship by examining two *E. elderi* populations in high and low grazing pressures. Seedhead and seedling densities were recorded in fifty randomly chosen 20x20 cm quadrats in Patches 2 and 7 (high grazing

- outside the Reserve) and Patches 9 and 10 (low grazing - inside the Reserve). Linear regressions between seedling density and seedhead density were calculated for each patch and departure from linearity tested with the runs test. An F-test was used to determine whether there were significant differences between the regression lines. This survey was conducted during the winter months (12-Jun-1995) at a time when there were large densities of *E. elderi* seedlings throughout the area.

The density of *E. elderi* seedlings and seedheads in the patches were analysed separately using non-parametric Kruskal-Wallis tests. Transforming the data was unsuccessful in removing the highly skewed nature of seedhead and seedling abundance data.

7.2.1.2 Effect of seedhead density on seedling germination

I manipulated *E. elderi* seedhead densities in the field and monitored subsequent recruitment to determine whether seedling densities increased with seedhead density. The experiment was established on 15-Jun-95 in Patches 2 and 7 (high grazing - outside Reserve) and Patches 9 and 10 (low grazing - inside Reserve).

Six replicate blocks divided into four 20x20 cm cells were established in each patch with wooden stakes placed horizontally on the ground and held with metal pins. This created a corral which prevented seedhead movement between cells, while remaining inconspicuous enough to attract minimal attention from animals. Densities of 0, 5, 25 and 75 seedheads per cell were randomly assigned to each of the four cells within each block. The zero seedhead density represented background seed densities in the soil seed bank. All vegetation and seedheads were removed carefully from within the cells and in the surrounding 50 cm of the block before seedheads were placed in the blocks. Seedling densities were monitored on 2-Jun-96 and 5-Apr-97. Although data were collected every field trip between these dates, germination had only occurred in one patch in the period to April 1997.

Data were analysed within each patch with a two-way mixed model ANOVA on ranks with block as a random factor and seedhead density as a fixed factor in JMP (SAS 1995) as recommended by Zar (1984) for analysing split plot designs. Differences between seedhead densities were determined with Dunn's multiple comparisons on the ranks.

7.2.2 Mature plant-seedling interactions

7.2.2.1 Seedhead and seedling density in relation to drift material

I conducted a survey to determine whether seedling and seedhead abundances are correlated with drift material accumulation on the ground. Drift material comprised of twigs, egesta, leaves, bones and occasionally, larger pieces of wood. This data was also used to estimate the proportion of ground covered in drift material. A series of sixty random quadrats, 20x20 cm each, were placed on the ground and seedling and seedhead abundances recorded on 31-Jan-1996 throughout Patch 6. Each quadrat was also classified into one of two classes: "open" or "drift material", depending on whether more or less than 50% of the quadrat was covered in drift material respectively.

Abundances were checked for normality and homogeneity of variances. Separate Mann-Whitney U-tests were performed on seedling and seedhead abundances to test whether there was a difference in open areas compared with the areas with drift material.

7.2.2.2 Seedhead and seedling density in relation to **E. elderi** *plants*

I measured seedhead and seedling densities to determine whether they were more common beneath adult *E. elderi* plants or in open areas. One random direction within each 90° quadrant was chosen and a transect layed out to ensure good coverage of the patch on 31-Jan-1996 within Patch 6. Whenever the transect intercepted a mature *E. elderi* plant (at this stage they were mostly dead) a 20x20 cm quadrat was placed with half on either side of the tape. The abundance of seedlings and seedheads was measured in each quadrat. Another quadrat was placed midway between the *E. elderi* on the transect and the nearest mature *E. elderi* to represent the open positions and sampled in the same manner.

Separate ANOVAs for seedlings and seedheads were performed on the differences between abundances in the open and under *E. elderi* plants to determine whether the data from the transects differed. Spearman Rank correlations were calculated for each transect to determine whether there was a spatial trend along the transects. As there were no spatial trends along the transects, and no difference between transect, future analyses considered values to be independent. Pearson correlation coefficients were calculated to determine whether pairing was effective.

Abundances of seedlings in the open compared with under *E. elderi* plants were analysed with a Mann-Whitney U-test while seedhead abundances were analysed with a t-test.

7.2.2.3 Seedling growth in soil taken from beneath dead **E. elderi** *plants and from open areas*

I grew *E. elderi* seedlings for three months to determine if the soil beneath dead *E. elderi* plants was more beneficial than soil from open areas. Soil was collected from beneath dead *E. elderi* plants and in the open spaces between plants to assess *E. elderi* seedling growth in the different soil. Soil samples of 20x20 cm and 5 cm deep were collected from beneath five randomly chosen dead *E. elderi* plants and the five corresponding neighbouring open areas. Each soil sample was placed into a pot in a glasshouse and five *E. elderi* seeds were planted per pot. Pots were watered regularly with all pots receiving the same quantity of water at each watering. Additional seedlings were germinated simultaneously so that seedlings could be transplanted to maintain the same number of seedlings per pot. All plants were harvested at the end of three months (27-May-1996) and the above ground dry weights measured. The above ground dry biomass data were analysed using a t-test.

In addition, soil characteristics were measured in the Soil Science Laboratories, Waite Institute, The University of Adelaide. The following variables were measured: pH, conductivity, texture, colour, the presence or absence of $CaCO_3$, available phosphorous, nitrogen and organic carbon content. Soil results were analysed with MANOVA and the response of each soil characteristic with the identity response matrix. In addition, the power of the tests were examined.

7.2.3 Seedling-seedling interactions

7.2.3.1 Seedling competition beneath dead adult **E. elderi**

To determine whether there were density-dependent effects between seedlings and whether litter enhanced seedling growth, I conducted a thinning experiment in areas with and without litter. Seedlings were either thinned in areas beneath dead *E. elderi* plants or left at the background density to determine if the thinned seedlings had higher survival or growth rates. In addition, I removed dead *E. elderi* material from half the treatments to determine whether litter enhanced seedling survival. Areas of high seedling density were chosen to enhance the ability to detect competitive effects as competition is often difficult to detect in the field (Waller 1981).

An 80x40 cm plot was marked in each of 24 high seedling density areas and divided into two adjacent 40x40 cm quadrats. Quadrats were positioned to obtain uniform seedling density within each 40x40 cm quadrat although, in some cases, this was not possible. The treatment of removal of dead material was randomly assigned to each block until half the plots had each treatment. The thinning treatment was randomly assigned to each pair of the cells. Two-thirds of the seedlings were removed from each 40x40 cm area in the thinned quadrats. Plants were removed by cutting them at the base which was previously found to be effective in killing seedlings without disturbing the surrounding area. Seedling abundances were counted in the central 20x20 cm quadrat of each of the 40x40 cm quadrats, thereby leaving a 10 cm buffer zone around them. The experiment was established on 31-Jan-1996, with subsequent readings taken on 20-Feb-1996, 5-Mar-1996, 3-Jun-1996 and 25-Aug-1996.

Seedling abundance data were tested separately for each data collection and the P_{sig} value Bonferroni adjusted to 0.0167 due to the lack of independence between readings (20-Feb-96, 5-Mar-96 and 3-Jun-96). Data were logit transformed to improve normality ($\ln(p/(1-p))$, where $p=(m+0.5)/(n+1)$, m = final abundance of seedlings, n = initial seedling abundance). This transformation removes problems associated with 0% and 100% survival proportions (Sokal and Rohlf 1981). Cell pairs were tested for the effectiveness of pairing using the Pearson correlation coefficient for leaf litter presence and absence. As this pairing was only strong in a couple of cases in the early readings data were analysed with two-way ANOVAs with thinning treatment and leaf litter presence as factors.

To test for an overall effect of seedling thinning, the means of the differences of the proportion of seedlings surviving in the thinned and non-thinned sides of the plots with treatments of with and without dead *E. elderi* litter were tested for a deviation from zero. A result greater than zero indicates that a higher proportion of seedlings survived in the thinned areas. The differences in the proportion of seedlings surviving in each treatment at each time were plotted.

7.2.3.2 Seedling competition in the open

I conducted a seedling competition experiment to determine whether density-dependent effects occurred between seedlings in areas without any dead material present. Areas of high seedling density (minimum of eight per 20x20 cm area) were chosen to enhance the ability to detect competition between seedlings. Instead of using a split plot design (as in the above experiment, section 7.2.3.1) which makes it difficult to maintain similar seedling abundances on either side of the plot, quadrats were chosen with high seedling density and paired with the nearest quadrat containing the same seedling density. One quadrat out of each pair was randomly assigned to be thinned by $^2/_3$. Quadrat pairs were generally within 0.5 m of each other. Each corner of the 40x40 cm quadrats was marked and the seedling removal treatment subjected to the entire area. *E. elderi* seedling abundances were recorded in the inner 20x20 cm leaving a 10 cm buffer zone around the inner quadrat. This experiment was established on 25-Aug-1996 with abundance measurements collected on 4-Oct-1996 and 10-Dec-1996.

The effectiveness of pairing was tested with the Pearson correlation co-efficient and paired t-tests were performed on the proportion of seedlings surviving in the thinned and unthinned plots.

All data were checked for normality and homogeneity of variances and non-parametric tests were used when these condition were not met. Data were analysed using PRISM (PRISM 1995) unless otherwise stated.

7.3 RESULTS

7.3.1 Effect of seedhead density on seedling germination and survival

7.3.1.1 Seedhead and seedling survey

The relationship between seedling abundances and seedhead abundances did not depart from linearity in any patch (runs test, $P>0.05$ in all cases; Table 7.1). However, the Goodness of Fit values were typically low (Linear regression, Patch 2: $r^2=0.36$, Patch 7: $r^2=0.22$, Patch 9: $r^2=0.29$, Patch 10: $r^2=0.52$; Figure 7.1) because of the range of seedling densities at high seedhead densities. In all cases, there was a positive relationship between seedhead and seedling abundance (*i.e.* slope of the regression lines were significantly different to zero and was positive, F-test, $P<0.05$ in all patches; Table 7.1). The slopes were bigger in the heavily grazed patches than for patches inside the Reserve (F-test, F=13.005, $\text{d.f}_{\text{num}}=3$, $\text{df}_{\text{den}}=191$, $P\leq0.0001$). In both patches outside the reserve, the intercepts were greater than zero suggesting that seedlings were present where there were no seedheads.

There were higher seedling densities in Patch 2 outside the Reserve than in both patches inside the Reserve (Kruskal-Wallis, $\chi^2= 44.44$, $P<0.0001$, n=4; Dunn's, $P<0.05$; Figure 7.2 a). Although there was no difference between seedhead abundances between patches (Kruskal-Wallis, $\chi^2= 4.552$, $P=0.2077$, n=4; Figure 7.2 b) the patches inside the Reserve had larger variances. Maximum seedhead densities per 20x20 cm^2 for the inside Reserve patches were 40 and 60 (Patch 9 and 10 respectively) while Patches 2 and 7 had lower maximum seedhead densities of 28 and 13 respectively.

Figure 7.1: Linear regressions between seedhead and seedling abundances for patches experiencing high and low grazing. Goodness of fit r^2 values indicated next to regression lines.

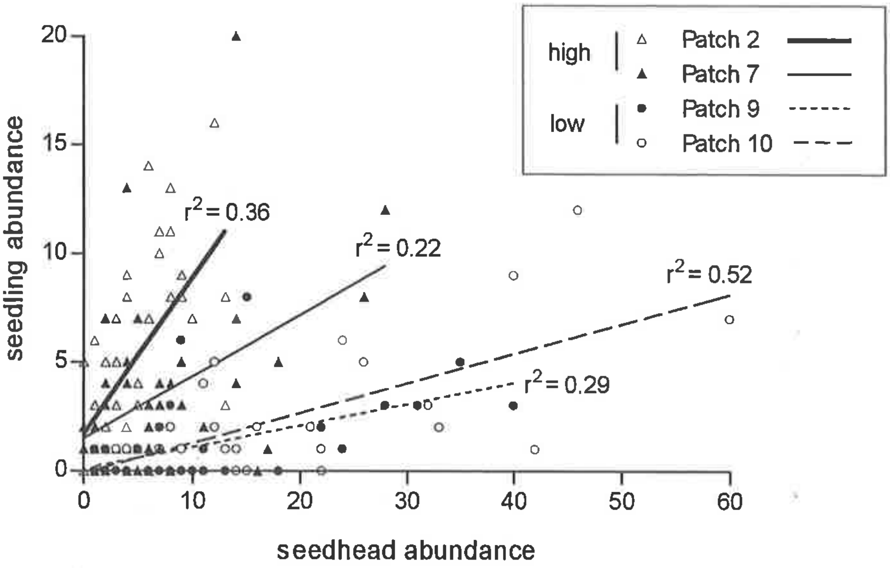


Figure 7.2: Abundances of a) seedlings and b) seedheads in each of the four patches on 12-Jun-1995. Different letters denote significant differences (Dunn's test, $P<0.05$). Box shows median, 25th and 75th percentiles and whiskers extend to minimum and maximum values.

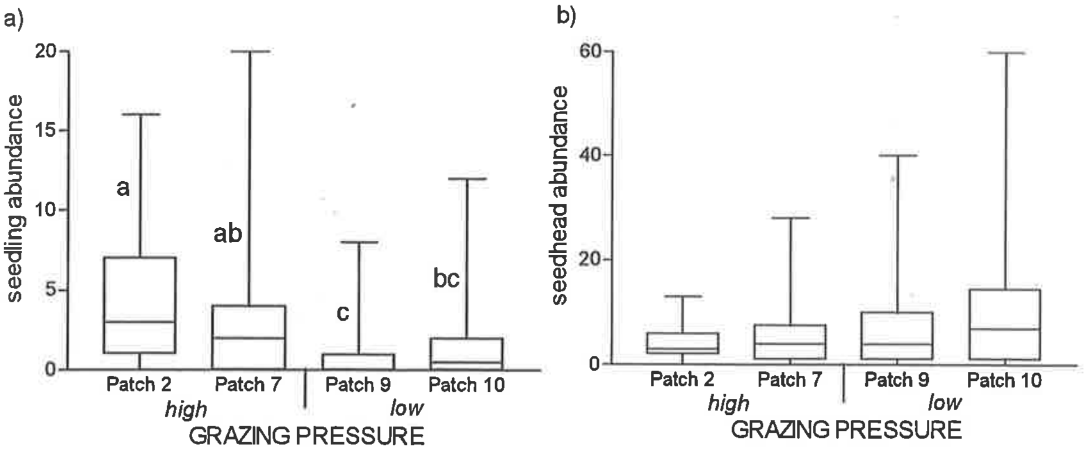


Table 7.1: Linear regression between seedhead and seedling abundances in patches experiencing high and low grazing. *m* is the slope of the line, c is the y-intercept, *P* determines if $m \neq 0$, and runs test examines departure from linearity.

	high		low	
	Patch 2	Patch 7	Patch 9	Patch 10
r^2	0.3636	0.2839	0.2938	0.5233
m	0.7216	0.2839	0.0985	0.1368
c	1.715	1.513	-0.1191	-0.0770
n	48	45	41	42
$P \leq$	0.0001	0.0010	0.0003	0.0001
runs test $P \leq$	0.9756	0.1426	0.9477	0.9850

7.3.1.2 Effect of seedhead density on seedling germination

Seedling germination in the corrals had only occurred in Patch 2 up to June 1996. At this stage seedling abundance was not correlated with seedhead density level. Germination was highly patchy and there were few *E. elderi* seedlings present. However, there were no seedlings in the cells with no seedheads present.

By 5-Apr-1997, germination had occurred in all *E. elderi* patches monitored. Seedling abundances increased with higher seedhead densities (ANOVA on ranks, seedhead density: $P<0.05$, df=3; Table 7.2 a-d). There were more seedlings in the cells with 75 seedheads present compared with all other seedhead densities in Patch 2 (Figure 7.3). In Patches 7, 9 and 10 the only significant effect was between the zero seedhead density and 75 seedhead density. This was because there was a large range of seedling densities in the high seedhead density categories. In Patches 2, 7 and 10 there was a strong spatial component for germination (ANOVA on ranks, block: $P<0.05$, df=5, Table 7.2 a-d). Few seedlings emerged in cells without seedheads. One replicate block in Patch 9 had been destroyed with sheet water flow.

Figure 7.3: Effect of seedhead density on seedling abundances in heavily grazed patches (a & b) and inside the Reserve (c & d) on 5-Apr-1997. Letters denote significant differences (Dunn's test, $P<0.05$). Boxes show median, 25th and 75th percentiles and whiskers extend to minimum and maximum values.

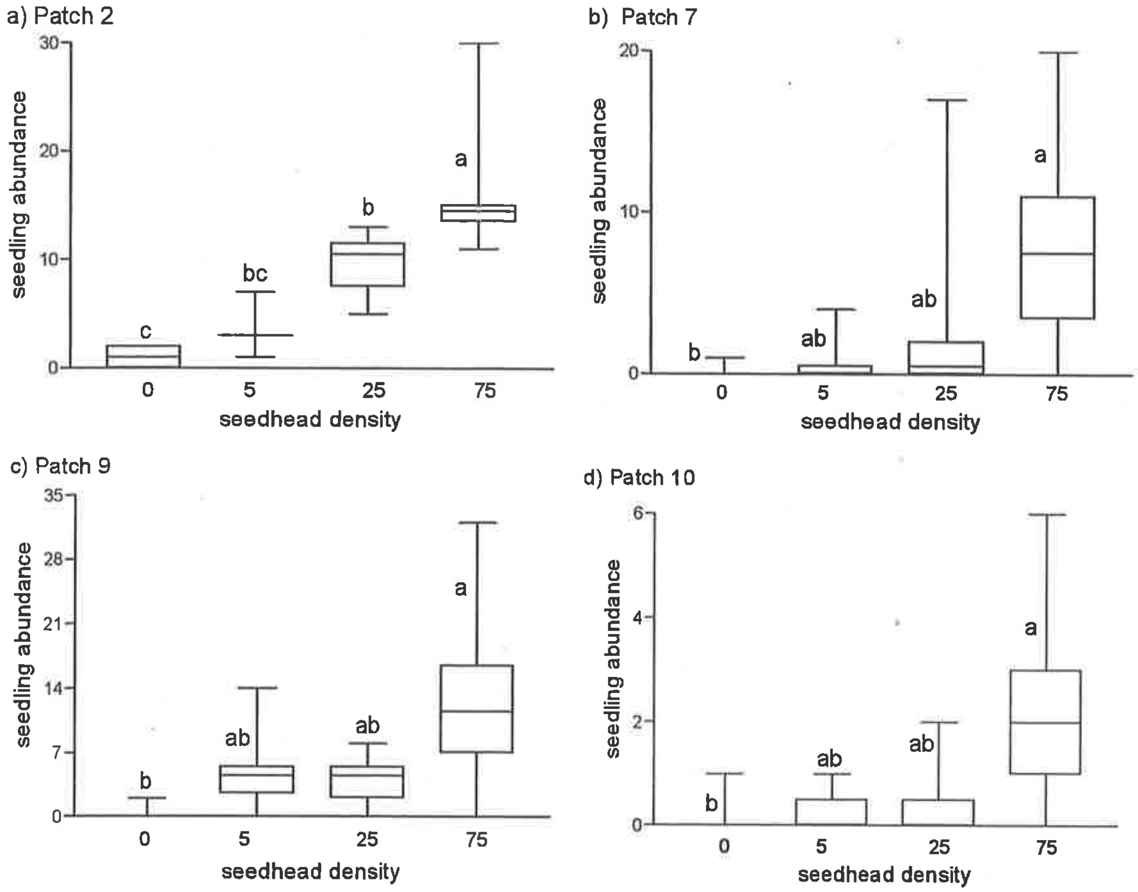


Table 7.2: Two-way mixed model rank ANOVA on seedling germination abundances for seedhead densities of 0, 5, 25 and 75 seedheads per cell. Each patch was analysed separately with block as a random factor.

high grazing		a) Patch			b) Patch 7		
source	df	MS	F	*P*≤	MS	F	*P*≤
total	8	135.017	29.527	0.0001	101.75	4.525	0.0057
seedhead density	3	329.111	71.893	0.0001	123	5.4911	0.0095
block	5	18.8	4.107	0.0150	89	3.973	0.0170
residual	15	4.578			22.4		

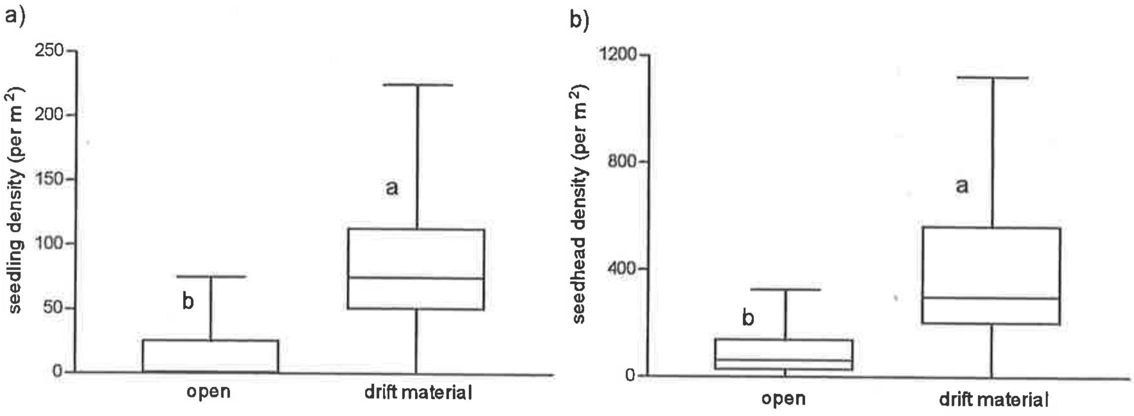
low grazing		d) Patch 9			e) Patch 10		
source	df	MS	F	*P*≤	MS	F	*P*≤
total	8	77.10	7.3839	0.0014	106.65	5.389	0.0025
seedhead density	3	76.067	7.285	0.0049	101.222	5.5536	0.0043
block	5	77.875	7.458	0.0029	109.9	5.1151	0.0123
residual	15	125.3			296.833		

7.3.2 *E. elderi* adult-seedling interactions

7.3.2.1 Seedhead and seedling density in relation to drift material

Exactly 50% of the random quadrats sampled were classified as open. Seedhead and seedling abundances were higher in areas with high drift material cover than in the open areas within Patch 6 (Mann-Whitney U-test, *P*<0.0001, U=104.0, n=30; *P*<0.0001, U=131.0, n=30 for seedlings and seedheads respectively; Figure 7.4). In both cases, the variability was greater in the areas with high drift material cover (F-test, seedlings: F=9.743, *P*<0.0001, seedheads: F=8.250, *P*<0.0001; df_{num}=29, df_{den}= 29 in both cases).

Figure 7.4: Abundances of a) seedlings and b) seedheads in areas with drift material cover (>50%) and in open areas. Boxes show median, 25th and 75th percentiles and whiskers extend to minimum and maximum values. Letters denote significant differences.



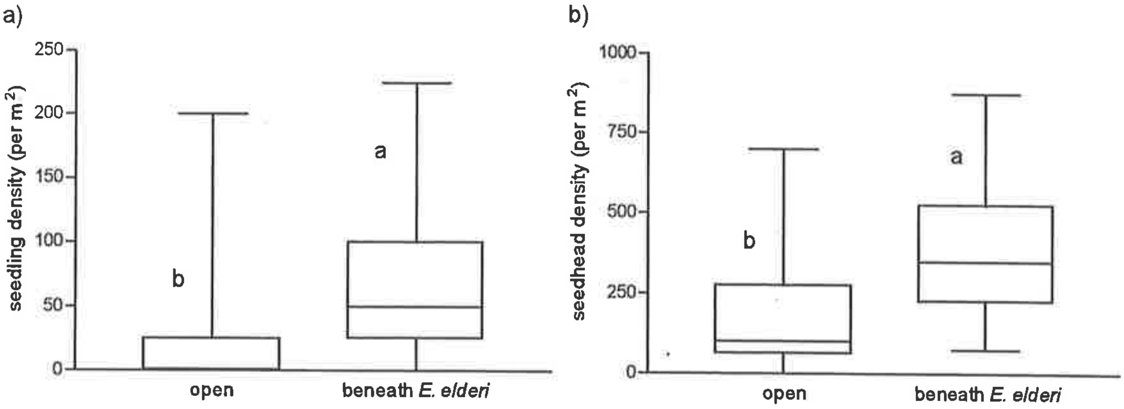
7.3.2.2 Seedhead and seedling density in relation to **E. elderi** *plants*

There were more seedlings and seedheads beneath *E. elderi* plants than in the open areas between *E. elderi* plants (seedlings: Mann-Whitney, U=214.0, n=60, *P*=0.0002; seedheads: t-test, t=4.188, df=60, *P*≤0.0001; Table 7.3; Figure 7.5). There was no spatial component of the abundance of seedheads in pairs of quadrats in the open and beneath *E. elderi* plant (Pearson correlation, *P*=0.3940; Table 7.3). However, the pairing for seedling densities between open areas and beneath *E. elderi* plant was borderline significant suggesting a spatial component (Pearson correlation, *P*=0.0597; Table 7.3).

Table 7.3: Mann-Whitney test for seedling abundances and t-test result for seedhead abundances beneath dead *E. elderi* plants and in open areas. Pearson Correlation coefficient (effectiveness of pairing) results for seedling and seedhead abundances.

		seedlings	seedheads
Mann-Whitney, t-test	*P*≤	0.0002	0.0001
	U, t	4.087	4.295
	d.f	60	60
effectiveness of pairing	r	0.2856	0.05039
	P≤	0.0597	0.3940

Figure 7.5: Abundances in open areas and beneath dead *E. elderi* plants for a) seedlings (boxes show median, 25th and 75th percentiles and whiskers extend to minimum and maximum values), and b) seedheads (mean ± SD). Letters denote significant differences.



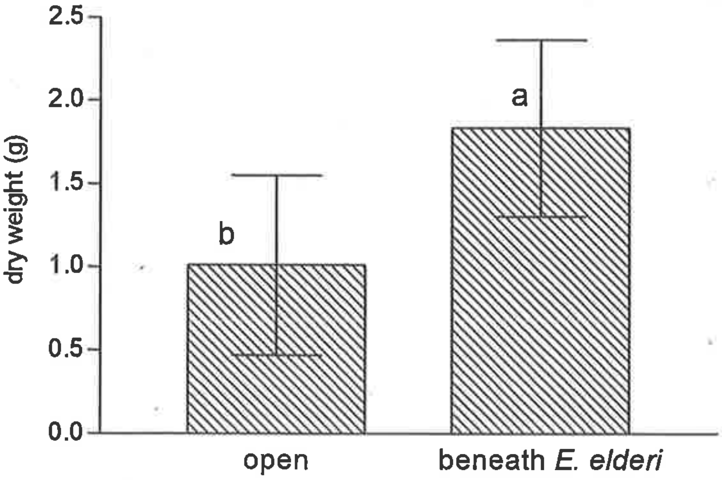
7.3.2.3 Seedling growth in soil taken from beneath dead **E. elderi** *plants and from open areas*

Seedlings were larger when grown in soil taken from beneath the dead *E. elderi* plants than from the open areas (t-test, P=0.0415, t=2.425, d.f.=8; Figure 7.6). However, there was no difference between variables examined in the soil from beneath dead *E. elderi* plants or in the areas in between (MANOVA, P=0.4935, F=1.0539, df_{num}=5, df_{den}=4; Table 7.4). Soil colour was consistently 5YRV4C6 (Munsell chart, anonymous 1954). Soil texture ranged from loamy sand to sandy loam, but there was no consistent difference between soil taken from beneath dead *E. elderi* plants or in the open areas between plants. In all cases, there was low power of the test statistics, which is most likely due to limited replication.

Table 7.4: MANOVA for soil collected from beneath dead *E. elderi* plants and from areas between *E. elderi* plants (position). Results from identity response matrix for phosphorous, nitrogen, organic carbon, pH, and conductivity with power details provided.

Source	Pillai's trace	approx. F	df_{num}	df_{den}	$P\leq$	Power
whole model	1.2559	1.3501	10	8	0.3421	
position	0.8242	2.8127	5	3	0.2120	
intercept	0.9992	753.613	5	3	0.0001	
phosphorous	0.2758	1.3332	2	7	0.3232	0.2025
nitrogen	0.3317	1.7369	2	7	0.2441	0.2523
organic carbon	0.3358	1.0801	2	7	0.3901	0.1716
pH	0.0580	0.2153	2	7	0.8114	0.0723
conductivity	0.2073	0.9151	2	7	0.4435	0.1518

Figure 7.6: Above ground dry biomass of seedlings grown in soil taken from beneath dead *E. elderi* plants and from open areas between plants. Mean ± SDs N=5. Letters denote significant differences.



7.3.3 Seedling-seedling interactions

7.3.3.1 Seedling competition beneath dead adult **E. elderi** *plants*

Leaf litter removal significantly decreased seedling survival (ANOVA, $P<0.0166$, df=1, in all cases; Table 7.5; Figure 7.7) while thinning seedlings had no effect on seedling survival (ANOVA, $P>0.0166$, df=1, in all cases; Table 7.5). Although there was no overall effect of thinning seedlings (*i.e.* mean of (the proportion surviving on the thinned side - the proportion surviving on the unthinned side) was not significantly different to zero in any case, t-test, $P>0.05$), removing individuals was associated with reduced seedling mortality in some quadrats, while in others, the opposite held (Figure 7.8). The variability of these effects was greater when the leaf litter was left (Figure 7.8).

Thinned and unthinned cells were effectively paired at all times with leaf litter removal (Pearson correlation, February 1996: r=0.5479, *P*=0.0326; March 1996: r=0.6371, *P*=0.129; June 1996: r=0.5364, *P* =0.0361). However, at no stage were the thinned and unthinned cells effectively paired for the quadrats with leaf litter.

Table 7.5: Two-way ANOVA on logit transformed survival proportions of seedlings. Leaf litter was either removed or left, and seedlings were either $^2/_3$ thinned or not. Results shown for a) 20-Feb-1996, b) 5-Mar-1996, and c) 6-Jun-1996.

		a) February			b) March			c) June		
source	df	MS	F	*P*	MS	F	*P*	MS	F	*P*
leaf litter	1	9.188	7.382	0.009	23.50	11.65	0.001	21.07	11.24	0.002
thinning	1	0.880	0.707	0.405	0.999	0.496	0.485	1.426	0.761	0.388
interaction	1	2.774	2.229	0.143	3.304	1.639	0.207	0.257	0.137	0.713
residual	44	1.245			2.016			1.875		

Figure 7.7: The proportion of seedlings surviving under treatments of leaving dead *E. elderi* material and removing it for a) 20-Feb-96, b) 5-Mar-96 and c) 3-Jun-96. Letters indicate significant differences. Values plotted are mean ± SDs.

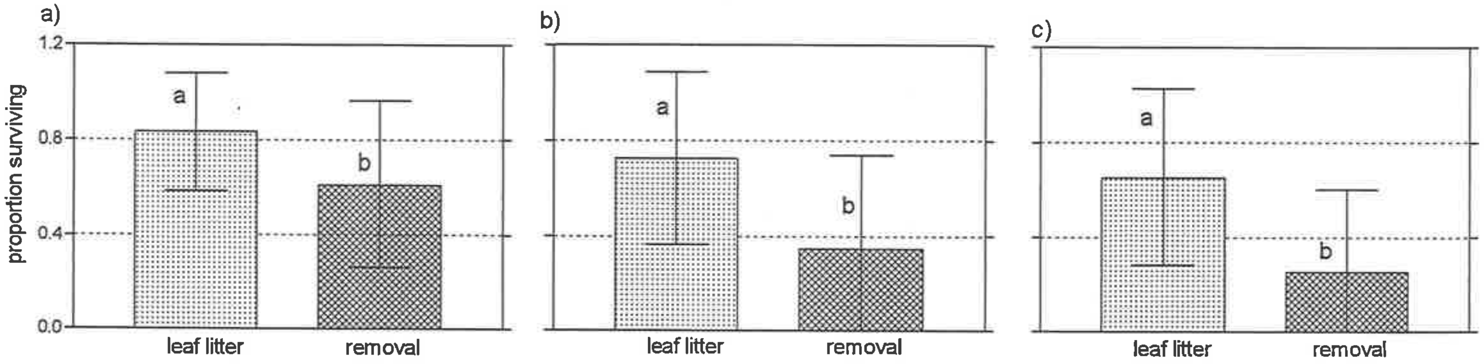
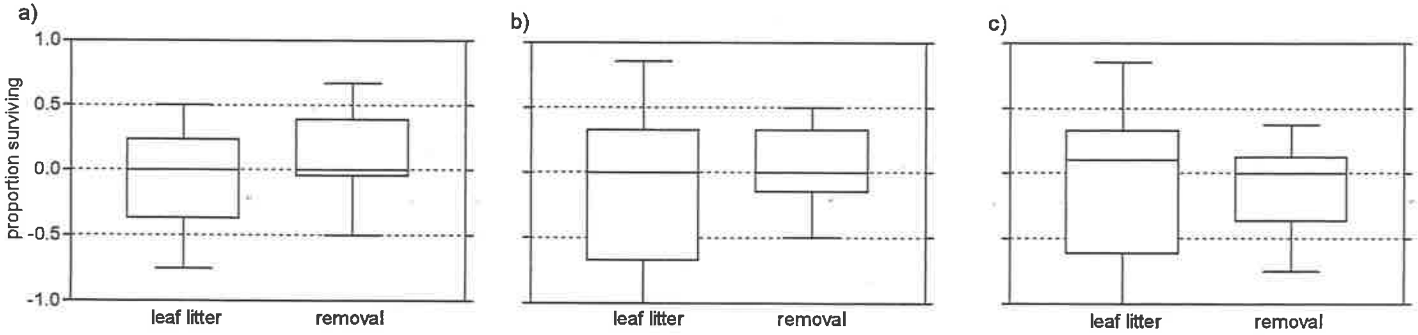


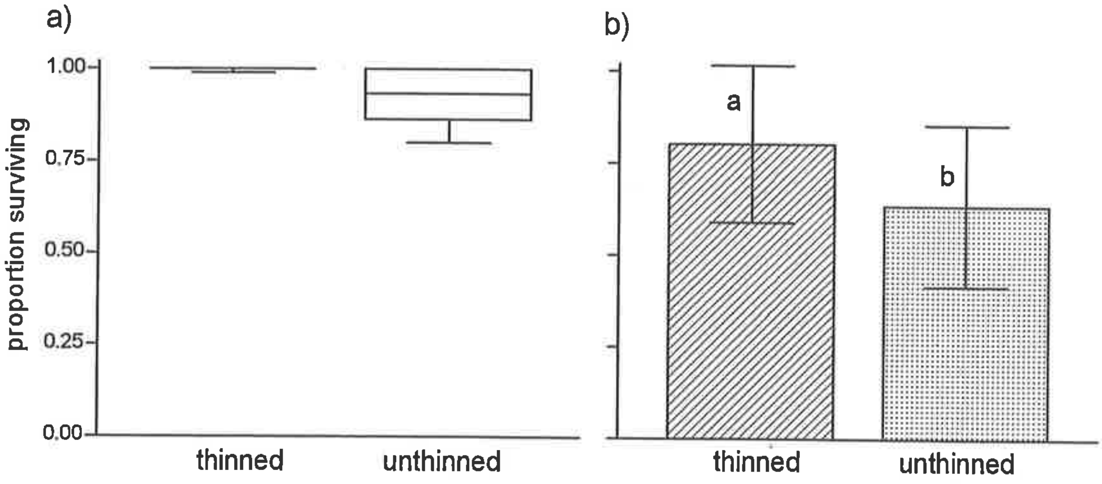
Figure 7.8: Difference between the proportion of thinned seedlings surviving - the proportion of unthinned side for each plot on a) 20-Feb-1996, b) 5-Mar-1996 and c) 3-Jun-1996. Treatment is the removal of dead *E. elderi* material. Values above 0 indicate that more seedlings survived in the thinned side of the plot. Boxes show 25th, 50th and 75th percentiles and whiskers extend to maximum and minimum values.



7.3.3.2 Seedling competition in the open

There was no effect of the $^2/_3$ thinning treatment on the logit proportion of seedlings surviving at the initial reading (Mann-Whitney, logit transformed proportions: U, U=69.00, *P*=0.8852; Figure 7.9) although the variance was higher for the unthinned treatments (F-test, F=18.53, *P*<0.0001, df_{num}=11, df_{den}=11). There was also no effectiveness of pairing for the initial reading (Pearson Correlation, 4-Oct-1996: r=0.2015, *P*=0.2650). In contrast, seedling survival was higher in the quadrats which had a $^2/_3$ thinning treatment in the final reading (paired t-test, *P*=0.0230, t=2.639, df=11; Figure 7.9) and the effectiveness of pairing was nearly significant (Pearson Correlation, , r=0.4839, *P*=0.0554).

Figure 7.9: Proportion of seedlings surviving in the thinned and unthinned sides of each plot for a) 4-Oct-1996 (boxes show 25th, 50th and 75th percentiles while whiskers extend to maximum and minimum values) and b) 10-Dec-1996 (mean ± SD). Letters denote significant differences (*P*<0.05).



7.4 DISCUSSION

There are many opposing forces which influence *Erodiophyllum elderi* seedling success. A conflict of site suitability for seed germination and seedling growth exists because areas with high *E. elderi* seedling emergence also have density dependent interactions between *E. elderi* seedlings. It appears that dead mature *E. elderi* plants have a facilitative effect on seedling survival as seedling survival was reduced when *E. elderi* leaf litter was removed. In contrast, living *E. elderi* plants may suppress seedling growth. Through directed dispersal and the facilitative effects of dead *E. elderi*, seedling establishment occurs preferentially in sites recently occupied by *E. elderi* plants. Site pre-emption by *E. elderi* over a period of many years and several generations may modify the soil structure which enhances seedling growth. Although seedlings grew much bigger in soil taken from beneath dead *E. elderi* plants, limited replication of soil samples meant that no differences in soil characteristics were detected. Site modification and facilitative effects are unlikely to occur after drought conditions or in heavily grazed areas.

Limited, directed dispersal through sheet water flow transports *E. elderi* seedheads to areas which are likely to be suitable for germination. The damming of water around drift material, which has been previously recorded in arid Australia (Tongway and Ludwig 1994), is likely to increase seedling germination beneath dead *E. elderi* plants and where debris accumulates. In addition to higher water availability in areas of accumulation, these areas may be 'islands of productivity' as debris accumulation results in increased organic matter (Tongway and Ludwig 1994). Limited seedhead dispersal and accumulation beneath *E. elderi* plants ensure that offspring do not move far from a site that was suitable for the maternal plant. Although some field studies indicate that high seedling densities inhibit subsequent germination (Inouye 1980), this was not detected for *E. elderi* seedlings in the field. This could be due to seedling densities not reaching the threshold, above which further germination is inhibited, in the field although thorough laboratory experiments are needed to determine whether further seed germination is inhibited with large seedling densities. As seedling density was linearly correlated with seedhead density in all patches examined, seed supply is probably the limiting factor in areas without seedlings.

The accumulation of seedheads in large densities can result in seed-seedling conflicts in site suitability where an area may be suitable for germination but not subsequent growth (Schupp 1995). Density dependent effects were observed between seedlings in areas with high seedling density and competitive interactions may also occur between seedlings and mature *E. elderi* plants. Seedling mortality may not be the direct effect of competition for water, as is common in many desert systems (Fonteyn and Mahall 1981), but the result of past competition. In such a situation, initial competitive interactions results in size asymmetry and the smaller individuals are then unable to survive when resources become limiting (Goldberg and Novoplansky 1997). Therefore, mortality of the smaller individuals may occur even though competition is no longer occurring. In addition to different pulses of competitive interactions, highly variable seedling density-dependent effects across a patch are probably due to variable site quality (Shaw 1987; Goldberg and Barton 1992) in terms of water or nutrient availability. All of these processes may contribute to different experiments in the same system giving conflicting results on the importance and strength of interactions (Connell 1983; Firbank *et al.* 1993).

Although living mature *E. elderi* plants had seedlings present beneath them, no seedlings survived to reach maturity (personal observation). This may reflect competitive interactions due to size differences, with the larger mature *E. elderi* plants having a competitive advantage (Connell 1983; Goldberg and Werner 1983; Schoener 1983; Callaway and Walker 1997). The strength of interactions between seedlings and adults and whether they are positive or negative may depend on the individuals life history stage (Callaway and Walker 1997).

While live mature *E. elderi* plants appear to inhibit seedling growth, dead *E. elderi* plants enhance seedling establishment during germination and seedling growth phases. Seedling densities may be higher beneath dead *E. elderi* through i) limited and directed dispersal increasing seed supply beneath *E. elderi* plants, ii) enhanced germination and growth conditions (Friedel *et al.* 1990) and iii) protection from herbivory (Osborn *et al.* 1932). The removal of dead *E. elderi* plants decreased seedling survival which may reflect the loss of benefits of *E. elderi* litter. The role of dead *E. elderi* plants in providing protection from grazing is unclear because seedling palatability is unknown, as is the degree of protection the dead plant provides. However, these beneficial effects are only likely to occur if seedling establishment occurs within a few years of adult plant death. Otherwise, the remains of dead plants would have decayed or dispersed (photo-records and personal observation).

The removal of dead *E. elderi* plants through heavy grazing and the deterioration of dead plants during drought reduces the number of areas suitable for *E. elderi* seedling germination and survival. In addition, negative seedling-seedling mortality effects may be high under heavy grazing because of the large seedling densities. In the heavily grazed areas, seedlings will not benefit from the presence of litter because plants never attain a large size to remain as substantial leaf litter after death. Likewise, the effects of drought is a reduction in standing biomass and the removal of any ameliorating effects associated with this standing biomass. The importance of litter removal is also likely to vary depending on the time of the year that removals occur. Facelli and Facelli (1993) found that removing litter at different times produced a complete shift in community structure in an oldfield in New Jersey. In this study, litter enhanced seedling survival. Therefore the role of dead adults in mediating spatial structure and competitive relationships may influence long term population dynamics (Bergelson 1990).

Seedlings grew larger when grown in soil collected from beneath dead *E. elderi* plants, although an investigation of soil characteristics revealed no differences. Alternative explanations for the difference in growth could be differences in micro-nutrients or mycorrhizal activity (eg. Tongway and Ludwig 1994). Essentially, micro-environments beneath plants can be from the creation of protective sites (eg. Osborn *et al.* 1932), the modification of resource availability (Gibson 1988; Tongway and Ludwig 1994), or site differences which enabled the plant to grow there initially (although see Gibson 1988). The modification of resources is important for plant growth and can produce a higher per unit area biomass than if resources were uniformly distributed (Noy-Meir 1973). However, soil modification beneath *E. elderi* is only likely to occur if plants establish in the same spot across generations because changes in the soil are likely to take longer than the life-span of a short-lived plant.

Seedlings preferentially establish beneath dead *E. elderi* plants which is probably due to both seed supply and the effects of litter. By pre-empting a site and through a series of antagonistic and facilitative effects, *E. elderi* plant influences last longer than between successive generations. Inter-generational effects show that living plants reduce seedling survival and dead adult grasses inhibit seedling germination (Bergelson

1990). In contrast, my results show *E. elderi* seedling establishment to be inhibited until the death of the adult *E. elderi* plant, after which, seedling establishment is enhanced. Therefore, *E. elderi* plants are likely to be replaced by *E. elderi* seedlings after large *E. elderi* plants die. Similar effects are well known for marine algal communities where dormant propagules beneath large alga exhibit rapid growth after disturbance (Santelices and Ojeda 1983; Dayton *et al.* 1992). A consequence of these recruitment patterns is that invaders are deterred from an occupied area while ensuring that plants recruit into areas which have previously been suitable for growth. For *E. elderi*, these effects will be most important during growth pulses. These pulses last for several years and are generally separated by periods which are longer than the growth pulses (see Chapter 4). During these pulses, facilitation and site pre-emption may help prolong growth pulses, increase individual plant growth and, as a result, increase input into the seed bank.

The importance of resource accumulation beneath a canopy declines from trees to short-lived species as relative plant longevity and size decreases (Tongway and Ludwig 1994). However, the propagation of historical effects through several generations may enable the modification of soil beneath the short-lived *E. elderi* plants. Through soil modification and other influences, there is small scale heterogeneity of site suitability which is important for seedling establishment. The importance of long term effects through site pre-emption over many generations may be relevant for short-lived species from a range of communities, particularly when there are limited sites suitable for establishment and growth.

8. Conclusions

My results indicate two time scales of relevance for *Erodiophyllum elderi* persistence. Over long time scales (*i.e.* a century or more), *E. elderi* may persist through dispersal between patches, as predicted by metapopulation theory for patchily distributed species. However, over shorter time scales, within patch persistence is achieved through a long-lived seed bank. This research highlights the importance of temporal and spatial scales of persistence mechanisms. Different temporal scales need to be considered when examining the persistence of patchy populations and, in particular, the relevance of patchy population models. It is possible that many other patchily distributed sessile organisms with limited dispersal may persist for a limited number of generations without metapopulation processes.

Arid land plants have conflicting selective pressures as a result of limited sites suitable for establishment and growth. Dispersal of arid land seeds is typically limited (Ellner and Shmida 1981) which ensures that seeds remain in areas which were beneficial to the parent plant. However, the patchy distribution of these species suggest that dispersal between patches, and hence long distance dispersal, is important for long term population persistence. Therefore, adaptations of arid land species are likely to increase within patch population persistence.

In contrast to sessile organisms, animals can easily move between patches should patch conditions become unsuitable. Rather than evolving mechanisms which allow within patch long term persistence, animal populations can persist through redistribution between patches. These issues highlight the relevance and the derivation of patchy population theory for mobile species.

8.1 CAUSES AND CONSEQUENCES OF PATCHY DISTRIBUTIONS

The distinctly patchy distribution of *E. elderi* results from both the limited and directed dispersal of the seed bank and from preferential growth conditions in low lying regions. Enhanced growth conditions are likely to result from the increase in soil water content and the increase in nutrients through run-on water flowing into low lying areas following rainfall (Ludwig *et al.* 1994), although these features were not explicitly examined for *E. elderi* patches. The homogeneity in soil characteristics suggests that there is no obvious physical reason why *E. elderi* populations can not expand to some degree given suitable climatic conditions and seed supply. In addition to the lack of differences in soil characteristics, very few species displayed a difference in the readily germinable soil seed bank inside and outside patches despite obvious differences in vegetation further away from the low lying areas. If causative effects for the restriction of *E. elderi* to the low lying areas are to be established, both the soil characteristics and the readily germinable seed bank need to be examined at greater distances from low-lying regions. Whatever the physical reasons, *E. elderi* plants are restricted to low-lying areas, creating a series of patches scattered throughout the area.

8.1.1 Population synchrony

Due to the rapid and direct response to rainfall, *E. elderi* populations had highly synchronous biomass dynamics across the Reserve over the 70 year period of photographic records. Spatial differences in individual rainfall events are unlikely to create asynchronous population fluctuations on this scale. Therefore, if local extinctions are driven by climatic conditions, these extinctions are also likely to be highly synchronous. Unless propagules are supplied from source patches during extended drought conditions, these populations may be highly vulnerable to widespread simultaneous extinction. Colonisation of some *E. elderi* patches may have occurred since 1925 because *E. elderi* plants were absent in the initial photo records in some populations. If colonisation has occurred during this time, then between patch dispersal events are important for population persistence over this spatial and temporal scale.

8.1.2 Seedhead dispersal: where average movement, is most suitable...

Seedhead dispersal experiments show that dispersal is limited, and is usually directed toward low lying *E. elderi* patches. Seedhead dispersal patterns not only promote the patchy distribution of *E. elderi* but also move seedheads to areas which are, on average, likely to be most suitable for subsequent germination and growth. Essentially there appear to be two modes of dispersal for *E. elderi* seedheads. The most frequent form is limited and directed seedhead dispersal toward lower regions which most likely have high resource availability. I hypothesise that large, infrequent rainfall events may allow seedheads to disperse between patches, and in so doing, "rescue" populations which are declining, recolonise temporally extinct patches or colonise new territory. If between patch dispersal occurs with deluges of rain, then the metapopulation framework is applicable to this species over that time scale.

8.2 SPECIES PERSISTENCE IN CORRELATED ENVIRONMENTS

There is a large degree of spatial synchrony between local populations for many short-lived arid land species because population fluctuations depend on rainfall, which does not vary greatly over large areas. Although population asynchrony is a commonly held pre-requisite for patchy population models (den Boer 1968; 1981), the occurrence of correlated environments does not necessarily preclude persistence through metapopulation processes. Harrison and Quinn (1989) suggest that regional persistence of short lived ephemerals may occur through their existence as large metapopulations, spread over partially or fully correlated environments. Population persistence may be achieved by a series of *groups* of populations, where each group behaves similarly to a patch in a metapopulation framework. In such a system, populations within a group have largely synchronous dynamics, while between groups populations have some degree of asynchrony. This allows regionally similar environmental conditions to drive population fluctuations, resulting in highly correlated population fluctuations. As with population fluctuations in a metapopulation context, extinctions are likely to be correlated within a group, although between groups extinction events are not correlated. In this model, groups of populations are connected by infrequent and very large dispersal events.

The degree of synchrony of *E. elderi* populations across the Reserve suggests that these populations are within the same group, due to the spatial homogeneity of the rainfall over this area. Following the above hypothesis, groups which are asynchronous with the Reserve group may exist some distance away and may be crucial to the overall population persistence. Very large and relatively infrequent deluges may flood large areas of this arid landscape, enabling widespread dispersal of seedheads between patches. This framework allows a range of possibilities for population persistence depending on the scale considered. For example, a group of populations may persist in partially correlated environments, with local colonisations and extinctions occurring until prolonged drought causes widespread correlated temporal extinction. A neighbouring group which does not experienced such harsh conditions may then provide propagules to the first group which can then continue to survive more-or-less independently for many generations. In addition, there is no reason for population persistence to be restricted to any one of the frameworks outlined in Chapter 1. Instead, populations may display features of several of these frameworks on different spatial and temporal scales. With the aid of molecular techniques, it will be possible to determine the degree of interactions between *E. elderi* populations, although this may simply detect movement of pollinators between patches.

As the important spatial and temporal scales for population processes vary between species (Thomas 1991), it is difficult to generalise about the relevance of metapopulation models. Many patchy populations have a high degree of environmental correlation (Harrison and Quinn 1989; Gilpin 1990; Ranta *et al.* 1995) and these populations persist through metapopulation processes in spite of highly correlated dynamics. Organisms are likely to adapt to common environmental risks by escaping in time or space (Venable and Lawlor 1980). Therefore, adaptations which increase within patch population persistence are selected (Harrison 1991), thereby increasing population independence. Although large rainfall events may enable the persistence of *E. elderi* populations through dispersal between patches, other mechanisms are needed to achieve within patch persistence over shorter temporal scales. Short-lived arid land species need to be able to store the benefits obtained during good years for persistence through unfavourable periods (Chesson and Huntly 1988).

8.2.1 Within patch persistence: The role of the seedhead

There are a range of mechanisms and life history strategies which allow *Erodiophyllum elderi* to persist between generations in local patches. The most important of these is the long lived seed bank, as it provides protection for the seeds during extended years of unsuitable conditions. The combination of long lived above-ground seed bank of *E. elderi* and the specialised conditions needed for successful establishment results in longer gaps between successful reproductive output pulses when compared to many annuals or ephemerals. The slow release of seeds from the seedhead results in temporal differences in germination and may reduce competitive interactions between sibling seedlings, and hence reduce widespread post release mortality (Inouye 1980; Westoby 1981; Ellner 1985a; Venable 1989).

The results of the Evolutionary Stable Strategy (ESS) model indicate no benefit for any particular release curve for many of the parameter combinations examined. However, I did not consider the effects of either predation or death of seeds once they had been released from the seedhead on the suitability of each release curve. If predator satiation is important during seed release (Louda 1989), then this may influence the outcome of the ESS release curve. These issues need to be explored further to fully appreciate the forces involved in the evolution of the seedhead structure and function. The role of woody seedheads may be to provide a structure for protecting seeds from predators (Kamenetsky and Gutterman 1994) and the ESS seed release curve may depend on the importance of the seedhead in protecting seeds against seed predation.

Another consequence of seed storage in seedheads is that this enables a potential ‘population’ of seeds to disperse as a group. This means that during long distance dispersal events, many seeds are dispersed at once. Hence, if conditions are unsuitable for establishment immediately after long distance dispersal has occurred and after initial seed release, additional seeds may be released at a later time. If the seedhead does manage to disperse to a suitable site, a single year with unsuccessful establishment will not fully deplete the recently dispersed seed bank.

8.3 DIRECT AND INDIRECT EFFECTS OF GRAZING

The most heavily grazed *E. elderi* patch examined persists in spite of having a smaller above ground seed bank than more lightly grazed patches. This suggests several possibilities: a) the reduction of input into the seed bank through *E. elderi* flowers being eaten by sheep is atypical, b) an occasional large input is sufficient to ensure local population survival, c) neighbouring source populations exist and supply propagules to areas unable to produce sufficient input into the seed bank, or d) extinction takes longer than a century of grazing.

Alien herbivores influence many population processes which affect the entire ephemeral herbland community in which *E. elderi* lives. Competitive interactions may be stronger in heavily grazed communities than in other areas due to the large seedling densities resulting from the creation of bare spaces (Tremont 1994). The reduction in plant growth in heavily grazed areas results in less accumulation of leaf litter. Therefore there is unlikely to be any substantial benefit of germinating beneath dead *E. elderi* plants in these patches. The lack of environmental amelioration may contribute to a reduction in the establishment and growth of *E. elderi* seedlings in heavily grazed areas, and may explain why seedhead production had a low variance in the heavily grazed areas.

Reduced standing biomass in heavily grazed areas results in the scattering of seedheads throughout patches and longer dispersal distances both away from and towards a patch. Seedlings are likely to germinate beneath maternal plant in lightly grazed areas due to limited seedhead dispersal in these areas. Seedlings growing beneath live maternal plants may experience negative effects, while the opposite is true when the maternal plant is dead. The accumulation of seedheads, either in open areas or beneath maternal plants, results in large seedhead densities, and is likely to result in strong competitive interactions between seedlings. Seedling mortality is associated with high seedling densities in an area which was lightly grazed, and these effects are likely to be amplified in the heavily grazed patches which have even higher seedling density. The presence of dead *E. elderi* plants increases the variability of survival in thinned areas.

In terms of patchy population persistence, the important issue is whether grazing is likely to cause widespread simultaneous local population extinction. My results suggest that this is unlikely, because the populations I monitored either survived a century of grazing or established despite grazing. For the heavily grazed *E. elderi* populations, grazing may result in their slow decline, or increase the probabilities of local extinctions. Although widespread simultaneous extinction is not likely to occur for *E. elderi*, it must be kept in mind that *E. elderi* has an extremely long-lived seed bank and the effects of grazing may take longer than a century to become apparent. In addition, when conditions permit, *E. elderi* can have very high reproductive output. Highly preferred species may not have this advantage and therefore the threat of grazing is stronger.

8.4 WHAT DOES IT ALL MEAN IN TERMS OF PATCHY POPULATION THEORY?

At the end of this study I can not definitely say that *Erodiophyllum elderi* is represented by any of the frameworks for patchy population theory outlined in Chapter 1. However, I can say for certain that the *E. elderi* population is not a 'patchy population' in terms of frequent dispersal between patches. The reason for this uncertainty is that the relevant spatial and temporal scales involved are greater than those I could investigate during this project.

There is some evidence that the *E. elderi* population may behave as an extended metapopulation, where population dynamics are highly synchronised within groups of populations which are interconnected, and asynchronous with other groups of populations. There is reason to believe that long term intense grazing may result in the regional decline of the *E. elderi* population, but the range of grazing pressures within a paddock means that the population is unlikely to experience a widespread decline. Instead, intense grazing is likely to result in a reduction in the current (or pre-European) range. Alternatively, if the current distribution reflects a series of remnant populations of a previously widespread species, this may indicate that the population is regionally declining. There is no evidence that the *E. elderi* population exists as a source-sink system, although finding and recognising source populations may simply be pragmatically difficult. However, experiments on seedhead dispersal suggest that dispersal between patches is likely to be rare. Consequently, *E. elderi* populations require a within patch persistence mechanism for between generation time scales, achieved through the long-lived seedhead.

Metapopulation theory on a short time scale is only likely to be important for plant species which are better adapted to long-distance dispersal than *E. elderi*. Furbish's lousewort (Menges 1990) and other early successional species (Harper 1977), are good examples of species which do persist through metapopulation processes. These species are particularly well adapted to long distance dispersal and are also good colonisers. The relevance of metapopulation theory therefore depends on the ability of a species to disperse and colonise, and its relevance for the above-mentioned species is probably the exception rather than the rule.

Appendix 1: Soil profile for each of the six patches for a 1m core inside and outside patches. Missing data implies that the auger hit rock on a minimum of three occasions and it was not possible to sample deeper.

a)

Patch 2	outside				inside			
depth (cm)	colour	pH	$CaCO_3$	texture	colour	pH	$CaCO_3$	texture
0-10	2.5YRV3C4	9.5	✓	medium clay	5YRV4C6	9.5	✓	heavy clay
10-20	5YRV4C4	"	✓	"	"	"	✓	"
20-30	2.5YRV3C4	"	✓	"	"	"	✓	"
30-40	"	"	✓	"	"	"	✓	"
40-50	2.5YRV4C4	"	✓	"	"	"	✓	"
50-60	5YRV5C4	"	✓	"	"	"	✓	"
60-70	5YRV4C6	"	✓	"	"	"	✓	"
70-80	5YRV5C6	"	✓	"	5YRV5C6	"	✓	"
80-90	"	"	✓	"	"	"	✓	"
90-100	"	"	✓	"	5YRV5C8	9.0	✓	"

b)

Patch 7	outside				inside			
depth (cm)	colour	pH	$CaCO_3$	texture	colour	pH	$CaCO_3$	texture
0-10	5YRV4C6	9.5	×	sand	5YRV4C6	8.5	×	medium clay
10-20	"	"	✓	loamy sand	"	"	×	"
20-30	"	"	✓	"	"	"	×	"
30-40	"	"	✓	"	"	"	×	hit rock
40-50	5YRV4C4	"	✓	"				
50-60	5YRV4C3	"	✓	hit rock				
60-70								
70-80								
80-90								
90-100								

c)

Patch 6	outside				inside			
depth (cm)	colour	pH	$CaCO_3$	texture	colour	pH	$CaCO_3$	texture
0-10	5YRV4C6	9.5	✓	sandy loam	5YRV4C6	9.5	✓	sandy loam
10-20	"	"	✓	sandy clay loam	"	"	✓	"
20-30	"	"	✓	sandy clay				
30-40	"	"	✓	"				
40-50	"	"	✓	"				
50-60	"	"	✓	medium clay				
60-70	"	"	✓	"				
70-80	"	"	✓	"				
80-90	"	"	✓	sandy clay				
90-100	"	"	✓	"				

d)

Patch 8	outside				inside			
depth (cm)	colour	pH	$CaCO_3$	texture	colour	pH	$CaCO_3$	texture
0-10	2.5YRV4C4	9.5	✓	sandy clay loam	2.5YRV4C4	8.5	×	sandy clay
10-20	5YRV5C6	"	✓	"	"	"	×	"
20-30	"	"	✓	"	"	"	×	medium clay
30-40	"	"	✓	"	"	"	×	"
40-50	"	"	✓	sandy loam	"	"	×	"
50-60	"	"	✓	"	"	"	×	heavy clay
60-70	"	"	✓	loamy sand	"	"	×	"
70-80	"	"	✓	"	"	"	✓	medium clay
80-90	"	"	✓	"	"	"	✓	sandy clay
90-100	"	"	✓	"	5YRV4C6	"	✓	sandy clay loam

NB obvious soil moisture at 40-50cm for outside and inside cores e)

Patch 9	outside				inside			
depth (cm)	colour	pH	$CaCO_3$	texture	colour	pH	$CaCO_3$	texture
0-10	5YRV4C6	8.5	×	medium clay	5YRV4C6	8.5	×	heavy clay
10-20	”	”	✓	”	”	”	✓	”
20-30	”	”	✓	”	”	”	✓	”
30-40	”	”	✓	”	”	”	✓	”
40-50	5YRV5C6	”	✓	”	”	”	✓	”
50-60	”	”	✓	heavy clay	”	”	✓	”
60-70	5YRV6C6	”	✓	”	”	”	✓	”
70-80					”	”	✓	”
80-90					”	”	✓	”
90-100					”	”	✓	”

f)

Patch 10	outside				inside			
depth (cm)	colour	pH	$CaCO_3$	texture	colour	pH	$CaCO_3$	texture
0-10	5YRV4C6	9.0	✓	sandy loam	2.5YRV4C6	8.0	×	loamy sand
10-20	”	”	✓	”	5YRV4C6	”	×	”
20-30					”	8.5	×	”
30-40					2.5YRV4C4	”	×	”
40-50					5YRV4C6	”	×	sandy loam
50-60					”	”	×	”
60-70					”	”	×	”
70-80					”	”	✓	”
80-90					”	”	✓	sandy clay loam
90-100					”	”	✓	”

Appendix 2: Description of the photo-point sites used for examining the long term population dynamics of *Erodiophyllum elderi* populations.

PP Q30 NW and PP Q30 NE: centre of Quadrat No. 300, a floodplain with few *Myoporum platycarpum*, *Acacia aneura*, *A. burkittii* and *Eremophila* spp. (Hall *et al.* 1964). The NW photo faces toward the patch, whilst the NE faces away from the population. The NW photo-series was a better representation of the *E. elderi* population dynamics.

PP Q40 NE and PP Q40 NW: centre of Quadrat No 400, a thick stand of *Casuarina cristata* trees with a few *M. platycarpum* and *Alectryon oleiofolium* on a sandplain. PP Q40 NW represented the *E. elderi* population dynamics better than the NE photo series as it faced toward the population.

PP Q6-80 NW: A stand of *A. aneura* on floodplain with clayey soils surrounded by sandy patches. An *Atriplex vesicaria* population surrounds this site along the higher ground while *E. elderi* was restricted to the lower region.

PP7: adjacent sand dunes, positioned on the southern fence-line. There were no clues as to the direction of the population with respect to this photo-point as no seedheads were found in the near vicinity.

PP9: desert loam with travertine soils in a small depression which collects run-on water (Noble 1977). The photo stake was positioned on a fence-line facing the *E. elderi* population. This area is surrounded by a *Maireana sedifolia* (bluebush) population.

PP8: positioned on sand dune looking down slope onto *E. elderi* population, the *E. elderi* population extends from the sandy soil in the dune onto the more clay soil of the depression running E-W.

PP4: adjacent bluebush population near Q300, see description for Q30.

PP3: flattish region in *A. vesicaria* community, slight depression, population extends towards Q200 along a long narrow corridor of *E. elderi* seedheads. Stones scattered over the surface of the area. Unlike many of the other sites there is no obvious region for water pooling at this site.

Appendix 3: Years and dates that photos were taken for each of the photo-points examined for long term biomass dynamics. Years with photos taken but no *E. elderi* biomass visible is marked with x, while *E. elderi* presence is indicated by ✓.

year	photo date	PP3	PP7 (KVR)	PP8	PP4	Q6-80 NW	PP9 (KVR)	Q30 E	Q30W	Q40 NE	Q40 NW
1923			x								
1924											
1925											
1926	27-Aug							✓	✓	x	x
1927	27-Aug					x	x	x	x	x	x
1928	27-Aug			x	x	x		✓	✓	x	x
1929	27-Aug					x		x	x	x	x
1930	27-Aug		x	✓	x	x	x	✓	✓	x	x
1931	26-Aug	x	x	x	✓	x	x	x	✓	x	x
1932	31-Aug	x	x		✓		x				
1933	28-May	x					x				
1934	24-May	x			x						
1935	24-Aug	x	x		x		x				
1936	27-May	x		x	x		x				
1937	31-May	✓	x	✓	✓		x				
1938	19-Aug	✓			✓		x				
1939	16-Aug	✓	x		x		x				
1940	28-May	✓	x		✓		x				
1941	28-May	x	x		x		x				
1942	28-May	x	x		x		x				
1943	20-Aug	x	x		x		x				
1944	19-Aug	x	x		x		x				
1945	19-Aug		x				x				
1946	8-Jun	x	x		x		x				
1947	3-Jun	x	x				✓				
1948	28-May	x	x				x				
1949	24-May	✓	x				x				
1950	26-May	✓	x		✓		x				
1951	26-Aug	✓	x		x		x				
1952	26-Aug				x		x				
1953	26-Aug						✓				
1954	30-May	x									
1955	30-May										
1956	30-May		x								
1957	26-Aug	x									
1958											
1959	26-Aug		x				x				
1960											
1961											
1962	26-Aug				x						
1963											
1964											
1965											
1966											
1967											
1968	Nov-31	x	x	x	x		x				
1969											
1970	1-Dec	✓	x	✓	✓		x		x		
1971	9-Jul	x	x	x	x		✓			x	

1972	14-Feb	✓	✓	✓	✓	✓	✓		✓		
1973	23-Jun	x	✓	x	x	x	x				
1974	7-Aug	✓	✓	✓	x	✓	✓	✓	✓	x	✓
1975	30-May	✓	x	x	✓	✓	x				
1976	14-Dec	x	x	x	✓	x	x	x	x	x	x
1977	17-Oct	x	x	x	x	x	x	x	x	x	x
1978	8-Jun	x	x	x	x	x	x	x	x	x	x
1979	21-Aug	x	x	x	x	x	x	x	x	x	x
1980	3-Jun	✓	x	x	x	x	x	x	x	x	x
1981	9-Dec	x	x	x	x	x	x	x	x	x	x
1982	5-Dec	x	x	x	x	x	x	x	x	x	x
1983	8-Dec	x	x	x	x	x	x	x	x	x	x
1984	12-Dec	x	x	x	x	x	x	x	x	x	x
1985	9-Dec	x	x	x		x	x	x	x	x	x
1986	9-Dec	x	x	x	x	x	✓	x	x	x	x
1987	7-Dec	x	x	x		x	✓	x	x	x	x
1988	7-Dec			x			x				
1989	12-Dec	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
1990	11-Dec	✓	✓	✓	✓	✓	✓	✓	x	x	✓
1991	10-Dec	✓	x	x	✓	x	x	x	x	✓	x
1992	15-Dec	x	x	x	x	✓	✓	✓	x	✓	✓
1993	14-Dec	✓	x	x	✓	✓	✓	✓	✓	✓	✓
1994	11-Dec	x	x	x	✓	x	x	x	x	x	x
total # photos		47	46	31	43	27	51	25	27	26	25

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