Encroachment of sandplain heathland (kwongan) by *Allocasuarina huegeliana* in the Western Australian wheatbelt: the role of herbivores, fire and other factors

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

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Abstract

Kwongan, also known as sandplain heathland, occurs in remnant vegetation throughout the fragmented landscape of the Western Australian wheatbelt. This vegetation community has high levels of species richness and endemism, and is of high conservation value. In many vegetation remnants in the wheatbelt the native tree species *Allocasuarina huegeliana* (rock sheoak) is expanding out from its normal range and encroaching into kwongan. *A. huegeliana* may ultimately dominate the kwongan, causing a decline in floristic diversity. Altered disturbance regimes, particularly the absence of fire and reduced or absent browsing mammal herbivores, are likely to be responsible for causing *A. huegeliana* encroachment.

This study used experimental and observational data from patches of kwongan in three Nature Reserves in the central and southern wheatbelt to investigate the role of fire, native mammal activities and interactions between these two factors in shaping *A. huegeliana* woodland–kwongan community boundaries. Investigations were carried out into the characteristics of encroaching *A. huegeliana* populations; the environmental factors affecting the extent of encroachment, naturally recruited juveniles, and seedling emergence and establishment; historical and current abundances of native mammals; and the effects of mammal herbivores on seedling establishment during inter-fire and post-fire periods.

Results from this study confirm that *A. huegeliana* has encroached into kwongan throughout the wheatbelt region and recruitment appears likely to continue in most areas. Few of the environmental factors measured in this study affected the extent of encroachment, the locations of naturally recruited *A. huegeliana* juveniles, and seedling germination and establishment. Western grey kangaroos (*Macropus fuliginosus*) browsed extensively on seedlings, which largely prevented them from establishing in open areas of kwongan. However, numerous *A. huegeliana* seedlings escaped browsing herbivores by establishing in perennial shrubs, where they appeared to be tolerant of increased levels of inter-specific competition.

There was no native mammal common to all three Reserves that declined around the time that *A. huegeliana* encroachment most likely began in the 1970s. In addition, tammar wallabies (*Macropus eugenii*) had little effect even where their densities were high. It is therefore unlikely that the decline of an individual mammal species initiated encroachment. *A. huegeliana* encroachment appears to be driven by increased propagule pressure, which is in turn caused by increased inter-fire intervals. Long periods of time without fire have enabled fire-sensitive *A. huegeliana* trees to produce increasing quantities of seed that are continuously released into kwongan. A range of other factors may interact synergistically with this process to affect encroachment and these are also discussed. This study considered the implications of these findings for management of remnant vegetation in fragmented landscapes, particularly kwongan in the Western Australian wheatbelt, and areas for further research are suggested.

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Chapter 1

General introduction

Ecosystems are complex and dynamic structures that change over time. The significance of disturbance in shaping ecosystem dynamics is well documented (White 1979; Sousa 1984; Pickett & White 1985; White & Jentsch 2001). Disturbances are relatively discrete events that affect or change ecosystem components and occur at different temporal and spatial scales. They range from localised modifications, such as small-scale soil disturbance by animals, to landscape scale disturbances, such as fire, drought and flood (Hobbs 1987). Many plant communities and species depend upon disturbance, particularly for regeneration (Pickett & White 1985). Disturbances provide novel conditions for seedling establishment and plant growth, and opportunities for plants to access resources that are otherwise unavailable (Spooner *et al.* 2004). Alterations to disturbance regimes will therefore result in changes to ecosystem dynamics, particularly to seedling recruitment.

Ecosystems worldwide have become increasingly subject to various forms of human modification including altered disturbance regimes as a result of fragmentation, cessation of traditional land use practises and human management (White & Jentsch 2001). The fragmentation process reduces the area of native ecosystems and leaves small patches that are increasingly isolated; reduces species population sizes of both flora and fauna; and alters landscape-scale processes (Hobbs & Yates 2003). In fragmented systems, it is highly likely that the pre-existing disturbance regimes will be significantly altered because of the changed landscape context, isolation of fragments and altered composition of vegetation (Hobbs 1987).

Disruption of disturbance regimes may cause dramatic successional changes in ecosystems that result in the loss of landscape and species diversity and ecological processes (White & Jentsch 2001), or changes in the abundances of many species (Tilman 1996). For example, fire regimes in fragmented ecosystems are likely to alter in one of two contrasting directions (Hobbs 2003). Fire can become almost entirely eliminated because of the lack of continuous vegetation cover and the cessation of active fire management, which could potentially lead to the disappearance of relatively short-lived species that require fire as a cue for germination. Alternatively, fire frequency can increase where fire is used in the surrounding landscape, for instance in stubble burning or "burning off" along road or rail reserves. In such cases, fires that escape into remnant vegetation can result in the death of particular native species and/or failure of some species to regenerate.

The increase of native tree and woody shrub species in vegetation communities from which they were formerly sparse has been variously referred to as expansion, encroachment, invasion and successional change. This process is becoming increasingly common in Australia (e.g. Withers & Ashton 1977; Gleadow & Ashton 1981; Bennett 1994; Fensham & Fairfax 1996; Crowley & Garnett 1998; Russell-Smith *et al.* 2004; Franco & Morgan 2007) and throughout the world (e.g. Veblen & Lorenz 1988; Rose *et al.* 2000; Soulé & Knapp 2000; Roques *et al.* 2001; Goslee *et al.* 2003; Bartolomé *et al.* 2005; Briggs *et al.* 2005; Norman & Taylor 2005). Due to the common association of the term invasion with exotic species, I will refer to this process as encroachment.

In the southwest of Western Australia anecdotal observations have been made about the encroachment of a native tree species *Allocasuarina huegeliana* into adjacent or nearby vegetation communities including kwongan (sandplain heathland) (Powell 1990; Little & Friend 1993; Main 1993; Bamford 1995). Historical vegetation surveys have shown that *A. huegeliana* was sparse or not recorded in many patches of kwongan in the Western Australian wheatbelt (Muir 1978b, c; Brown & Hopkins 1983).

Several shrub species in eastern Australia, including *Leptospermum laevigatum*, *Kunzea ambigua* and *Acacia sophorae*, have encroached into heathland from adjacent communities and are considered woody plant invaders (Burrell 1981; Cheal 1996; McMahon *et al.* 1996). The change from heathland to *Callitris verrucosa* woodland has, in contrast, been described as a cyclical change because *C. verrucosa* is present in the heathland from the earliest post-fire regeneration (Cheal 1996). This is not the case with *Allocasuarina huegeliana* in kwongan.

Encroachment may have a range of impacts including the decline of species richness and diversity, decline of landscape diversity, loss of conservation-value habitats and an increase in erosion (Crowley & Garnett 1998; Costello *et al.* 2000; Rose *et al.* 2000; Foster & Motzkin 2003; Bartolomé *et al.* 2005; Briggs *et al.* 2005; Butler *et al.* 2006; Fredrickson *et al.* 2006). *A. huegeliana* encroachment may cause a decline in floristic diversity in kwongan because this species appears to be able to dominate the vegetation types it encroaches into (Main 1993). Other *Allocasuarina* species have altered the composition and structure of vegetation communities that they have encroached into (Lunt 1998a; Kirkpatrick 2004).

The southwest of Western Australia has high levels of plant diversity and endemism that is recognised as being of global significance, with the flora richest in the coastal and inland kwongan (Hopper & Gioia 2004; Mittermeier *et al.* 2005). Much of this area is now occupied by wheat and sheep farming, known as the wheatbelt, and covers more than 150 000 km^2 in the southwest of the state. Since European settlement 93% of native vegetation in the Western Australian wheatbelt has been cleared and the remaining vegetation exists in small, scattered remnants in what is now a highly fragmented landscape (Hobbs *et al.* 1993). This degree of habitat removal has had obvious consequences for the biota in terms of both representation of native vegetation types and abundance and range of fauna (Hobbs 2001).

The wheatbelt region is dominated by old landscapes with nutrient-deficient, highly weathered soils (Hopper *et al.* 1996) and experiences a Mediterranean climate of hot dry summers and cool wet winters. The geology is dominated by the extensive Yilgarn Block. The bedrock of gneisses and granites is largely covered by laterite and its derived products (Johnstone *et al.* 1973). Prior to clearing the wheatbelt region consisted of a complex mosaic of vegetation types, the distribution of which was largely determined by soils, landforms and climate (Beard 1981, 1990; McArthur 1991; Gibson *et al.* 2004).

Kwongan is ecologically complex and its component species exhibit a wide range of life forms, regenerative strategies and habitat requirements (Pate & Beard 1984; Brown 1989). This vegetation community occurs throughout the wheatbelt and is comparable with the maquis, chaparral and fynbos of other countries with Mediterranean-type systems. Kwongan is characterised by a high diversity within homogeneous habitats (ά-diversity), high plant species turnover along habitat or environmental gradients (β-diversity), high plant species turnover among equivalent habitats across geographical gradients (γ-diversity) and a large proportion of locally endemic flora (Hopper 1979; Brown 1989; Hopper 1992; Hopper *et al.* 1996; Hopper & Gioia 2004). Remnants of this rich flora are located in landscapes that have been extensively cleared through European land-use practices and are therefore of high conservation value (Hopper & Gioia 2004).

In many areas of remnant vegetation in the wheatbelt, kwongan occurs adjacent to or near woodland dominated by the native tree species *Allocasuarina huegeliana* (Beadle 1981). *A. huegeliana* often occurs on and around granite outcrops; however, it also occurs on the sandplains and has been recorded from a wide range of other soil types (Doran & Hall 1981). *A. huegeliana* stands vary from open to very dense and range from 5−10m in height. This species forms a thick layer of leaf litter beneath its canopy and the species present in the understorey vary according to the density of the overstorey (Beard 1990).

The causes of encroachment have been much debated and are often complex and interactive. The most commonly identified causes of encroachment are altered browsing and grazing regimes, including both overgrazing by livestock and the absence or decline of herbivore populations; altered fire regimes, particularly a reduction in fire frequency; and interactions between these processes.

Herbivores may determine the relative abundance of different plant species in a habitat through selective defoliation causing seedling death, trampling, nutrient relocation and other factors (Harper 1977). Grazing from domestic livestock has caused encroachment in many systems through reduced competition from grasses and herbs for soil moisture and nutrients, and reduced fine fuel in the understorey, which limits fire and subsequent seedling mortality (Madany & West 1983; Savage & Swetnam 1990; Roques *et al.* 2001; Harris *et al.* 2003; Briggs *et al.* 2005). The loss or decline of various herbivores, such as the black-tailed prairie dog (Weltzin *et al.* 1997), reindeer (Cairns & Moen 2004) and bettongs and bridled nailtail wallabies (Noble & Grice 2002), have also caused encroachment in a range of systems through reduced levels of browsing on seedlings of the encroaching species.

Fire has the potential to affect plant populations by killing fire-sensitive species. Local extinction of fire-sensitive species will occur if the interval between successive fires is shorter than the time that plants require to reach first reproduction. In many systems where encroachment is occurring reduced fire frequencies have enabled seedlings of fire-sensitive species to establish (Veblen & Lorenz 1988; Crowley & Garnett 1998; Lunt 1998b; Russell-Smith *et al.* 2004; Bartolomé *et al.* 2005; Norman & Taylor 2005; Coop & Givnish 2007). Disturbance processes such as fire and herbivory may also interact with each other to influence seedling mortality, particularly in post-fire environments where grazing can promote or eliminate particular plant species (Noble & Grice 2002; Hobbs 2003; Kirkpatrick 2004).

No systematic scientific investigations have been undertaken into *A. huegeliana* encroachment. However, anecdotal observations suggest that altered fire and browsing regimes may be responsible for driving this process (Powell 1990; Main 1993; Bamford 1995). Disturbance regimes have been fundamentally altered across the Australian landscape since European colonization (Hobbs 1987). Kwongan is fire-prone and is thought to have historically been subject to frequent fires, set by Aboriginal people or by lightening, at intervals from 1 to 20 years (Pate & Beard 1984). However, many reserves have currently not been burned for more than 50 years. *A. huegeliana* is very fire-sensitive and historical fire intervals may have maintained the kwongan structures by eliminating seedlings establishing in kwongan before they reached first reproduction. *A. huegeliana* can, unlike many kwongan species, establish seedlings without disturbance (Ladd 1989). The decline of fire frequency in these reserves may have enabled large numbers of *A. huegeliana* seedlings to establish and reach maturity.

Grazing and browsing regimes have also been dramatically altered in remnant vegetation in Australia through the loss or decline of most medium-sized mammal fauna such as small wallabies, bandicoots and large rodents. The loss or decline of these fauna has been attributed to habitat loss, predation by foxes and cats, and other factors (Burbidge & McKenzie 1989). These mammals probably had important effects on ecosystem and regeneration processes in post-fire and inter-fire periods. For example, when fire was absent for long periods of time in the past, herbivores such as the tammar wallaby might have controlled the recruitment of *A. huegeliana* seedlings to a large extent through browsing (Main 1993). However, like many similar species, tammars are now absent from many reserves. As a result of the absence of fire and reduced herbivore populations, many remnant areas in the wheatbelt now lack two key processes that may have previously been important drivers of ecosystem dynamics.

In addition to factors such as fire, grazing and climate, the initiation, rate and extent encroachment would also depend on factors that affect all colonizing plants. These factors may include the availability of propagules, dispersal capacity, availability of safe sites, conditions suitable for germination and establishment, and competitive interactions with resident vegetation (Harper 1977; Oliver & Larson 1990). It is not surprising that in complex systems, changes in ecosystem dynamics reflect the influence of multiple factors. However, there are few studies that address all of these components or their interactions simultaneously.

If anecdotal observations that *A. huegeliana* is encroaching into kwongan and populations are surviving to maturity are correct, management strategies may be required to ensure the conservation of kwongan communities. However, the extent to which management is required will depend on the impact of *A. huegeliana* on kwongan. Little is currently known about *A. huegeliana* populations encroaching into kwongan, factors affecting the rate and extent of encroachment, the processes driving these changes or the impacts of encroachment. As a consequence there are no scientific guidelines for managing the remaining areas of kwongan to ensure the continued retention of species in these communities.

I considered a number of factors that may potentially be contributing to *A. huegeliana* encroachment, including altered fire and browsing regimes, altered climatic conditions and atmospheric carbon dioxide concentrations, and altered levels of seed predation. However, the research in this thesis focuses on the role of fire and browsing by native herbivores for several reasons. Fire and browsing are commonly identified as driving encroachment in a range of systems worldwide, including heathlands in Australia. These factors have also been identified as enabling *Allocasuarina* species to encroach into other vegetation communities in Australia. Additionally, other research scientists who have observed *A. huegeliana* encroachment in the wheatbelt over several decades have suggested that fire and browsing are key factors likely to be causing encroachment (e.g. Main 1993).

There is currently an important and unique opportunity to examine the effects of fire interval and mammal herbivore activity by using a mixture of natural and targeted experimentation. Native mammals have increased recently in several Nature Reserves due to predator control. The vegetation communities within these Reserves have experienced a range of known fire intervals. It was beyond the scope of this study to carry out experimental fires in kwongan that has been encroached upon by *A. huegeliana*. An area of *A. huegeliana* woodland was burned at the beginning of the study and this opportunity was used to monitor the effects of herbivore exclusion on post-fire recruitment. The research undertaken for this thesis aimed to use the aforementioned opportunities to develop an understanding of the role of fire, native mammal activities and the interactions between the two in shaping *A. huegeliana*–kwongan community boundaries in remnant vegetation.

The major research questions addressed in this thesis were:

- What is the extent of *A. huegeliana* encroachment in kwongan in remnant vegetation in the Western Australian wheatbelt and is it likely to be a long-term problem?
- Which environmental factors affect *A. huegeliana* establishment in kwongan during inter-fire periods?
- How does native mammal browsing affect *A. huegeliana* establishment in the inter-fire and immediate post-fire periods?
- What are the likely outcomes of long inter-fire periods in remnants where native herbivores are largely absent?

More detailed research questions were addressed within each chapter (Figure 1.1).

The current chapter provided an overview of the problem of encroachment, its ecological significance, potential causal factors and historical background to the study. The structure of the remaining chapters is illustrated in Figure 1.1. Chapter Two describes the characteristics of encroaching *A. huegeliana* populations and the patches of kwongan in which this phenomenon is occurring. Chapter Three introduces the mammals that were historically present in the study areas and explores the pattern of their decline since the 1800s. Chapter Four investigates the relative abundance of mammal herbivores currently present in the study areas. Chapter Five characterises the locations where naturally recruited juvenile *A. huegeliana* are both present and absent. Chapter Six examines the effects of perennial vegetation and herbivore exclusion on *A. huegeliana* seedling establishment. Chapter Seven explores the effects of a range of environmental factors on *A. huegeliana* seedling establishment. Chapter Eight differentiates between the impacts of individual mammal herbivore species on *A. huegeliana* seedling establishment. Chapter Nine describes the effects of mammal exclusion on the recovery of *A. huegeliana* woodland following fire. Chapter Ten summarises the main findings and discusses the implications for management of remnant vegetation in fragmented landscapes.

Note: Chapter 2 forms the basis of the following paper: Maher, K.A, Hobbs, R.J. & Yates, C.J., Invasion of kwongan by the native tree species rock sheoak (*Allocasuarina huegeliana*) in the Western Australian wheatbelt: population and patch characteristics. *Austral Ecology*, in revision.

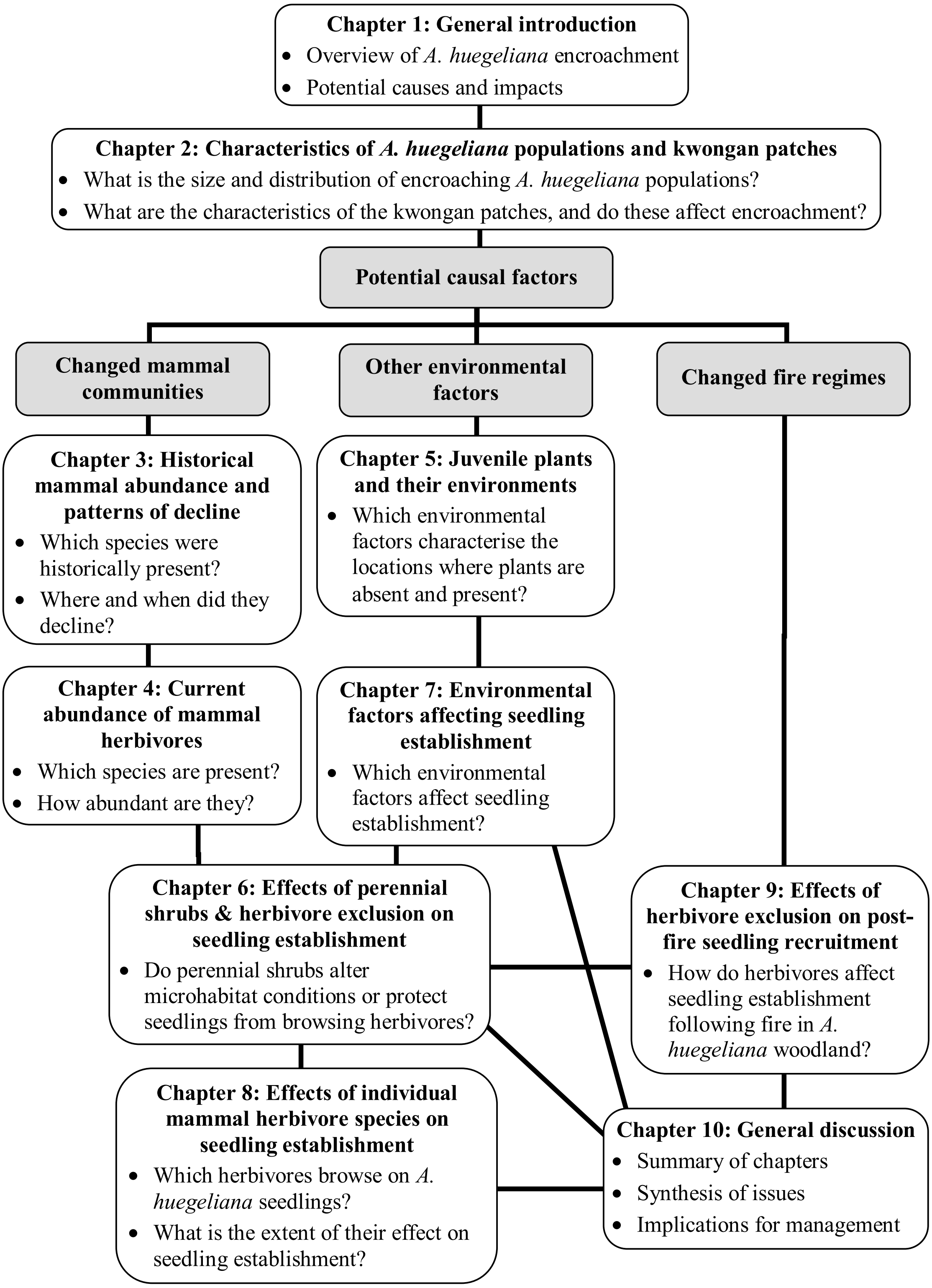
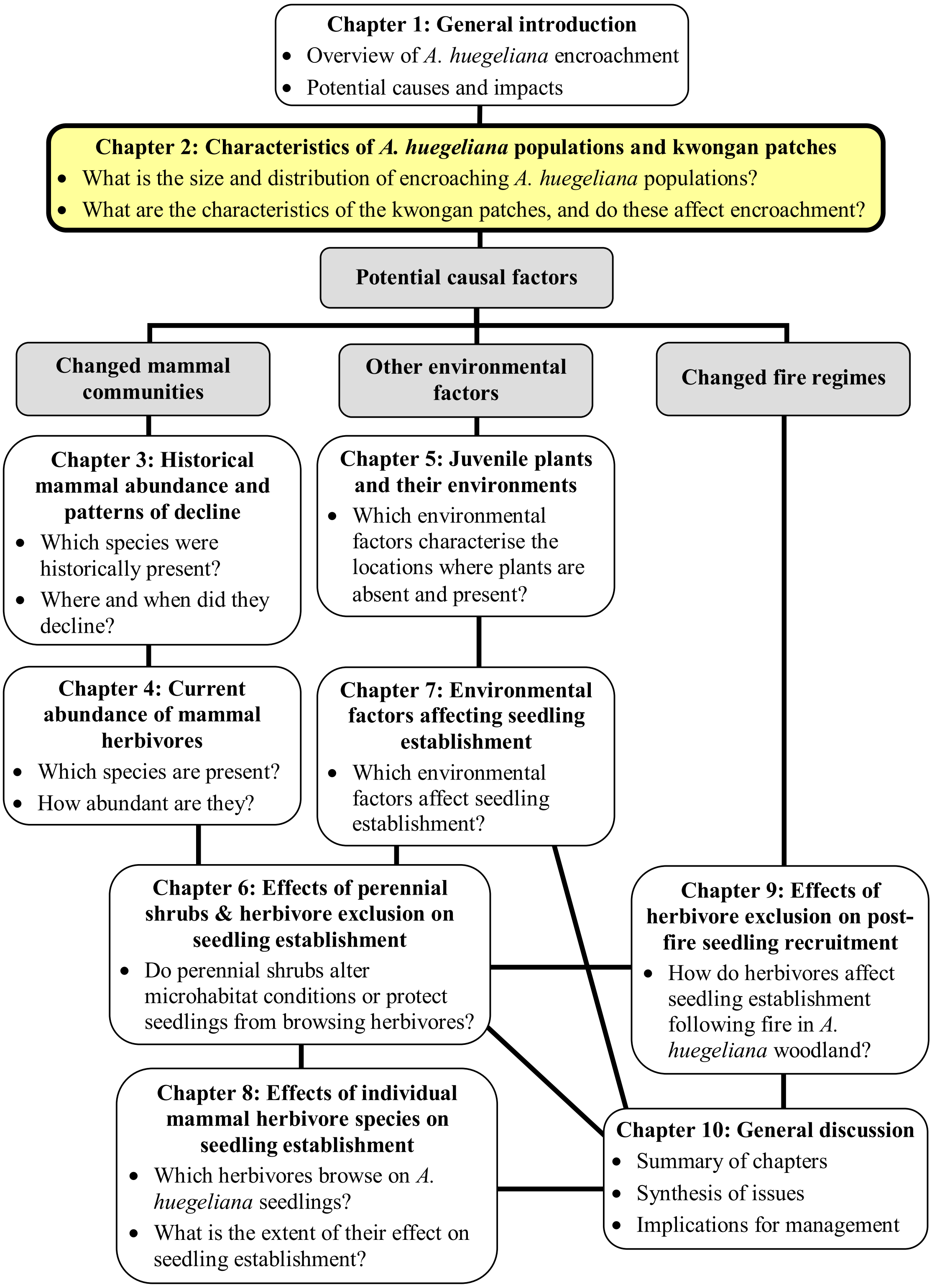


Figure 1.1: Diagram of thesis structure, order of the chapters and key questions.

Chapter 2

Population and patch characteristics



2.1 Introduction

As discussed in Chapter 1, anecdotal observations have been made on the encroachment of *A. huegeliana* at a range of sites located throughout the wheatbelt (Powell 1990; Little & Friend 1993; Main 1993; Bamford 1995). However, little is currently known about the characteristics of the encroaching *A. huegeliana* populations or the sites where this is occurring.

Population structure studies may give insight into regeneration patterns and whether recruitment is continuous or fluctuates in response to disturbance events, competitive interactions or climatic changes (Ågren & Zackrisson 1990). Age is often a more accurate measure of a population structure; however, age is difficult to determine for most native plant species in Australia because the production of annual rings is constrained due to the opportunistic response of most tree taxa to unpredictable rainfall and temperatures (LaMarche *et al.* 1979; Mucha 1979; Ogden 1978). In the absence of an appropriate method for age determination girth is often a reasonable approximation of a tree's age (Pearson and Searson 2002). Although estimates of population size through time are preferable (Condit *et al.* 1998; Kohira & Ninomiya 2003), single-year 'snapshot' data may give some indication of the future of a population. Size-class distributions have been successfully used in numerous studies (e.g. Hett & Loucks 1976; Fensham & Bowman 1992; Kelly *et al.* 2001; George et al 2005; Souza 2007).

The size distribution of a population is a synthesis of the demographic events of recruitment, mortality and individual growth rates over time (Kelly *et al.* 2001). In a population with a constant recruitment rate, and a mortality rate that is either constant or decreasing with age, the expected age structure has a 'reverse-J' shape, (Hett & Loucks 1976). These populations have many small stems and gradually declining numbers of larger stem sizes. Large numbers of juvenile plants relative to adult plants indicates that a population is stable or perhaps growing, but few juveniles may indicate that the population is in decline (Condit *et al.* 1998). Distinct gaps or peaks in abundance of one or more size classes indicate the episodic establishment from recruitment events or the death of juvenile plants (Fensham & Bowman 1992). Such structures may be found in populations where recruitment is only possible during periods following major disturbances; only at certain intervals because of competitive interactions; or in climatically marginal populations, only during periods of favourable weather conditions (Ågren & Zackrisson 1990). Studies of *A. huegeliana* population structures should indicate whether recruitment is continuous or episodic, and whether recruitment is likely to continue or decline.

The *A. huegeliana*–kwongan system is complex and a number of factors are likely to interact to affect encroachment. The initiation, rate and extent of encroachment will depend on a range of factors that determine whether a plant establishes, including seed availability and dispersal capacity, biotic interactions and abiotic conditions (Harper 1977). Propagule pressure has consistently been associated with invasion success (Colautti *et al.* 2006). If two habitats exert equally negative effects on new species, but one receives greater propagule input, the habitat receiving more propagules is more likely to become invaded (Thomsen *et al.* 2006). However, invasion may be unlikely when propagule density is below a threshold value because of the sensitivity of small populations to stochastic events (Tilman 2004) and Allee effects (Leung *et al.* 2004). Encroachment is thus more likely to occur in kwongan patches that are bordered by *A. huegeliana* woodland than patches that are not.

Site characteristics such as time-since-fire and soil type may interact with propagule pressure to affect *A. huegeliana* encroachment. Since *A. huegeliana* is killed by fire, the amount of time that encroachment could occur is indicated by the number of years since the last fire. The size of the encroaching *A. huegeliana* populations is therefore likely to be lower at sites with shorter time-since-fire. *A. huegeliana* has been recorded from a wide range of soil types (Doran & Hall 1981). However, vegetation community boundaries in the southwest are thought to be controlled largely by soils, landforms and climate (Beard 1981, 1990; McArthur 1991; Gibson *et al.* 2004). Soil types at some sites may therefore inhibit seedling survival. If so, *A. huegeliana* populations would be smaller at such sites.

This chapter investigates the characteristics of *A. huegeliana* populations that have encroached into kwongan in three Nature Reserves in the Western Australian wheatbelt. This chapter aims to describe the density, reproductive capacity, and size structure of *A. huegeliana* populations, and the effects of the characteristics of the kwongan patches on the extent of encroachment.

2.2 Methods and materials

2.2.1 Study species

Allocasuarina huegeliana is a dioecious tree that ranges from 5–10 m in height. Few studies have been conducted into *A. huegeliana* and little is known about a number of its biological and ecological characteristics. Little is also known about *A. huegeliana* growth rates in kwongan; however, plants that recruited after a wildfire at a granite outcrop in the wheatbelt grew to around 1 metre in the first three years and were greater than 4 metres eleven years after the fire (Yates *et al.* 2003). At the same site, *A. huegeliana* plants took around 9 years before fruit occurred to any significant extent (Hopper 2000). Personal observations of *A. huegeliana* at other sites with known fire ages indicate that this species may live for around 100 years.

A. huegeliana has winged seeds that are wind dispersed and although distances are unknown, it is considered to have a good dispersal capacity (Main 1993). Seed is released continually, and although there may be peaks in release at some times of the year, there is always carry-over of propagules in the canopy from year to year (Ladd, 1989). *A. huegeliana* has been found to germinate readily in moist conditions at rates ranging from 60 to 100% (Turnbull & Martensz 1981; Piggott *et al.* 1987; Schmidberger 1997).

A. huegeliana is very fire sensitive and can establish at high densities following fire (e.g. Yates *et al.* 2003) because a heavy seed rain is produced (Ladd 1989). However, survival can decline rapidly as a consequence of irregular rain and protracted drought (Yates *et al.* 2003). *A. huegeliana* is also able to establish seedlings without disturbance, although often not particularly abundantly, which is likely to be related to their shade and drought tolerance (Ladd 1989).

2.2.2 Study sites

Kwongan is a sclerophyllous shrub-dominated community commonly dominated by the families Proteaceae (genera such as *Banksia*, *Dryandra* and *Hakea*), Myrtaceae

(*Verticordia* and *Melaleuca*) and Papilionaceae (*Daviesia* and *Jacksonia*), although a range of other families are also well represented including the Cyperaceae, Mimosaceae, Epacridaceae, Leguminosae, Orchidaceae, Stylidaeceae, Asteraceae, Poaceae and Liliaceae (Pate & Beard 1984; Brown 1989; Brown & Hopkins 1983). In many areas of remnant vegetation in the wheatbelt, kwongan commonly occurs adjacent to or near woodland dominated by the native tree species *Allocasuarina huegeliana* (Beadle 1981). Boundaries between these two vegetation communities are generally sharp (e.g. Figure 2.1).

Figure 2.1: Photograph of a patch of kwongan at Tutanning Nature Reserve showing the sharp boundary between the kwongan (foreground) and *A. huegeliana* woodland (background) communities.

The characteristics of *A. huegeliana* populations were investigated at twelve kwongan patches at Durokoppin, Dongolocking and Tutanning Nature Reserves in the Western Australian wheatbelt in 2004 (Figure 2.2). These reserves are set aside for the conservation and restoration of the natural environment, and the protection, care and study of indigenous flora and fauna. Durokoppin Nature Reserve is located in the central wheatbelt *ca* 26 km north of Kellerberrin, has an area of 1030 ha and an average annual rainfall of 330 mm. Tutanning Nature Reserve is located *ca* 18 km east of Pingelly, has an area of 2140 ha and an average annual rainfall of 454 mm. Dongolocking Nature Reserve is located *ca* 80 km west of Lake Grace and consists of a large number of remnants, including eleven that are protected by the reserve system and have a total area of 3450 ha, and an average annual rainfall of 430mm.

These particular reserves were selected because they are located in similar topographic locations high in the landscape, contain similar vegetation mosaics and experience similar management regimes i.e. are not frequently burned. They include a geographic spread across the central and southern wheatbelt to give some idea of the regional extent of where *A. huegeliana* is encroaching into kwongan. These reserves were also selected because they have different mammal herbivore communities and the patches of kwongan within the reserves have been burned at different times in the past. These differences may give some indication how fire regimes and browsing herbivores affect *A. huegeliana* encroachment and are investigated in subsequent chapters.

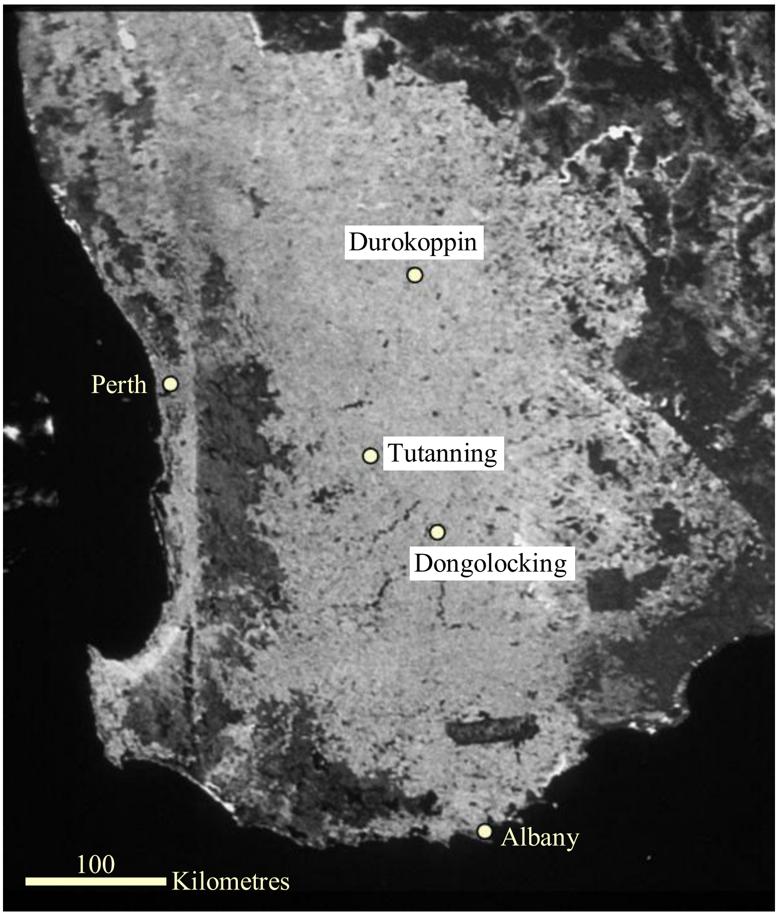


Figure 2.2: Satellite image of southwest Western Australia showing the extent of the wheatbelt region (light grey), areas of native vegetation (dark grey), and the location of three Nature Reserves studied.

Each patch was an area of kwongan that was separated from other areas of kwongan by different types of vegetation, cleared land, or adjoining areas of kwongan with different ages since last fire. Such adjoining patches only occurred at Durokoppin and time-since-fire ages were obtained from Friend *et al.* (1997) and Muir (1978*a*). The patches encompassed a broad range of characteristics including patch size, soil type, percentage of the kwongan bordering on *A. huegeliana* woodland and time since last fire (Table 2.1). The uneven number of patches selected for study in each reserve was due to the number of kwongan patches present at each reserve.

Table 2.1: Characteristics of the 12 patches of kwongan invaded by *Allocasuarina huegeliana* in three Nature Reserves.

Patch	Patch size	*A. huegeliana* border	Time since fire	Soil type	Citations
	(ha)	(%)	(years)		
Durokoppin 1	25	10	65 (1939)	yellow sand	Hobbs *et al.* 1989
Durokoppin 2	50	20	15 (1989)	yellow sand	Muir 1978a
Dongolocking 1	34	1	76 (1928)	grey sand	Chapman 1978
Dongolocking 2	59	1	76 (1928)	grey sand	Beecham *et al.* 1998
Dongolocking 3	31	1	76 (1928)	grey sand	Lloyd 1998
Tutanning 1	3	3	44 (1960)	yellow sand	Brown & Hopkins 1983 Friend *et al.* 1997 Little & Friend 1993 Nyagba 1976
Tutanning 2	14	1	44 (1940)	grey sand	
Tutanning 3	1	100	64 (1940)	duplex	
Tutanning 4	4	35	64 (1940)	shallow duplex	
Tutanning 5	6	35	14 (1990)	duplex	
Tutanning 6	2	100	72 (1932)	shallow duplex	
Tutanning 7	4	100	38 (1966)	shallow duplex	

2.2.2 Stem density, plant size and population structure

At each patch, three parallel transects were located from the patch boundary into the kwongan. The patch boundary was defined by bordering *A. huegeliana* woodland or other vegetation community. At sites where there was no clear boundary and *A. huegeliana* plants were scattered throughout the patch transects were located at a selected point, e.g. a track or road. The three transects were spaced evenly across the patch and transect length varied, depending on the size of the patch. Transects extended across the entire patch or to a maximum of 520m (at Durokoppin 1 and 2, and Dongolocking 1).

From the patch boundary, 10 × 10 m quadrats were located at 30 m intervals along each transect. In each quadrat, the height of all live *A. huegeliana* individuals was recorded using an extendable pole and tape measure, whether the individual was bearing fruit or not, and the stem diameter of live and dead individuals using vernier calipers at 40 cm above the ground or for smaller plants (< 0.6 m) at 10 cm above the ground. Almost all trees were single-stemmed, but in the case of multi-stemmed individuals the diameter of the largest stem was recorded.

Mean *A. huegeliana* stem density and fruit-bearing tree density were calculated for each patch by averaging data across all quadrats. Mean height and stem diameter, and the percentage of fruit-bearing trees were calculated from data pooled across all quadrats and transects. Reserve values were then obtained by averaging data across the patches at each reserve. The relationships between the percentage of trees bearing fruit, height and stem diameter among the patches were analysed using Spearman's rank order correlation in SPSS 15.0 (SPSS 2006).

Preliminary investigations indicated that age classes could not be determined for *A. huegeliana* due to the absence of reliable growth ring markers. In the absence of an appropriate method for age determination, girth is often a reasonable approximation of a tree's age (Pearson & Searson 2002). Therefore stem diameter classes were used to analyse the *A. huegeliana* population structures. A population was considered to include all the trees within a patch. Stem-class frequency histograms were produced for each patch by pooling data from all quadrats.

The populations were visually categorized into three distribution types. Type 1 distributions had a 'reverse-J' distribution, with many small trees and decreased toward larger diameter classes. Type 2 distributions were discontinuous (i.e. a larger size class had more individuals than a smaller size class), but the smallest classes still had the largest proportion. Type 3 distributions were unimodal with a few or no trees in small classes or had even distributions across size classes. The classification was done visually, but the following statistical inspections were also performed to see if both results agreed. For each population, the midpoint for each size class range (e.g. the midpoint of size class 0−20 was 10) and the corresponding number of plants were natural log transformed, and their relationship was tested using linear regressions in SPSS 15.0 (SPSS 2006). The log-linear relationship should be highly significant in Type 1 distributions, less so in Type 2 and not significant in Type 3 (Kohira & Ninomiya 2003). The distribution of *A. huegeliana* across each patch was illustrated by producing graphs of the number of individuals that were/not bearing fruit within the quadrats. Quadrats located at specific distances from the patch edge were pooled across the three transects.

2.2.3 Effects of patch characteristics on the extent of encroachment

The effect of the patch characteristics, including patch size, the percentage of the kwongan patch that bordered on *A. huegeliana* woodland, number of years since last fire and edge–area ratio (patch size/percentage *A. huegeliana*–kwongan border) on the level of encroachment (*A. huegeliana* density and plant height) was examined using linear regression. The effect of soil type (categorised as yellow sand, grey sand or duplex) was examined using one way ANOVA. Percentage values were converted to proportions and arcsine square root transformed. Assumptions of homogeneity of variance and normality were checked with residual plots, box-plots and using the Levene test. These data met the assumptions. All analyses were undertaken using SPSS 15.0 (SPSS 2006).

The effect of interactions among patch-scale characteristics on the extent of encroachment at each patch could not be analysed because there were not enough patches to fit multiple regression models. Although the twelve patches occurred within three reserves they were treated independently due to the large degree of heterogeneity. Kwongan in the wheatbelt exhibits a low level of floristic uniformity between stands at both the regional scale and the local scale between stands that are located close together (Brown 1989).

2.3 Results

2.3.1 Stem density and plant size

Mean *A. huegeliana* stem density was similar among reserves (Table 2.2). The proportion of trees bearing fruit was larger at Tutanning (21%) than Dongolocking and Durokoppin (13–14%). Plants were largest (in height and stem diameter) at Tutanning, followed by Dongolocking and were smallest at Durokoppin.

The density of *A. huegeliana* trees within the 12 patches differed markedly among patches at the same reserve and patches at other reserves, from 138–908 plants ha^{-1} (Table 2.2). The largest trees were located at Tutanning 3, 6 and 7 with both the tallest (4.6–7.2 m) and broadest trees (74–133 mm). Mean plant sizes at the remaining patches averaged between 2.0–3.6 m in height and 21–49 mm in diameter. The percentage of trees that were bearing fruit increased as both height and stem diameter increased (stem diameter $P = 0.004$, $r_s = 0.760$; height $P = 0.003$, $r_s = 0.760$). Fruit-bearing plants had a minimum height of 2.1 m at Durokoppin, 3.2 m at Dongolocking and 2.7 m at Tutanning. It should be noted that these figures included trees that had just begun to bear fruit i.e. only had one or two cones.

Table 2.2: Characteristics of the *Allocasuarina huegeliana* populations in 12 patches of kwongan in three Nature Reserves.

Site (patch)	Density (mean ± SE)	Fruit-bearing tree density (mean ± SE)	Fruit-bearing trees	Height (mean ± SE)	Stem diameter (mean ± SE)
	(trees ha^{-1})	**(trees ha^{-1})**	**(%)**	**(m)**	**(mm)**
Durokoppin 1	167 ± 49	31 ± 11	19	3.3 ± 0.21	43 ± 4
Durokoppin 2	456 ± 195	37 ± 13	8	2.1 ± 0.08	21 ± 1.3
Durokoppin mean	**312 ± 145**	**34 ± 3**	**14 ± 6**	**2.7 ± 0.62**	**32 ± 11**
Dongolocking 1	446 ± 234	25 ± 21	6	3.0 ± 0.16	43 ± 4
Dongolocking 2	387 ± 109	59 ± 22	15	3.6 ± 0.16	49 ± 3
Dongolocking 3	185 ± 68	31 ± 15	17	3.4 ± 0.22	47 ± 5
Dongolocking mean	**339 ± 79**	**38 ± 10**	**13 ± 3**	**3.3 ± 0.19**	**46 ± 2**
Tutanning 1	333 ± 128	10 ± 10	3	2.0 ± 0.21	25 ± 5
Tutanning 2	138 ± 61	38 ± 22	27	3.4 ± 0.63	48 ± 12
Tutanning 3	236 ± 62	91 ± 28	38	7.2 ± 0.35	133 ± 14
Tutanning 4	229 ± 105	17 ± 10	7	2.6 ± 0.23	33 ± 5
Tutanning 5	296 ± 56	21 ± 8	7	2.9 ± 0.18	40 ± 3
Tutanning 6	908 ± 158	400 ± 66	44	6.1 ± 0.17	93 ± 6
Tutanning 7	171 ± 30	40 ± 12	24	4.6 ± 0.19	74 ± 5
Tutanning mean	**330 ± 100**	**88 ± 53**	**21 ± 6**	**4.1 ± 0.73**	**64 ± 15**

2.3.2 Population structure

Eight populations were classified as having Type 1 (‘reverse-J’ shape) distributions, one population as Type 2 (discontinuous but most stems in smaller classes) and three populations as having Type 3 (even or unimodal distributions). Visual classification of the observed distributions was strongly supported by the statistical tests: ANOVA F-tests were markedly significant ($P < 0.01$) for species classified as Type 1; intermediate ($0.01 < P < 0.05$) for Type 2; and not significant for Type 3 (Table 2.3).

A. huegeliana populations at all patches at Durokoppin and Dongolockings, and three patches at Tutanning (1, 2 and 4) indicated continual recruitment, with a large proportion of individuals in the smaller size classes and few individuals in the larger size classes (Figure 2.3 a–g and i). Tutanning 5 was also dominated by plants in smaller size classes; however, there were fewer plants in the smallest size class (0–19mm) than the number in the larger size class. This population structure indicates a possible reduction in recruitment (Figure 2.3 j).

The *A. huegeliana* population at Tutanning 3 had an even distribution across size classes (Figure 2.3 h). *A. huegeliana* encroachment into this patch was extensive and the canopy of *A. huegeliana* trees shaded much of the kwongan.

A. huegeliana populations at Tutanning 6 and 7 had unimodal population distributions, with the majority of individuals in the 40–100 cm size classes (Figure 2.3 k–l). There were a few larger trees at these patches and many individuals were reaching maturity (beginning to flower or bear fruit). Despite similar size-class distributions the difference in plant densities was great. Tutanning 6 was dominated by larger trees at much greater densities (Table 2.2) which formed an almost closed canopy over much of the kwongan. Although large trees were present at Tutanning 7 they were at much lower densities and the canopy was open.

Table 2.3: Size distribution types of *Allocasuarina huegeliana* populations in 12 patches of kwongan at three Nature Reserves and the parameter estimates (standard error) for the intercepts and slopes (standard error) of the log-linear relationship between the number of individuals and size class. For significant relationships: $P < 0.01^{**}$, $P < 0.05^{*}$.

Patch	**Intercept (SE)**	**Slope (SE)**	***P***	**Distribution Type**
Durokoppin 1	6.95 (1.19)	−1.26 (0.28)	0.003**	1
Durokoppin 2	9.97 (0.97)	−1.97 (0.23)	0.001**	1
Dongolocking 1	7.14 (0.98)	−1.27 (0.22)	0.001**	1
Dongolocking 2	7.91 (1.20)	−1.39 (0.27)	0.001**	1
Dongolocking 3	6.37 (1.07)	−1.15 (0.25)	0.002**	1
Tutanning 1	6.71 (0.95)	−1.33 (0.23)	0.002**	1
Tutanning 2	4.26 (0.61)	−0.76 (0.14)	0.001**	1
Tutanning 3	1.18 (1.26)	−0.09 (0.26)	0.730	3
Tutanning 4	5.81 (0.54)	−1.04 (0.13)	0.001**	1
Tutanning 5	6.04 (1.30)	−1.06 (0.32)	0.021*	2
Tutanning 6	4.17 (1.36)	−0.54 (0.29)	0.092	3
Tutanning 7	3.91 (1.64)	−0.55 (0.37)	0.177	3

2.3.3 Effects of patch characteristics on the extent of encroachment

Few of the relationships between the patch characteristics and the measures of encroachment were significant; plant height was the only measure of encroachment that could be significantly explained. Mean plant height was taller at patches with a larger percentage of the kwongan patch bordering on *A. huegeliana* woodland (Table 2.4). Soil type did not significantly impact on plant density or height (Table 2.5).

Table 2.4: Results from linear regression analyses between patch-scale characteristics and extent of *Allocasuarina huegeliana* encroachment (stem density and plant height) in twelve patches of kwongan. For significant relationships: $P < 0.01$**, $P < 0.05$*.

Patch characteristic	**Measure of encroachment**	P	r^2
Stem density	Patch size	0.878	0.002
	Time-since-fire	0.633	0.024
	A. huegeliana woodland–kwongan border	0.352	0.087
	Edge–area ratio	0.994	0.000
Plant height	Patch size	0.226	0.143
	Time-since-fire	0.258	0.126
	A. huegeliana woodland–kwongan border	0.002**	0.629
	Edge–area ratio	0.649	0.021

Table 2.5: Results from ANOVA analyses between soil type (yellow sand, grey sand or duplex) and extent of *Allocasuarina huegeliana* encroachment (stem density and plant height) in twelve patches of kwongan. For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	**Degrees of freedom**	**Stem density**			**Plant height**		
		Mean Square	F	P	Mean Square	F	P
Soil type	2	7245.68	0.14	0.875	4.93	2.63	0.126
Error	9	53616.97			1.88		

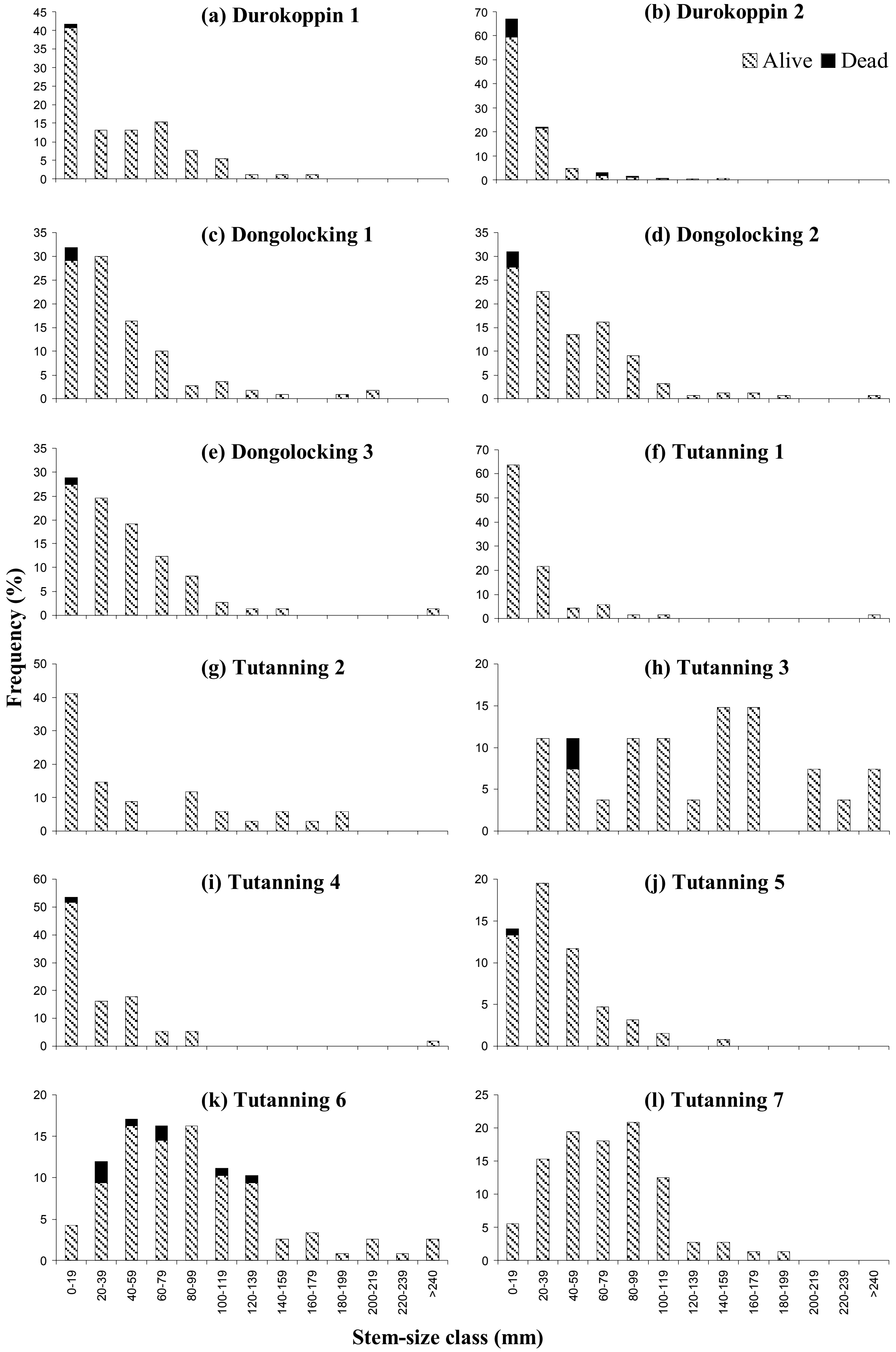


Figure 2.3: The percentage frequencies of *Allocasuarina huegeliana* individuals in each stem size class (pooled across all quadrats and transects) in 12 patches of kwongan at three Nature Reserves.

2.4 Discussion

Results from this study confirm anecdotal observations that *A. huegeliana* has encroached into kwongan at the reserves studied, which are located in the central and southern wheatbelt (Powell 1990; Little & Friend 1993; Main 1993; Bamford 1995). The progress of encroachment was substantially different among the kwongan patches, indicated by the variation in *A. huegeliana* population characteristics and size class structures.

Since the study species did not produce reliable annual growth rings it was not possible to accurately age individuals. Therefore, the initiation of encroachment could not be determined. At Durokoppin and Dongolocking, *A. huegeliana* was not recorded in the patches of kwongan studied in the late 1970s (Muir 1978b, c). In the early 1980s at Tutanning, Brown and Hopkins (1983) recorded *A. huegeliana* within quadrats at a number of kwongan patches, and outside the quadrats but within the community at other patches. At most sites, however, they described *A. huegeliana* as 'rare emergent' or 'very rare emergent', and above kwongan shrublands 1.5–2 m in height. Although little is known about *A. huegeliana* growth rates, Yates *et al.* (2003) found that the mean plant height of 10-year-old *A. huegeliana* plants was greater than 3.5 m. In addition, a large proportion of *A. huegeliana* plants that recruited after a fire in 1990 (i.e. 14 years old) at Tutanning 5 were greater than 3 m in height. Therefore the 'emergent' *A. huegeliana* plants recorded by Brown and Hopkins (1983) were most likely less than 10 years old and established during the 1970s.

Not all encroachment, however, has occurred since the 1970s. Large isolated individuals were present in several patches e.g. Dongolocking 2 and 3, and Tutanning

1 and 4 (Figure 2.3), and were probably present prior to the 1970s. Field observations suggest that isolated individuals are not uncommon in kwongan, including patches that are not bordered by *A. huegeliana* woodland (Figure 2.4). Very few of the isolated individuals observed at the study sites or other Nature Reserves in areas that had and had not been encroached upon were producing fruit. Therefore, I do not consider that the establishment of individual isolated *A. huegeliana* trees is the 'initiation of encroachment'. Instead I consider that encroachment began (although this is only a rough estimate) when several plants had established; hence the majority of plants have established in kwongan since the 1970s.

Figure 2.4: Photographs of isolated *A. huegeliana* trees that have established in kwongan.

The size structure of *A. huegeliana* populations (live plants only) at most patches was a ‘reverse J’ shape, which indicates continual recruitment (Hett & Loucks 1976; Smith *et al.* 1997). Encroachment does not visually appear to be dramatic in many kwongan patches because most *A. huegeliana* populations were dominated by seedlings and saplings with few larger trees. However, the visual and ecological impacts of encroachment on the kwongan species will increase dramatically as the current *A. huegeliana* populations mature and come to dominate the kwongan.

The continuing recruitment patterns of most of the populations indicate that plant density will increase within the patches studied. These populations have already reached densities of between 138–456 stems per hectare. The size-class distribution of an area of *A. huegeliana* woodland on a granite site indicated continuous recruitment up to a carrying capacity of approximately 2 000 trees per hectare (Ladd 1989). Whether *A. huegeliana* can establish to such densities in kwongan is unknown.

A. huegeliana populations at two patches at Tutanning (6 and 7) had unimodal size structures and were dominated by plants in the mid-size classes with few plants in the smallest size classes, indicating a recent decline in recruitment. However the density and average size of the plants was considerably different between these patches. The stem density was much higher and plant size was larger at Tutanning 6 and the encroaching populations had formed an almost closed canopy over much of the kwongan (Figure 2.6). Further seedling recruitment at this site is most likely prevented by shading and competition from the established trees (Oliver & Larson 1990). Dead individuals in the larger size classes indicate that self-thinning may be occurring, where tree death occurs due to suppression by a more competitive neighbour (Peet & Christensen 1987). This process was commonly observed in the dense sheoak woodlands surrounding the kwongan.

Figure 2.5: Photograph showing extensive *A. huegeliana* encroachment in kwongan at Tutanning 6.

While the *A. huegeliana* population at Tutanning 7 had a unimodal size structure, the stem density and plant size was much smaller at this patch. The stem density was also much lower at Tutanning 3, which had an even size-class distribution and no stems in the smallest size class, but there were a number of trees in large size classes. The reasons why *A. huegeliana* is establishing at lower densities at these two patches are uncertain. A range of factors determine whether a plant establishes including the supply of available propagules, and biotic and abiotic site conditions (Harper 1977; Oliver & Larson 1990). These factors will therefore affect the density of plants and the size structure of a population establishing within a patch.

Propagule pressure is unlikely to be the cause of the differences in recruitment between patches 3, 6 and 7 at Tutanning, which had even or unimodal size distributions, because all patches were small in size and entirely surrounded by *A. huegeliana* woodland. The soil type at these sites was also similar (all were duplex soils) and rainfall would be similar because these patches occur within the same reserve. Additionally, the encroaching *A. huegeliana* stands were not triggered by fire because *A. huegeliana* was spare in these areas in the early 1980s (Brown & Hopkins 1983), 15−40 years after the last fire occurred at each patch (Table 2.1). Other environmental factors that are different between these patches must therefore be responsible for differences in extent of encroachment.

The density at which *A. huegeliana* is able to establish and grow to maturity within different kwongan patches is extremely important because this will determine the impact that these trees will have on the kwongan understorey. Small numbers of *A. huegeliana* individuals at low densities are much less likely to negatively impact on the kwongan that a large number of individuals that have established at high densities. An understanding of the factors affecting recruitment is therefore essential to determine which sites are most at risk of extensive encroachment and to assist with prioritising the sites for management.

Colonisation by an expanding or invading species can occur as both advancing fronts from existing populations and as satellites that arise from them. The progression of a frontier is generally limited by the time required for new generations to establish; new recruits at a population boundary must reach seed-bearing age before they can disperse their seed beyond the advancing front (Clark *et al.* 1998). Satellite populations establish when individuals disperse widely and then increase sufficiently to become self-perpetuating populations (Moody & Mack 1988). Such colonists that detach from the main population accelerate spread well beyond that expected from the average dispersal distance, and also make the rate of spread highly variable (Clark *et al.* 1998). It has therefore been suggested that measures to reduce the overall population spread of a species should be more effective if control tactics are focused on satellite populations (Cousens & Mortimer 1995; Moody & Mack 1988).

Personal observations indicate that *A. huegeliana* plants have established widely throughout most patches, including patches where *A. huegeliana* woodland was an adjacent community and where it was not. Therefore patches of kwongan that are not adjacent to *A. huegeliana* woodland still appear to be susceptible to encroachment. Although this study did not assess the patterns of encroachment, observations indicated that *A. huegeliana* was establishing both in large numbers adjacent to areas of woodland i.e. an encroachment front, and also in scattered populations that have thickened and spread i.e. satellites. Further investigations into the pattern of *A. huegeliana* encroachment are needed to provide a greater understanding of the encroachment process. This information may be useful for prioritising sites for management and management practises.

There appeared to be no obvious patch-scale characteristics limiting *A. huegeliana* encroachment into kwongan. We can therefore assume that encroachment is likely to occur throughout the region, at least in remnants in the central and southern wheatbelt that have similar characteristics to the reserves selected for this study (Section 2.2.2). It is also possible that *A. huegeliana* could be encroaching on kwongan in remnants further north and south of the study reserves. The occurrence of kwongan and distribution of *A. huegeliana* overlaps throughout the southwest region (Beard 1984, 1990) therefore all kwongan remnants in this area could be at risk of encroachment.

The patches that are being encroached upon encompassed a range of characteristics. *A. huegeliana* plants were significantly larger (both height and stem diameter) in patches that shared a greater percentage of their boundary with *A. huegeliana* woodland and therefore experienced higher propagule pressure. In the absence of an appropriate method for age determination, girth is often a reasonable approximation of a tree's age (Pearson & Searson 2002) and thus the length of time that encroachment has been occurring. Therefore, *A. huegeliana* appears to have been encroaching into patches of kwongan that experience higher propagule pressure for a longer period of time than patches with lower propagule pressure. Alternatively, encroachment may have occurred over the same period of time but has occurred more rapidly at the sites that experience higher propagule pressure.

Since propagule pressure was greater at kwongan patches where encroachment had been occurring either for a longer period of time or more rapidly, we would also expect higher *A. huegeliana* stem densities. However, none of the patch-scale characteristics explained the variation in stem density among the patches, including propagule pressure (i.e. *A. huegeliana* woodland–kwongan border and the edge–area ratio). Other environmental factors must therefore affect the density of seedlings that are able to establish within a patch.

In patches with higher densities of fruit-bearing trees, which should therefore have higher propagule pressure, the stem densities of younger plants (in the smallest size category) were low. The highest densities of fruit-bearing trees occurred in Dongolocking 2 and Tutanning 3, 6 and 7. Three of these were the patches that showed evidence of declining recruitment, which were all at Tutanning. This pattern would suggest that *A. huegeliana* establishment was inversely related to propagule pressure. However, most seed entering the kwongan patch is from bordering *A. huegeliana* woodland. Fruit-bearing trees within kwongan patches would also contribute seed; however, field observations indicated that the heights, canopy sizes and seed loads were much smaller than for fruit-bearing trees in the surrounding woodland. The decline in recruitment is instead more likely due to increased shading and competition from the larger *A. huegeliana* plants present at these sites, and other factors that affect the carrying capacity of the site such as biotic and abiotic site conditions, as discussed previously.

Soil type did not significantly affect plant density or size. Plants of all sizes had established across entire patches of kwongan, which indicates that *A. huegeliana* can prosper on a range of soil types. This characteristic is unsurprising considering that *A. huegeliana* has been recorded from a wide range of soil types ranging from yellow sand-clays to sandy and gravely loans, sandy clays, sandy types of all gradations and lateritic clays (Doran & Hall 1981). Such a wide tolerance for different soil types increases the range of sites that are at risk of encroachment and raises the question why *A. huegeliana* hasn't always occurred within these patches.

Historical vegetation surveys have indicated that *A. huegeliana* was sparse or not recorded in the patches of kwongan studied (Muir 1978b, c; Brown & Hopkins 1983). Therefore, the historical *A. huegeliana* and kwongan community boundaries were probably maintained by interactions between soils and disturbance regimes. These results are particularly significant in southwest Australia where there is considered to be a close correlation between vegetation type and soil type (Beard 1990; McArthur 1991; Gibson *et al.* 2004). However, it should be noted that the analysis only included broad soil type and did not include a detailed analysis of soil physical and chemical properties.

Fire and grazing regimes have been altered across much of Australia, including the Western Australian wheatbelt (Hobbs 1987). Alterations to fire and grazing regimes have been identified as factors contributing to the encroachment of *Allocasuarina* in other vegetation communities (Withers & Ashton 1977; Lunt 1998a, b; Main 2001; Crosti *et al.* in press) and the encroachment of other woody species into heathland (Burrell 1981; Cheal 1996; McMahon *et al.* 1996). However, time-since-fire did not significantly explain variation in the stem density or plant size (age) of *A. huegeliana* populations among patches.

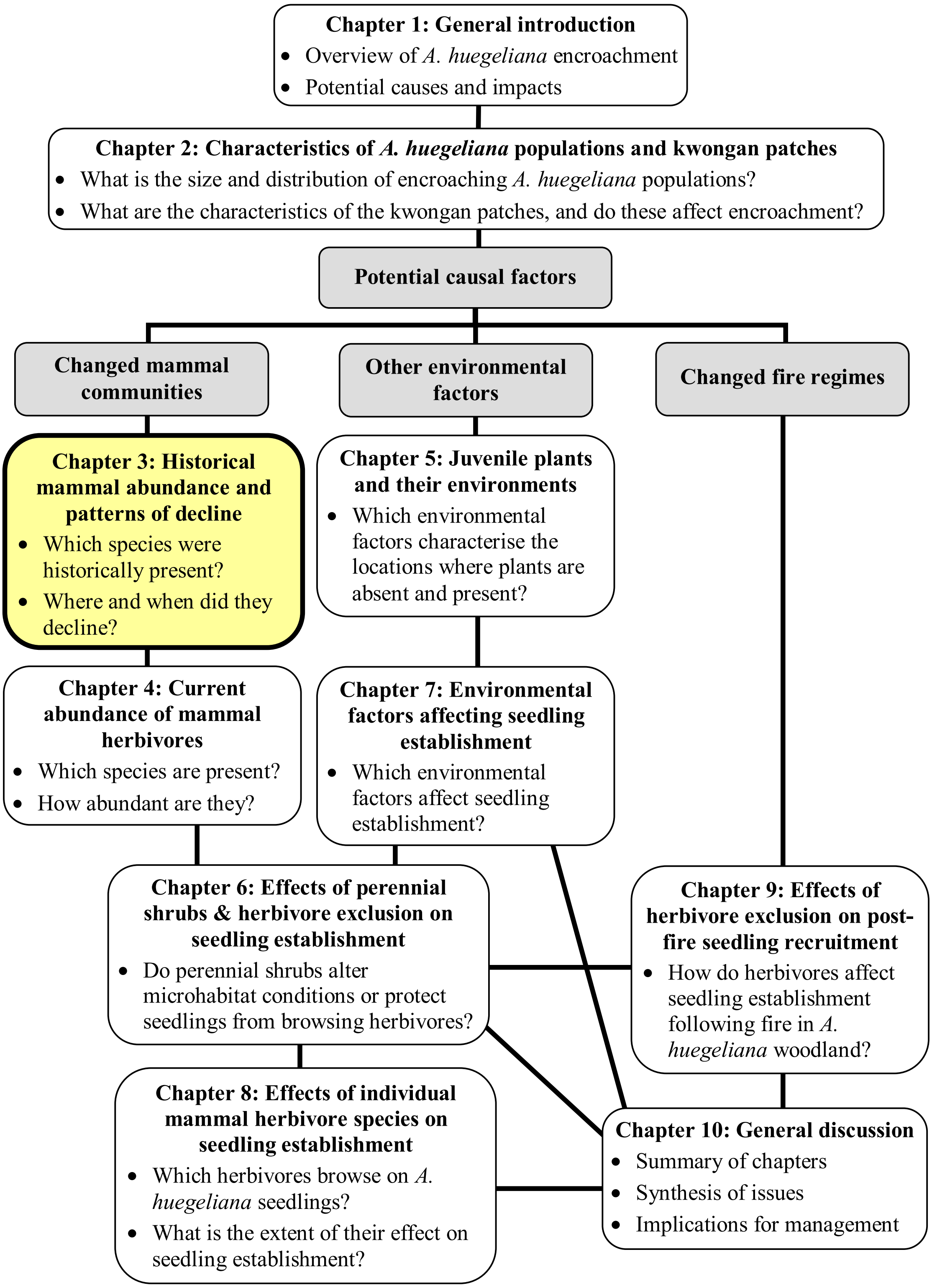
A. huegeliana is killed by fire and can regenerate prolifically following fire or soil disturbance (Yates *et al.* 2003). However, *A. huegeliana* is also able to establish seedlings without disturbance (Ladd 1989). Plant age, indicated by stem diameter (if this measure is a reasonable approximation of age), should therefore be greater at patches with a longer period of time since the last fire. However, the stem diameters of plants were not larger at sites with a longer time-since-fire. The initiation and rate of encroachment may be affected by interactions with other factors such as propagule pressure, herbivore browsing, and other biotic and abiotic site characteristics.

The effect of interactions among the patch-scale characteristics (e.g. time-since-fire, propagule pressure, soil type etc.) could not be analysed because there were not enough patches to fit multiple regression models. Interactions among patch-scale characteristics may have a more significant effect on the extent of encroachment than individual characteristics alone. The survey design used in this study was constrained by the history of land-use in the wheatbelt and replication at the patch and reserve scale was limited due to the small amount of remnant vegetation remaining in the region. A broader survey of kwongan patches throughout the wheatbelt, which includes sites that have not been encroached upon by *A. huegeliana* and additional characteristics such as herbivore abundance, is required to better understand how reserve and management factors are affecting encroachment.

This chapter has demonstrated that *A. huegeliana* has successfully established in patches of kwongan that encompass a broad range of characteristics and occur throughout the central and southern wheatbelt. *A. huegeliana* appears to have dispersed widely throughout these patches, recruitment is continuous in most populations and most plants appear able to survive to maturity. Kwongan that occurs throughout the wheatbelt where *A. huegeliana* is nearby is therefore likely to be at risk from encroachment. In contrast to the commonly held understanding that vegetation communities in southwest Western Australia are largely controlled by soil factors, these do not appear to limit *A. huegeliana* establishment in kwongan. Subsequent chapters will investigate the environmental conditions affecting seedling recruitment and the effects of herbivore browsing during inter- and post-fire periods to better understand the factors driving *A. huegeliana* encroachment.

Chapter 3

Historical abundances of native mammals and patterns of decline since European settlement



3.1 Introduction

Chapter 1 explained suggestions that altered browsing regimes, as a consequence of the loss of much of the medium-sized mammal fauna throughout the wheatbelt, may be potentially responsible for encroachment.

Australia has suffered more mammal extinctions, range contractions and population declines than any other biogeographical realm (Kinnear *et al.* 2002). Currently 18 Australian mammal species are believed extinct and another 40 are considered under threat (Short *et al.* 2005). Most extinctions and declines have occurred within the medium-sized terrestrial species in the weight range 0.35–5.5kg (Burbidge & McKenzie 1989) and omnivores and herbivores have declined to a greater extent than carnivores (Short & Smith 1994). The two most affected areas are the southern arid zone and the wheatbelt of Western Australia (Short & Smith 1994). Many species from the wheatbelt now persist only as small populations in remnant patches of native habitat or on offshore islands.

A large number of factors have been identified as potential contributors to mammal decline in Australia. These factors include habitat loss, fragmentation, changed fire regimes, introduction of stock and rabbits, predation by foxes and cats, disease and climate change (Short *et al.* 2005). The loss or decline of mammals may have a number of important indirect effects on ecosystem dynamics through the loss of the functional role of these species (Hobbs & Mooney 1998).

Several mammals that suffered the greatest declines were important disturbance agents. Bettongs, potoroos, bilbies and bandicoots turn plant litter and dig shallow scratchings, pits and holes when foraging for food (Strahan 1995). Such digging activity mixes organic matter into the soil; spreads mycorrhizal fungi and seeds; and alters the conditions for water infiltration, nutrient cycling and seed germination (Christensen 1980b; Claridge *et al.* 1992; Noble 1995; Garkaklis *et al.* 1998; Garkaklis *et al.* 2000; Martin 2003). Brush-tailed bettongs (Bettongia penicillata) make between 38 and 114 diggings a night each and turn over almost 5 tonnes of soil each year (Garkaklis *et al.* 2004). The loss of these mammals removed this soil turnover and its subsequent effects on soil characteristics and vegetation dynamics. Similar declines of herbivore species have altered grazing and browsing regimes which is likely to have had widespread effects on vegetation dynamics.

Main (1993) proposed that the reduction of browsing that occurred with the decline of native mammal herbivores was responsible for *A. huegeliana* encroachment. In particular, the author suggested that *A. huegeliana* encroachment into kwongan at Tutanning Nature Reserve was caused by reduced levels of browsing on seedlings as a result of the decline of tammar wallabies during the 1970s. *A. huegeliana* has encroached into kwongan at several reserves in the wheatbelt and the factors driving this process are assumed to be similar. If the decline of a particular mammal species, such as tammars, has caused *A. huegeliana* encroachment, the timing and extent of decline should be similar at the reserves where encroachment has occurred.

Prior to the 1970s, knowledge and information about the distribution and abundance of mammal populations, and the timing of major changes in abundance is scarce. Hence the information available is largely anecdotal or dependent upon the small collection of specimens held in the Western Australian Museum (Kitchener *et al.*

1980). This chapter uses museum collections, survey data, naturalist diaries, and anecdotal observations to explore the historical abundance of native mammals, and the pattern, timing and extent of their decline in the areas surrounding Durokoppin, Dongolocking and Tutanning Nature Reserves. It will then discuss the potential role of mammal decline in driving *A. huegeliana* encroachment. Most of the anecdotal observations of mammal abundances and changes to their populations were by local residents and largely recorded in social history books of the region. All books and manuscripts written by residents that lived in the region around the three Nature Reserves studied, that were held in the J. S. Battye Library of West Australian History (Perth) were searched for discussion of native mammals and their abundances.

3.2 Early observations of mammal abundance

Throughout this chapter, many locations are identified by the Local Government District that they occur in (Table 3.1). These Districts are now known as Local Government Shires. Durokoppin is located in the Shire of Kellerberrin, Dongolocking is located on the border between the Shires of Wickepin, Dumbleyung and Wagin, and Tutanning is located in the Shire of Pingelly. Although the boundaries of the Districts and Shires have changed over the past 100 years, the areas that they refer to are generally similar (Figure 3.1).

Table 3.1: Local Government Shires and former Districts that Durokoppin, Dongolocking and Tutanning Nature Reserves are located in, and nearby Shires/Districts.

Reserve	**Located in Shire/District**	**Adjacent Shires/Districts (direction)**
Durokoppin	Kellerberrin	Bruce Rock (south and east), Tammin (west), Cunderdin/Meckering (adjoins the western border of Tammin)
Dongolocking	Border between Wickepin, Dumbleyung and Wagin	Katanning (south of Dumbleyung)
Tutanning	Pingelly	Brookton (north), Corrigin (northeast), Wickepin (southeast), Cuballing (south)

Figure 3.1: Location of the Local Government Shires within the Western Australian wheatbelt (Wheatbelt Development Commission n.d.)

At the time of European settlement there were about 43 species of mammals in the wheatbelt region (Kitchener *et al.* 1980), including those listed in Table 3.2. Bruce Leake, whose father had property near Doodlakine (15 km east of Kellerberrin), observed numerous mammals in this part of the eastern wheatbelt in the 1890s including the grey kangaroo, rock-wallaby, tammar, woylie, boodie, bertie, wurrung, wurrup, numbat, merrnine, possums, dalgyte, red-tailed phascogale and native cat (Leake 1962). Leake also noted that in the early 1900s the brush wallaby and euro extended their range into the Kellerberrin district as a result of rapid agricultural expansion pushing them out of their former range.

In the nearby Meckering (now Cunderdin) district Thomas Kelly (n.d.) recalled that in the 1880s the “wildlife in the bush was plentiful” including the tammar wallaby, brushtail and ringtail possum, dalgyte, boodie, numbat, pig-footed bandicoot and the brush wallaby which “ranged everywhere in the scrub country”. Other observations indicate that brush wallabies were also abundant in 1906 in the Bruce Rock district (Ewers 1959) and the Meckering [Cunderdin] district in 1924 (Stokes 1986).

Guy Shortridge made extensive collections of mammals in southern Australia in the years 1904 to 1907 for the British Museum of Natural History. Shortridge found abundant fauna at Dwaladine (18 km north of Tutanning) and Woyaline (5 km east of Tutanning), including the grey kangaroo, brush wallaby, tammar wallaby, nailtail wallaby, banded hare-wallaby, burrowing bettong, brush-tailed bettong, bilby, brushtail possum, western quoll, numbat and bandicoots (Short 2005). In the nearby area of Aldersyde (16 km north of Tutanning), Charles Smith reported that there were large numbers of boodie rats, dalgytes, dunnarts, warrens, bandicoots and native cats in the district in 1903 (Knox-Thompson 1975). In the 1920s the Dowling family noted that a number of mammals were abundant including kangaroos, brush wallabies, tammars, boodie rats, possums and dalgytes in areas of bush near Popanyinning (18 km southwest of Tutanning) (Lange 1981).

Job Haddleton recalled that when the first settlers came to the Katanning district during the 1860s kangaroos, brush wallabies, tammar wallabies, kangaroo rats, boodie rats, dalgytes, brushtail and ringtail possums, bandicoots, marls, numbats and native cats were found in the area, and several species were so abundant that they were considered pests (Haddleton 1952). At this time, the kangaroo, brush wallaby, tammar and possums were also common in the Wagin district (Pederick 1979) and there were hundreds of brush wallabies in the Dongolocking area (Lloyd 1999b). The brushtail possum, kangaroo, brush and tammar wallaby were eaten by landholders in the Dongolocking area, especially during the Depression (Lloyd 1999a) and thus were presumably abundant at this time.

3.3 Patterns of mammal decline

3.3.1 The late 1800s to the 1920s

A number of species became extinct from the wheatbelt region soon after settlement in the late 1800s and early 1900s. In 1904 Shortridge detected a widespread decline of mammals in arid and semi-arid parts of Western Australia and a lack of fauna in the mesic southwest where agriculture was well developed (Short 2005). However, no fauna decline was evident in mesic woodland, scrub and forest in the wheatbelt except in areas close to settlements (Short 2005).

Table 3.2: The common and indigenous names of some of the mammal species observed by settlers in the Western Australian wheatbelt (from Strahan 1995).

Common Names	**Species**
Banded hare-wallaby, warren, merrnine (indigenous)	*Lagostrophus fasciatus*
Bilby, dalgyte (indigenous)	*Macrotis lagotis*
Black-footed rock-wallaby, rock-wallaby	*Petrogale lateralis*
Western brush wallaby, brush wallaby, black-gloved wallaby	*Macropus irma*
Brushtail possum	*Trichosurus vulpecula*
Brush-tailed bettong, kangaroo rat, woylie (indigenous)	*Bettongia penicillata*
Burrowing bettong, boodie, boodie rat	*Bettongia lesueur*
Dunnart	*Sminthopsis murina*
Euro, common wallaroo	*Macropus robustus*
Western grey kangaroo, grey kangaroo, kangaroo	*Macropus fuliginosus*
Crescent nailtail wallaby, nailtail wallaby, wurrung (indigenous)	*Onychogalea lunata*
Western quoll, native cat	*Dasyurus geoffroii*
Numbat	*Myrmecobius fasciatus*
Pig-footed bandicoot, bertie (indigenous)	*Chaeropus ecaudatus*
Red-tailed phascogale	*Phascogale calura*
Western ringtail possum, ringtail possum	*Pseudocheirus occidentalis*
Rufous hare-wallaby, whistler, mala (indigenous), wurrup (indigenous)	*Lagorchestus hirsutus*
Southern brown bandicoot, short-nosed bandicoot, quenda (indigenous)	*Isoodon obesulus*
Tammar wallaby, tammar	*Macropus eugenii*
Western barred bandicoot, marl	*Perameles bougainville*

Leake (1962) noted that a number of smaller mammals were lost from the Kellerberrin district between 1894 to 1899 including the woylie, boodie, wurrung, merrnine, wurrup, short-nosed bandicoot, pig-footed bandicoot, numbat and native cat. Tammars and the brushtail possum were lost from the district a few years later in 1902 (Leake 1962). Charles Masters noted that most brushtail possums had disappeared from the nearby Tammin district by early 1902 and boodies by 1904 (Masters & Masters 1999). However, specimens received by the Western Australian Museum from the central wheatbelt indicate that the bilby, brushtail possum and numbat persisted in the area until the late 1920s to early 1930s (Kitchener & Vicker 1981).

There were no reports of widespread decline in mammals in the area around Tutanning. However, several species appear to have declined in the early 1900s in the districts surrounding Dongolocking. Haddleton (1952) considered that many of the smaller mammals in the Katanning district disappeared from 1898 to 1905 including the boodie, wurrung, ringtail possum and kangaroo rat, although the bilby survived to 1935. John Drummond noted in 1911 the early demise of tammar wallabies in the Katanning district (Prince 1984).

3.3.2 Continued decline through the 1930s and 1940s

The first wave of extinctions and general decline in abundance of many mammals appears to have slowed by about 1930 (Kitchener *et al.* 1978). However, another serious decline occurred throughout the southwest from the early 1930s to the mid 1940s which particularly affected medium-sized mammals. This decline in the native fauna has largely been attributed to predation by the fox which spread throughout the southwest during the 1930s (Christensen 1980a).

The distribution of a number of mammals in Western Australia was described by Glauret (1933). At the time, the ringtail possum remained only in small isolated colonies in the lower southwest; the brushtail possum was still plentiful in the southwest but its distribution was restricted; the banded hare-wallaby was rare; the rufous hare-wallaby only survived in the northern desert regions; the black-footed rock-wallaby was rare in the settled districts of the southwest and wheatbelt; and the nailtail wallaby was on the verge of extinction (Glauert 1933). The distribution of both the brush and tammar wallaby was described as ‘southwestern Australia’, however their abundance was not mentioned (Glauert 1933).

Perry (1973) concluded from his observations and discussions with other people that there was a catastrophic collapse of number of species populations during the period 1938–1944 in the southwest including brushtail and ringtail possums, woylies and tammars. Although brush wallaby populations were reduced, they did not appear to be as seriously affected as other mammals (Perry 1973). However, a serious decline in brush wallabies was observed in the Kulin district from 1938, where they were previously considered to be plentiful (Serventy 1954).

3.3.3 A small increase during the 1950s

An increase in the abundance of several native mammals that had been long regarded as scarce or rare in the southwest was reported during the 1950s (Serventy 1954). The recovery of some species of fauna at this time appears to have been due to the decrease in fox populations. The introduction of broad-scale rabbit poisoning using 1080 baits caused large numbers of foxes to be killed through secondary poisoning from eating the poisoned rabbits (Christensen 1980a).

The toxin fluoroacetate contained in the 1080 baits occurs naturally in many plant species of the genera *Gastrolobium* which are abundant throughout southwest Western Australia. A number of species of native fauna in the southwest have a high level of tolerance to fluoroacetate (Oliver *et al.* 1977; King *et al.* 1978; Oliver *et al.*

1979; King *et al.* 1981). However, introduced species such as rabbits and foxes are highly susceptible to 1080.

The mammal community at Tutanning continued to be relatively unaffected by the decline experienced in other areas (Kinnear *et al.* 2002). A number of medium-sized marsupials were present within Tutanning in the 1960s including the numbat, quenda, ringtail possum, brushtail possum, tammar wallaby and woylie (Sampson 1971). Woylies, brushtail possums and kangaroos were abundant at nearby Dryandra Forestry Station (35 km southwest), and brush wallabies and tammars were also present in the area (Serventy 1954).

The decline of mammals continued throughout much of the rest of the wheatbelt, including the areas around Durokoppin and Dongolocking. During the early 1950s in the Katanning district, Haddleton (1952) noted that kangaroos and brush wallabies were still abundant, the brushtail possum was not present in large numbers, and tammars were very scarce. By the early 1960s in the Kellerberrin district, Leake (1962) considered that the grey kangaroo was common but less abundant, the rock-wallaby had almost disappeared, and the brush wallaby was rare. Ewers (1959) similarly reported that in the Bruce Rock district by the 1950s, only the kangaroo and brush wallaby were still occasionally seen, and only a few black-footed rock-wallabies remained.

3.3.4 Drastic decline from the 1960 to mid-1980s

Medium-sized mammal populations that persisted on Nature Reserves in the wheatbelt suffered a further drastic decline in the 1970s, and some species declined to extinction (Kinnear 1993). This decline followed the reduction in broad-scale rabbit poisoning using 1080 during the early 1970s (Christensen 1980a). An unintended consequence of this was an unprecedented increase in fox populations due to the lack of secondary poisoning from eating poisoned rabbits (King *et al.* 1981). Native species subsequently declined drastically in numbers and remained under constant pressure from foxes (Christensen 1980a).

During the 1970s, the Western Australian Museum conducted detailed surveys of flora and fauna at 23 Nature Reserves in the wheatbelt. Of the 43 mammal species thought to have been present in the wheatbelt at the time of European settlement, 18 species were recorded in the Museum surveys in the 1970s and only 12 species were considered to be moderately common to abundant (Kitchener *et al.* 1980).

The Museum survey at Durokoppin found that the western grey kangaroo and euro were common, but the brush wallaby was uncommon and was only seen on occasions (Chapman & Kitchener 1978). A similar survey at Dongolocking found that the western grey kangaroo was common, on average a solitary individual brush wallaby was sighted each day and only two brushtail possums were captured (Kitchener & Chapman 1978). The tammar, woylie, quenda and numbat were considered to be locally extinct at Dongolocking by the late 1990s (Beecham *et al.* 1998). The mammal community at Tutanning was severely affected during the early 1970s and by 1978 the numbat, quenda and the ringtail possum had disappeared from the reserve, the tammar wallaby and brushtail possum were infrequently sighted and sightings of the woylie ceased (Kinnear *et al.* 2002).

3.3.5 From the instigation of fox baiting in the mid 1980s to present

Fox baiting programs were introduced at several reserves in the wheatbelt during the 1980s, including Tutanning and Dongolocking, and had a profound affect on native fauna. The tammar population at Tutanning experienced a 12 to 20 fold increase in abundance over the 12 years following fox control, locally elevating the species from rarity to pest status (Kinnear *et al.* 2002). Tutanning now supports one of the largest populations of tammars in Western Australia; 429 tammars were removed from this reserve from 1998−2004 and translocated other locations without any measurable impact on the Tutanning population (DEH 2004). The brushtail possum population at this reserve is now thriving and appears stable, and the woylie population remains relatively low but stable (Orell 2004). Brush wallaby numbers have increased since fox baiting was implemented, but the species is still uncommon at Tutanning (Courtenay 1996).

There has been a large increase in brush wallabies at Dongolocking; however, brushtail possums remain uncommon at this reserve (Orell 2004). The quenda has been successfully reintroduced to the reserve (Kinnear *et al.* 2002). There have been unconfirmed reports of tammar wallabies in the reserve, and it is fair to assume that western grey kangaroos are also abundant in the area (P. Orell pers. comm.).

Euros and western grey kangaroos are present in high densities at Durokoppin and are thought to probably represent the near natural status of population distribution and abundance in this environment (Arnold *et al.* 1994). Brush wallabies are believed to persist as a very small relictual population and were sighted about once a year from 1986 to 1992 (Arnold *et al.* 1994).

The western grey kangaroo is considered to be common throughout its distribution. In some remaining extensive areas of natural habitat it appears to be as abundant as it was at the time of European settlement (Prince 1984). However, western grey kangaroo populations have almost certainly been reduced in abundance since the 1930s (Prince 1984), but probably by less than 10% (Kennedy 1992). Rock-wallaby populations have also recovered significantly at the four sites where this species is located, Mt Caroline, Nangeen Hill, Sales Rock and Tutakin (Eldridge *et al.* 2004). No rock-wallabies occur at the three reserves in this study.

3.4 Implications for *A. huegeliana* encroachment

Anecdotal observations clearly indicate that numerous mammal species were present in the region around the three reserves around the time of settlement. Many species were abundant and most were common to all three areas. Many of these mammals suffered massive declines or have been lost from the areas around Durokoppin, Dongolocking and Tutanning. However, the pattern, timing and extent of decline were substantially different among these reserves.

Mammal decline occurred at a much earlier stage at Durokoppin, primarily before the 1930s. The extent of decline was also more dramatic at this reserve and many species became locally extinct. Substantial decline also occurred at Dongolocking in the decades following settlement; however, many species were able to persist in small numbers until the 1970s and 1980s. The decline of mammals was relatively limited at Tutanning until the 1970s, when most species were either lost from the reserve or declined to very small numbers.

The majority of the *A. huegeliana* populations studied appear to have established in kwongan from the 1970s (Chapter 2). Therefore, the extinction of several mammal species prior to 1950s probably did not directly cause the more recent encroachment of *A. huegeliana* into kwongan. The establishment of *A. huegeliana* in kwongan from the 1970s coincides with the decline of remaining mammal populations throughout the wheatbelt at this time. However, no mammal species was common to all three areas that declined during the period between the 1960s and 1980s. For example, western grey kangaroos were common to all three areas but did not experience a decline at this time. Brush wallabies had already declined to small numbers at Durokoppin by the 1950s. Tammar wallabies had been lost from Durokoppin in the early 1900s, were scarce at Dongolocking by the 1950s and were only abundant at Tutanning where they declined dramatically during the 1970s. The decline of a single mammal species, including tammars, is therefore unlikely to have enabled large numbers of *A. huegeliana* seedlings to establish in kwongan at this time.

While the decline of individual mammal species may not be responsible for driving *A. huegeliana* encroachment, the cumulative effects of mammal decline needs to be taken into account. Ecosystems in this region may have been resilient to the initial mammal losses, with other species fulfilling the functions lost with successive declines or extinctions. The most recent losses and declines during the 1970s may have pushed these ecosystems past a threshold where remaining species, such as kangaroos, can no longer compensate for the absence of other mammals. However, it should be noted that encroachment has continued (Chapter 2) despite populations of several mammal species recovering in some areas including Tutanning.

Rabbits became abundant throughout the wheatbelt from the 1920s, soon after many native mammals were lost from the region. The activities of these native mammals such as digging, burrowing and browsing, may have been replaced to an extent by the activities of rabbits. Graziers have suggested that rabbits to some extent controlled the encroachment of several woody shrubs species in semi-arid pastoral lands in eastern Australia prior to the 1950s by browsing seedlings and ringbarking larger shrubs (Noble & Grice 2002). Browsing by rabbits has been shown to limit shrub and tree recruitment in many parts of Australia (Johnston 1968; Crisp & Lange 1976; Lange & Graham 1983; Cooke 1987; Auld 1990; Cohn & Bradstock 2000).

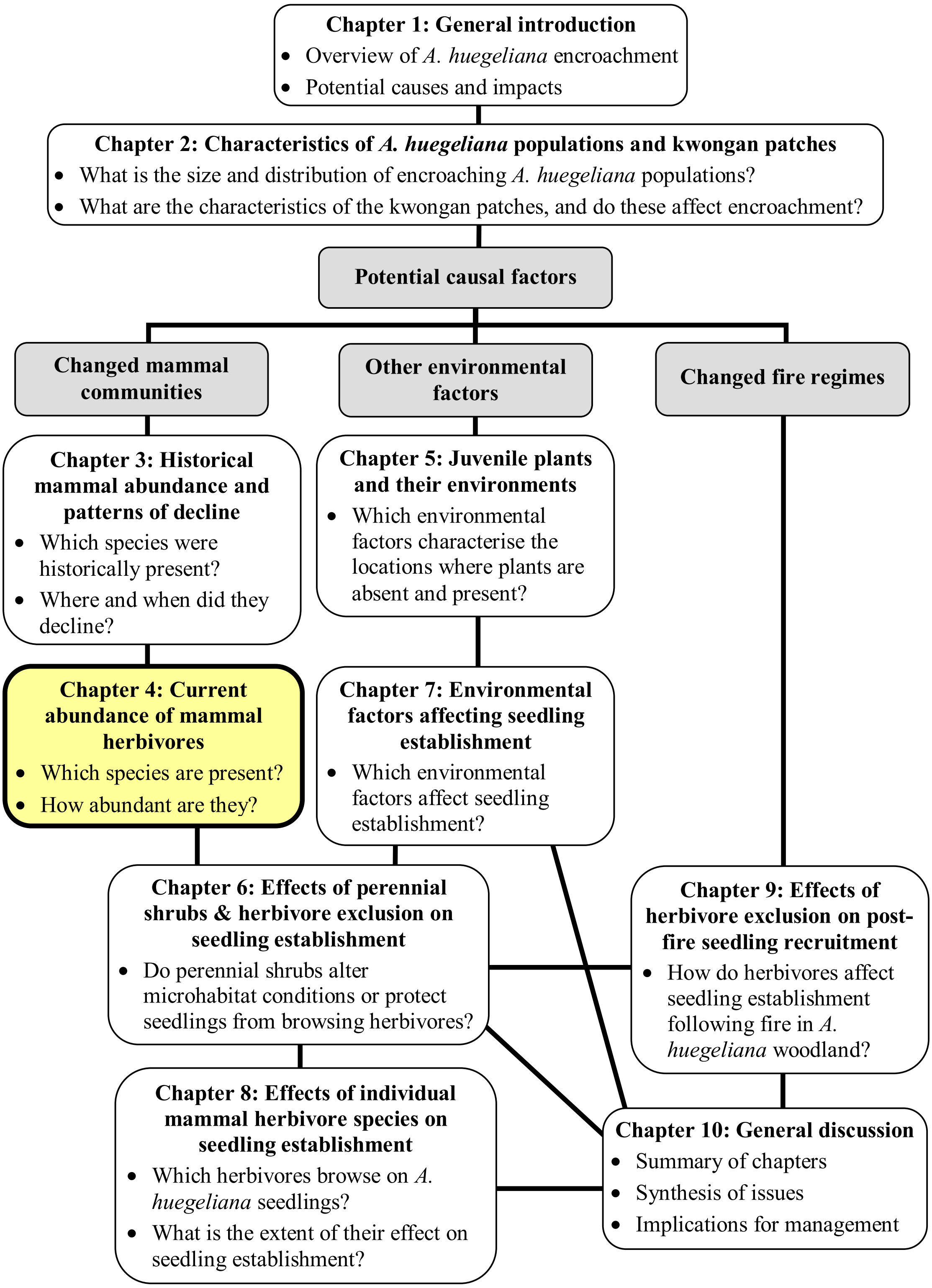
Rabbits may have similarly buffered the effects of mammal decline on ecosystem dynamics in the wheatbelt and potentially limited the recruitment of *A. huegeliana* seedlings in kwongan. Rabbit populations declined from the 1950s with the introduction of broad scale 1080 poisoning and the disease myxomatosis. A further substantial decline in rabbit populations occurred when the rabbit flea was introduced in 1969 and increased the transmission of myxomatosis (King *et al.* 1985; King & Wheeler 1985). The decline of rabbit populations from the late 1960s corresponds with the estimates of the initiation of *A. huegeliana* encroachment. Rabbit decline may have contributed to this process of encroachment, but the extent to which rabbits replaced previous herbivory by native mammals is unknown.

Although *A. huegeliana* encroachment into kwongan corresponds with the crash of many mammal populations in the 1970s, it is also important to note that the Reserves had not been burned for 20 to 50 years. These intervals are most likely much longer than historical inter-fire intervals. Therefore, the decline of mammals and long fire intervals may have had interactive effects that caused *A. huegeliana* encroachment. The absence of fire may have enabled trees to grow larger, and produce and disperse more seed into kwongan where seedlings have established because browsing mammals were largely absent. The effect of mammal herbivores on the establishment of *A. huegeliana* seedlings is investigated in Chapters 6 and 8. Other factors that might cause or exacerbate encroachment are considered in Chapter 10.

This chapter has shown that a diverse range of mammals were present at the time of European settlement in the areas around the three studied Nature Reserves. Most species were common to the three areas and many were abundant. From the 1900s onwards, the patterns of the mammal population decline varied among the reserves. Additionally, there was no native mammal common to all three reserves that declined around the time that *A. huegeliana* encroachment is estimated to have begun during the 1970s. It is therefore unlikely that the decline of a single mammal species triggered encroachment. However, the cumulative effects of mammal decline, the decline of rabbits, or both may have contributed to the progress of encroachment.

Chapter 4

Current abundance of mammal herbivores in kwongan



Chapter 1: General introduction
- Overview of *A. huegeliana* encroachment
- Potential causes and impacts

Chapter 2: Characteristics of *A. huegeliana* populations and kwongan patches
- What is the size and distribution of encroaching *A. huegeliana* populations?
- What are the characteristics of the kwongan patches, and do these affect encroachment?

Potential causal factors

Changed mammal communities

Other environmental factors

Changed fire regimes

Chapter 3: Historical mammal abundance and patterns of decline
- Which species were historically present?
- Where and when did they decline?

Chapter 5: Juvenile plants and their environments
- Which environmental factors characterise the locations where plants are absent and present?

Chapter 4: Current abundance of mammal herbivores
- Which species are present?
- How abundant are they?

Chapter 7: Environmental factors affecting seedling establishment
- Which environmental factors affect seedling establishment?

Chapter 6: Effects of perennial shrubs & herbivore exclusion on seedling establishment
- Do perennial shrubs alter microhabitat conditions or protect seedlings from browsing herbivores?

Chapter 9: Effects of herbivore exclusion on post-fire seedling recruitment
- How do herbivores affect seedling establishment following fire in *A. huegeliana* woodland?

Chapter 8: Effects of individual mammal herbivore species on seedling establishment
- Which herbivores browse on *A. huegeliana* seedlings?
- What is the extent of their effect on seedling establishment?

Chapter 10: General discussion
- Summary of chapters
- Synthesis of issues
- Implications for management

4.1 Introduction

Chapter 2 demonstrated that the extent of *A. huegeliana* encroachment varied among the patches of kwongan studied. The abundance of mammal herbivores was suggested as a factor potentially affecting *A. huegeliana* encroachment. Chapter 3 indicated that the mammal herbivore communities are currently different among the reserves, but did not investigate possible differences in the abundance of mammals at each reserve.

Mammal abundances can be measured either as a population size, an absolute density or as a density index, i.e. some measurable correlate of absolute density (Caughley 1977). Provided an appropriate index is used, relative indices of density can be just as effective as measurements of absolute density in monitoring abundance and are often far cheaper and easier to obtain (Southwell 1989). A commonly used index based on indirect counts is faecal pellet (or scat) accumulation. This method requires the measurement of scat accumulation per unit area over a defined time. Initially, permanent plots need to be marked and cleared of scats. The number of scats deposited over a defined time by the species of interest is then counted at regular intervals. These data can then be used directly as a measure of relative abundance or, if the defecation rate of a mammal is known, the scat abundance index can be converted to an estimate of absolute density (Southwell 1989).

Faecal scat counts have been used to study trends in the abundance of a wide range of vertebrate species including deer (e.g. Neff 1968; Bailey & Putman 1981; Freddy & Bowden 1983), elk (e.g. Edge & Marcum 1989; Ripple 2001), and rabbits (e.g. Taylor & Williams 1956; Wood 1988). Faecal scat counts have also been used in studies of macropods in Australia including the red kangaroo (*Macropus rufus*), eastern grey kangaroo (*Macropus giganteus*), western grey kangaroo (*Macropus fuliginosus*), wallaroo/euro (*Macropus robustus*), red-necked wallaby (*Macropus rufogriseus*) and swamp/black wallaby (*Wallabia bicolour*) (e.g. Caughley 1964; Floyd 1980; Hill 1981; Andrew & Lange 1986; Johnson & Jarman 1987; Arnold *et al.* 1994; Meers & Adams 2003).

Macropod scat counts of have been used to assess patterns of habitat utilisation (e.g. Caughley 1964; Hill 1982; Arnold *et al.* 1995), and to estimate absolute density using a known defecation rate (e.g. Coulson & Raines 1985; Perry & Braysher 1986; Johnson & Jarman 1987). However, knowledge of the defecation rates of macropods is currently very poor. Most information comes from captive animals (either in laboratory cages or in small enclosures), and only two studies have been conducted on wild macropods (Southwell 1989). Without accurate knowledge of defecation rates the general use of the scat accumulation method as a monitoring technique of macropods is limited. This method is effective, however, for specific problems in small areas, for example monitoring the abundance of small localized populations of macropods (Southwell 1989).

Scat abundance indicates the presence of an animal rather than the particular activity it is performing such as resting, browsing, or moving between areas. However, Caughley (1964), Hill (1978), and Johnson *et al.* (1987) found that defecation by macropods was strongly associated with feeding. Consequently, several studies have been used scat counts as an indicator of browsing/grazing pressure. Andrew and Lange (1986) used this method to show that kangaroos prefer to graze in different areas that sheep. Hill (1982) used scat counts to determine the seasonal movements of kangaroos associated with grazing. Floyd (1980) also used this method to determine the browsing habits of the swamp wallaby in Eucalypt plantations of different ages. Scat counts of macropods in this study should therefore be reasonable indicator of browsing activity in kwongan.

There are several errors associated with the scat accumulation method, including incorrectly identified scats, missing scats, scat decay, and variation in faecal output among seasons and years (Johnson & Jarman 1987; Arnold & Maller 1987; Southwell 1989; Bulinski & McArthur 2000). However, many of these errors may be overcome if the ability of workers to accurately identify scats is tested, search effort in plots with taller or denser vegetation is more thorough, studies of scat decay are carried out and incorporated into abundance calculations, and studies are conducted over longer periods of time.

Studies that have been carried out where several macropod species inhabit the same geographic region have required workers to identify between scats of the different species. Shepherd *et al.* (1997) stated that faecal scats for the western grey kangaroo, western brush wallaby (*Macropus irma*), tammar wallaby (*Macropus eugenii*), were distinctive in shape and size and could be easily separated. Wann and Bell (1987) had little difficulty discriminating between faecal scats of western brush wallabies and western grey kangaroos, also according to their shape and size. These studies were able to differentiate between scats of the species present in the reserves in this study (Section 2.2.2); therefore, the scat accumulation method should be suitable to assess the relative abundance of these mammal herbivores.

This chapter aims to determine: (1) which mammal herbivore species are currently present in patches of kwongan at Durokoppin, Dongolocking and Tutanning Nature Reserves in the Western Australian wheatbelt; and (2) identify differences in the relative abundance of each species among patches of kwongan within these reserves using the scat accumulation method. A greater understanding of the abundances of the herbivores present in kwongan at these reserves may provide some indication of the potential differences in browsing pressure that these remnants of vegetation experience.

4.2 Methods and materials

4.2.1 Study sites

The abundance of mammal herbivores was investigated at eight patches of kwongan, including four at Tutanning (1, 4, 5 and 7), two at Dongolocking (1, 2) and two at Durokoppin (1, 2) (see Section 2.2.2).

4.2.2 Scat identification

Western grey kangaroo (*Macropus fuliginosus)*, tammar wallaby (*Macropus eugenii*), brush wallaby (*Macropus irma*) and rabbit (*Oryctolagus cuniculus*) scats were identified using descriptions and photographs in Wann and Bell (1997) and Triggs (2004). Kangaroo and euro scats could not be differentiated; however, surveys have shown a significant difference in distribution of the two species around Durokoppin (the only reserve where euros are located) (Arnold *et al.* 1994). Western grey kangaroos favoured short heathland whilst the euro showed a strong preference for dense tall shrubland (primarily *Allocasuarina* sp.) and in areas of *Eucalyptus loxophleba*, *Acacia acuminata* woodland with rock outcrops (Arnold *et al.* 1994).

To ensure that the species belonging to each type of scat was identified consistently, all scats found during the first four periods were collected and stored in the laboratory. The scats collected at the different reserves and patches were visually compared and checked regularly throughout the duration of the study, and the scats of the different herbivore species were easily identifiable.

Scats can decay through attacks of insects, such as scarabaeid dung-beetles and flies, and tend to disappear quickly during warm, wet conditions (Johnson & Jarman 1987). Scat decay was assessed in June (winter), September (spring) and January (summer). Scats from the herbivores present at each reserve were collected, and for each species 10 scats were placed under a shrub and 10 in an open area with no vegetation cover. Decay was subsequently observed by visually inspection between collection periods. Little decay was detected within the 4–6 week periods and all scats remained visible. Scat decay was not considered to be a problem in the reserves studied; therefore, the results did not require adjustment.

4.2.3 Size and shape of plots

Two basic sampling shapes have been used in macropod scat accumulation surveys; circular plots and belt transects (see review by Southwell 1989). Circular plots have the advantages over transects of having a lower perimeter to area ratio, thus reducing the chance of incorrectly judging a scat or scat-group as in or out of the sampling unit, and are easier to set up and count. Belt transects have the advantage of increasing the dispersion of effort and hence improving sampling efficiency. Line-plot designs, where circular plots are systematically spaced along transects, effectively combine the advantages of both methods (Southwell 1989). Most studies of rabbit densities using the scat accumulation method have used belt or line-plot designs (Taylor & Williams 1956; Wood 1988; Moreno & Villafuerte 1995; Fa *et al.* 1999). Transects used in these studies were not located towards ‘latrine sites’ or ‘dung hills’; they were systematically or randomly located across the study area. Because the line-plot design has been successfully used in both macropod and rabbit studies this method was considered to be an appropriate design for this study.

At each patch, three parallel transects were located from the patch boundary into the kwongan. The patch boundary was defined by bordering *A. huegeliana* woodland or other vegetation community. At sites where there was no clear boundary and *A. huegeliana* plants were scattered throughout the patch transects were located at a selected point, e.g. a track or road. The three transects were evenly spaced across the patch and were 150 m in length. From the beginning of each transect, 8 m^2 circular plots were located at 10m intervals along each transect (15 plots × 8 m^2 = 120 m^2/transect) and cleared of scats at the end of August 2005. Areas of the basic estimation unit for line-plot designs have ranged from 3 to 250 m^2, with the most common size around 50 m^2 (Southwell 1989).

4.2.4 Scat counting (groups versus individuals)

Scat groups or individual scats may be counted in a scat accumulation survey. Several studies have addressed the question of scats versus scat groups for macropod surveys. The general consensus is for counting scats rather than scat-groups (e.g. Hill 1978; Perry & Braysher 1986; Arnold & Maller 1987) largely due to the difficulty of defining scat-groups. However, there are disadvantages to counting individual scats because they are likely to decay more quickly, to be obliterated if stepped on while fresh and soft and are more easily missed by a surveyor. The assumption that all scat groups are independent should also cause less distortion than the assumption that all individual scats are independent (Johnson & Jarman 1987).

All individual scats deposited in the plots after clearing in August 2005 were collected at intervals of 4−6 weeks, from September 2005 to March 2007, identified and counted. More time was spent searching for scats where vegetation height and cover was greater, because the number of scats found in a plot may be partially related to the vegetation characteristics, and the probability of 'missing' scats is often related to vegetation height and cover (Bulinski & McArthur 2000).

4.2.5 Abundance of mammal herbivore scats

The total number of scats deposited by each herbivore species within all of the 8 m^2 plots located on each transect was pooled for the duration of the study. The number of scats deposited by each species per hectare, per day for the duration of the study (scats ha^{-1} day^{-1}) was then calculated for each transect (total area 120 m^2) and averaged across the three transects at each site. Differences in the abundance of scats of each mammal herbivore among the reserves and patches were examined using ANOVA. The reserves (Durokoppin, Dongolocking and Tutanning) were treated as a fixed factor and the patches as a random factor nested within reserve. Since tammar scats were only found at Tutanning, reserve was not included as a factor and patch was treated as a random factor for the tammar scat ANOVA. Post hoc comparisons of reserve means were made using Tukey HSD tests (Quinn & Keough 2002). Assumptions of homogeneity of variance and normality were checked with residual plots and box-plots. The data were cube root transformed. All analyses were undertaken using SPSS 15.0 (SPSS 2006).

4.3 Results

4.3.1 Mammal herbivores identified

Western grey kangaroos, brush wallabies and rabbits were present at all three reserves, and tammars were present only at Tutanning. Kangaroo scats were the most abundant and large numbers of scats were recorded at all reserves (Figure 4.1). The number of scats deposited by kangaroos, brush wallabies and rabbit was not affected by the reserves, but was affected by the patches within the reserves (Table 4.1).

4.3.2 Abundance of mammal herbivore scats

Kangaroo scats were more abundant within patches 5 and 7 at Tutanning than all other patches (Figure 4.1). Brush wallaby scats were particularly abundant at Dongolocking 2, but were only recorded in small numbers at Dongolocking 1 and patches at the other reserves (Figure 4.1). Rabbit scats were most abundant at Dongolocking 2 and also relatively abundant at Durokoppin 1 and 2. However, rabbits scats were practically absent from the kwongan patches at Tutanning and Dongolocking 1 (Figure 4.1). Tammar wallaby scats occurred in similar densities in the four patches at Tutanning (Table 4.1; Figure 4.1).

Table 4.1: Results from the ANOVA investigating the effects of the reserves and patches on the abundance of mammal herbivore scats among eight patches of kwongan at three Nature Reserves. For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	**Kangaroo/euro**				**Brush wallaby**			**Rabbit**			**Tammar**			
	d.f.	Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*	d.f.	Mean Square	*F*	*P*
Reserve	2	2.12	4.53	0.075	3.90	2.64	0.165	8.58	3.68	0.104				
Patch (Reserve)	5	0.47	7.18	0.001**	1.48	5.33	0.005**	2.33	18.13	0.001**	3	0.02	0.19	0.901
Error	16	0.07			0.28			0.13			8	0.12		

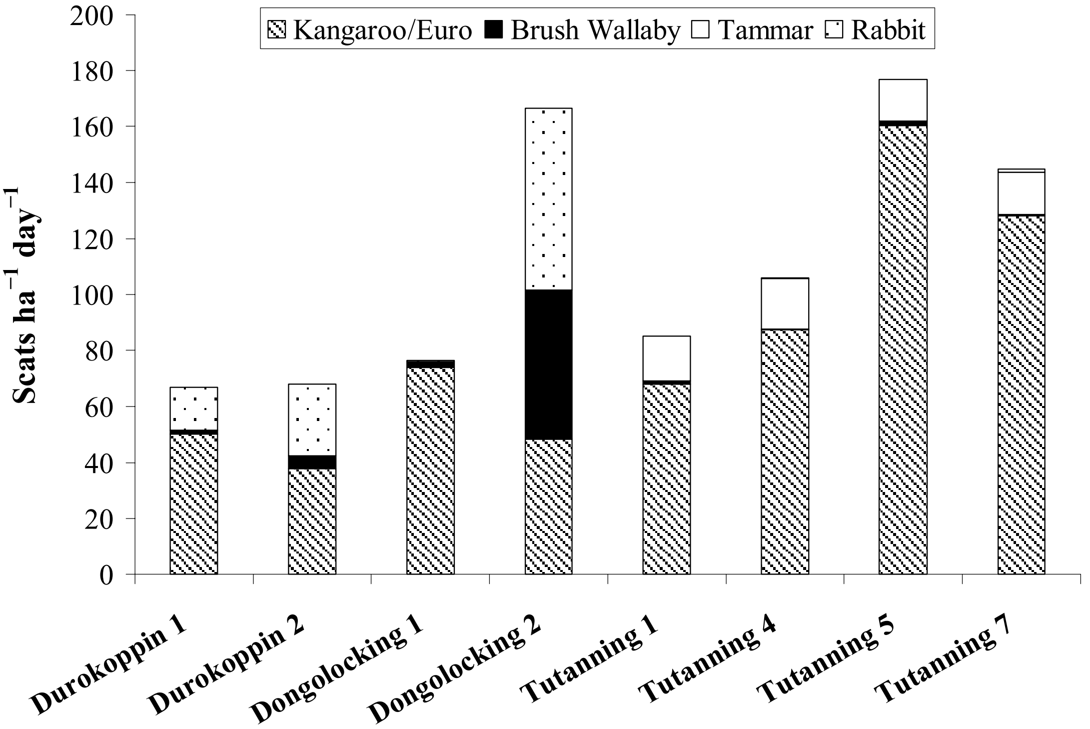


Figure 4.1: Mean number of scats deposited by each mammal herbivore species, per hectare, per day, in eight patches of kwongan at three Nature Reserves.

4.4 Discussion

Western grey kangaroo and western brush wallaby scats were found in kwongan at all three reserves and tammar wallaby scats were found only at Tutanning. The collection of brush wallaby scats at Durokoppin is particularly significant because individual brush wallabies were only sighted about once a year from 1986–92 (Arnold *et al.* 1994) and the persistence of this species was uncertain.

Scat accumulation provides an index of the relative abundance of mammals among patches of kwongan. Macropods have been found to deposit most scats while they are actively feeding (Caughley 1964; Hill 1978; Johnson *et al.* 1987); therefore, most scats found in kwongan are likely to have been deposited when the animals were feeding or moving around. Consequently, differences in scat accumulation among the reserves and patches within the reserves indicate corresponding differences in browsing pressure among these areas to some degree.

The abundance of kangaroos was reasonably similar among the reserves and most kwongan patches. These results suggest that kangaroo populations may be as abundant in similar sized or larger remnants of vegetation in the wheatbelt. However, kangaroos may be scarcer in smaller remnants. Their populations may vary according to the vegetation types within the remnants, the degree of isolation from human disturbance and the distance to nearby remnants (Arnold *et al.* 1995). Kangaroos at Durokoppin and Tutanning obtain nearly all their resources from native vegetation (Arnold & Steven 1988; Arnold *et al.* 1994). The grazing and browsing pressure imposed by kangaroos is therefore likely to be similar among the reserves.

Kangaroos were particularly abundant at two patches of kwongan within Tutanning (5 and 7), which are located in the western part of the reserve. Arnold and Steven (1988) considered that the western part of Tutanning has a higher proportion of vegetation that provided food for kangaroos, including short kwongan and woodland with *Eucalyptus wandoo* and *E. accedens*. Kangaroos were less abundant at patches 1 and 4 at Tutanning. Field observations indicate that the kwongan Tutanning 1 was the tallest of the four patches studied at this reserve. Tall kwongan is considered to provide little or no feed for kangaroos (Arnold & Steven 1988). The vegetation at the other three Tutanning patches (4, 5 and 7) was much shorter, but the abundance of scats was also low at Tutanning 4. The variation in kangaroo abundance among the patches may reflect the overall suitability of the surrounding vegetation mosaics to provide both food and shelter for kangaroos, rather than just the availability of food (Arnold & Steven 1988).

The abundance of brush wallabies, tammar wallabies and rabbits varied substantially among the patches of kwongan at the three reserves. Therefore, the occurrence of these herbivores at other reserves is likely to be more idiosyncratic than kangaroos. The numbers of native mammal species in a remnant and their population sizes is affected by the size of the reserve (Kitchener *et al.* 1980), whether fox baiting is carried out (Kinnear *et al.* 2002), and the incidence of *Gastrolobium* plants which are highly toxic to exotic species, but not to native animals (Short *et al.* 2005).

Brush wallabies were abundant at Dongolocking 2, but were relatively scarce at Dongolocking 1 and the other patches at Durokoppin and Tutanning. Unlike the patches of kwongan within the other reserves, the two patches at Dongolocking were separated by about 8 km of farmland and brush wallabies may not have been able to move between the two areas. Dongolocking 2 is about twice the size of Dongolocking 1 and the vegetation communities within the remnants varied to some extent (Beecham *et al.* 1998). Such differences may affect the ability of these remnants to provide food and shelter for brush wallabies and thus affect the abundance of this species within the remnants. It is interesting to note that the brush wallabies appear to remain scarce at Tutanning, while tammars densities have increased dramatically following fox baiting at this reserve (Chapter 3).

Tammar wallabies were only present at Tutanning and their abundance did not vary a great deal among the patches of kwongan within the reserve. Tammars are therefore likely to exert similar levels of browsing pressure on the vegetation in these patches. The similarity in tammar abundance is interesting considering that there were a number of characteristics that varied among the patches, such as vegetation height, dominant plant species (Brown & Hopkins 1983) and the amount of surrounding *A. huegeliana* woodland (Chapter 2), which may provide shelter. Such differences apparently did not affect the tammar populations among the patches at Tutanning.

Rabbits were scarce at Dongolocking 1 and all patches of kwongan at Tutanning, but were much more abundant at Dongolocking 2 and both patches at Durokoppin. The soil type at both Dongolocking patches was deep grey sand. This factor is therefore is unlikely to be responsible for the variation in rabbit abundance among the patches at this reserve. Variation in rabbit abundances among the reserves and the patches within Dongolocking (which are separated by farmland) may be due to the effectiveness of past outbreaks of the myxoma virus (King & Wheeler 1985) and rabbit haemorrhagic disease (Pech & Hood 1998), or the use of other control methods such as poisoning, refuge removal, ripping, fencing and shooting in surrounding areas of farmland.

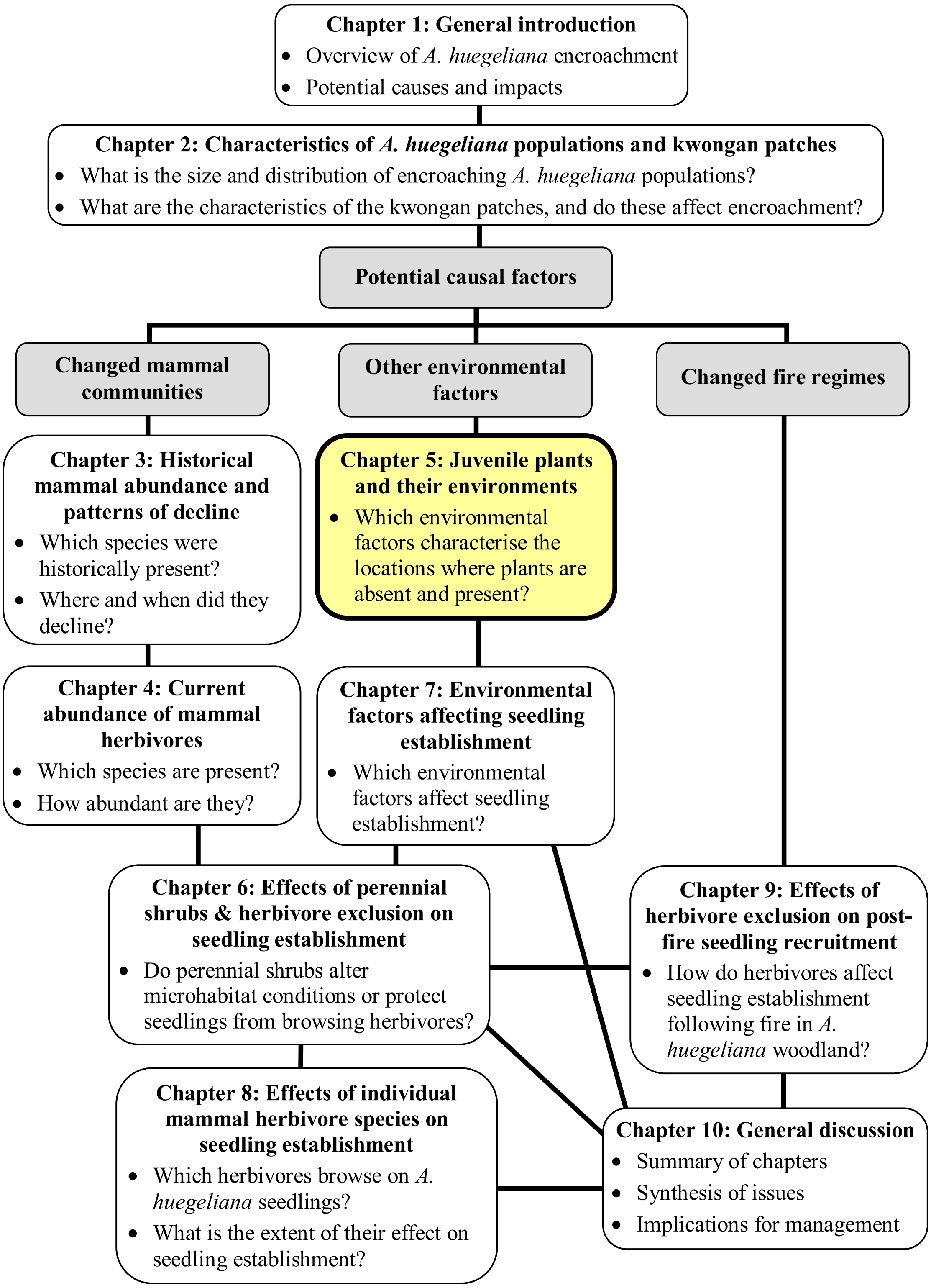
The total number of herbivore scats and the proportion of the scats contributed by each species varied considerably among the reserves and individual patches of kwongan. Browsing pressure may therefore vary among the reserves and patches of kwongan. However, the mammal herbivores vary substantially in size and consequently consume different amounts of vegetation. The impact of browsing by each herbivore species on kwongan and on *A. huegeliana* seedlings establishing within kwongan will also depend on their dietary preferences.

Western grey kangaroos consume a broad range of plant species. Their diets have been found to range from predominantly grasses (Wann & Bell 1997), to equal proportions of grasses and shrubs (Halford *et al.* 1984), to mainly shrubs (Shepherd *et al.* 1997). The western brush wallaby has a similarly variable diet, from a mixture of grasses, other monocotyledons and shrubs (Wann & Bell 1997), to largely shrubs (Shepherd *et al.* 1997). The diets of tammar wallabies also vary from mostly grasses (Christensen 1980b; Bell *et al.* 1987), to primarily shrubs (Shepherd *et al.* 1997). Shepherd *et al.* (1997) suggested that variations in diet most likely reflect a difference in the predominance of the available food source. All of the mammal herbivores found at the reserves studied may potentially browse on *A. huegeliana* seedlings. However, their impact on seedling establishment can only be determined experimentally and this is investigated in Chapters 6 and 8.

This chapter has shown that the western grey kangaroo and western brush wallaby are present at Tutanning, Durokoppin and Dongolocking Nature Reserves, but the tammar wallaby is only present at Tutanning. The abundance of kangaroos was similar among the reserves; therefore the browsing pressure exerted by this herbivore is likely to be similar among these areas. It also appears likely that this herbivore would be as abundant at other similar sized reserves. Brush wallabies remain reasonably scarce in most areas, but have become abundant in kwongan at one remnant at Dongolocking. The abundance of tammar wallabies was similar among the patches of kwongan at Tutanning. Rabbits were practically absent from Tutanning but were more abundant at Durokoppin and Dongolocking. The differences in mammal abundances among the reserves and patches of kwongan of indicate that browsing pressure is also likely to vary and may affect *A. huegeliana* establishment. The effects of browsing by mammal herbivores on *A. huegeliana* seedling establishment are investigated in subsequent chapters.

Chapter 5

Juvenile *Allocasuarina huegeliana* plants and their environments



Chapter 1: General introduction
- Overview of *A. huegeliana* encroachment
- Potential causes and impacts

Chapter 2: Characteristics of *A. huegeliana* populations and kwongan patches
- What is the size and distribution of encroaching *A. huegeliana* populations?
- What are the characteristics of the kwongan patches, and do these affect encroachment?

Potential causal factors

Changed mammal communities

Other environmental factors

Changed fire regimes

Chapter 3: Historical mammal abundance and patterns of decline
- Which species were historically present?
- Where and when did they decline?

Chapter 5: Juvenile plants and their environments
- Which environmental factors characterise the locations where plants are absent and present?

Chapter 4: Current abundance of mammal herbivores
- Which species are present?
- How abundant are they?

Chapter 7: Environmental factors affecting seedling establishment
- Which environmental factors affect seedling establishment?

Chapter 6: Effects of perennial shrubs & herbivore exclusion on seedling establishment
- Do perennial shrubs alter microhabitat conditions or protect seedlings from browsing herbivores?

Chapter 9: Effects of herbivore exclusion on post-fire seedling recruitment
- How do herbivores affect seedling establishment following fire in *A. huegeliana* woodland?

Chapter 8: Effects of individual mammal herbivore species on seedling establishment
- Which herbivores browse on *A. huegeliana* seedlings?
- What is the extent of their effect on seedling establishment?

Chapter 10: General discussion
- Summary of chapters
- Synthesis of issues
- Implications for management

5.1 Introduction

Chapter 2 demonstrated that *A. huegeliana* has encroached into patches of kwongan in Nature Reserves in the central and southern wheatbelt. *A. huegeliana* has dispersed widely throughout these patches and recruitment appears likely to continue in most patches. The extent of encroachment varied among the patches, and some of this variation could be attributed to propagule pressure. However, a range of environmental factors affect plant establishment and these factors will affect *A. huegeliana* plants encroaching into kwongan.

For a plant to establish, viable seed must be dispersed and persist until conditions suitable for germination occur, and the young plant must then grow and survive. A range of environmental factors affect plant establishment including soil conditions, temperature, rainfall, and interactions such as competition and herbivory (Harper 1977). Interactions with other plants may be particularly important for establishing *A. huegeliana* plants because they have to compete with existing flora that is well adapted to the site conditions.

Neighbouring plants compete for limited resources and interfere with each other's activities according to their age, size and distance apart (Harper 1977). Shrubs can impede seedling establishment through litter accumulation, reducing light and soil water, or by excreting allelopathic substances (Callaway & Walker 1997; Holmgren *et al.* 1997). However, shrubs can enhance seedling establishment by protecting them from browsing herbivores, or by improving microhabitat conditions through reducing thermal or water stress, and increasing soil nutrients and organic matter (Hunter & Aarssen 1988; Callaway 1995; Stachowicz 2001; Bruno *et al.* 2003). Shrubs that facilitate the growth or survival of other plants that establish within them are known as ‘nurse plants’ (Callaway 1995).

Seedlings of many *Casuarina* and *Allocasuarina* species appear to be tolerant of competition with established vegetation (*Allocasuarina* was previously included in the *Casuarina* genus, but was separated in the 1980s: all genus and species names in this thesis have been updated to their current status). Ladd (1989) suggested that most *Casuarina/Allocasuarina* species are able to regenerate under an overstorey canopy. He also found that the growth of *Casuarina cunninghamiana* seedlings, a riparian species on the eastern coast of Australia, was affected by only very high levels of shading (95%). Withers (1978) found that *A. littoralis* and *A. verticillata* seedlings were able to establish in dense grass swards and under dense canopy cover at Ocean Grove, Victoria. Withers (1979) showed that 30% shading actually increased the height growth of *A. verticillata* and *A. littoralis* seedlings; however, intense shading (92%) caused etoliation and decreased growth. The author concluded that *Allocasuarina* seedlings were able to survive in dense grass swards because their foliage had achieved a balance between shade tolerance and drought resistance.

The ability of *A. huegeliana* to regenerate sporadically in grassy swards in the wheatbelt has been attributed its high drought resistance (Ladd 1989). However, a lack of rainfall can have a significant effect on *Casuarina/Allocasuarina* seedling survival. Yates *et al.* (2003) suggested that lower rates of seedling recruitment including *A. huegeliana* after a fire in granite outcrop vegetation in the wheatbelt were a consequence of irregular rain and protracted drought during the rainy season resulting in poor germination and survival. *A. huegeliana* seedlings establishing under the canopy of a fallen tree at a site in the wheatbelt were found to have only a 3% survival rate, which was attributed to a long dry summer (Ladd 1989). Low levels of rainfall has also been attributed to the lack of regeneration success of *A. fraseriana* seedlings in jarrah forest in Western Australia (Abbott 1984) and *C. pauper* seedlings in the semi-arid region of western New South Wales (Auld 1995).

Casuarina/Allocasuarina seedlings appear to be palatable to a range of native and introduced herbivores. Seedling regeneration of *C. pauper* has been found to be strongly limited by rabbits, stock and goats in the arid and semi-arid regions of southeastern Australia (Chesterfield and Parsons 1985; Auld 1995). Main (1993) commented that it was common to see sheoak seedlings cropped and frequently killed by herbivores at a reserve in the Western Australian wheatbelt. Workers on revegetation projects in the wheatbelt region have also observed that planted *Casuarina* and *Allocasuarina* seedlings are often preferentially browsed over other seedlings by kangaroos. Faecal studies of western grey kangaroos have shown that these herbivores consume *Casuarina/Allocasuarina* species (Halford *et al.* 1984).

If *A. huegeliana* is palatable to herbivores present at the reserves studied, kwongan shrubs may act as ‘nurse plants’ by protecting seedlings from browsing. The strong drought and shade tolerance of many *Casuarina* and *Allocasuarina* species indicates that seedlings of *A. huegeliana* may be able to successfully establish in kwongan vegetation while avoiding browsing herbivores. However, the ability of seedlings to survive may also depend on other factors such as litter, annual plants and soil conditions.

Many *Casuarina* and *Allocasuarina* species appear to be tolerant of competition; however, field experiments have shown that annual plants significantly reduced the survival of seedlings of the shrub *A. campestris* in the Western Australian wheatbelt (Hobbs & Atkins 1991). Plant litter may also affect germination and establishment; however few studies have been conducted into such effects on *Casuarina* or *Allocasuarina* seedlings. Ladd (1989) suggested that a thin layer of litter would provide protection for seedlings, while a thicker layer would intercept much precipitation, leaving them in a dry micro-environment, and may have allelopathic effects. *A. huegeliana* seedlings in kwongan may be less likely to survive in areas where levels of annual cover or plant litter are high.

Substrate quality has been found to affect recruitment of some *Casuarina* and *Allocasuarina* species. In a glasshouse experiment, Woolfrey and Ladd (2001) confirmed field observations that seedlings of *C. cunninghamiana* grew better on a cobble substrate than on sand. Ladd (1989) suggested that where site quality is poor, such as where soils are shallow over rock, *Casuarina/Allocasuarina* seedling recruitment may become sporadic after a carrying capacity is reached. Kwongan occurs on a range of soil types, including lateritic duricrust, gravels, deep yellow sands and grey sands, sandy loams, gravel/clay duplex soils and clay (Brown & Hopkins (1983). Although *A. huegeliana* has also been recorded from a wide range of soil types (Doran & Hall 1981), soil conditions in some types of kwongan may affect its ability to survive in these areas.

This chapter aims to determine which environmental factors best predict where *A. huegeliana* plants have successfully established and where they have not. The characteristics of the environments that surround *A. huegeliana* plants and the environments where plants are absent should identify the factors that favour or inhibit *A. huegeliana* encroachment into kwongan.

5.2 Methods and materials

5.2.1 Study sites

The environments associated with juvenile *A. huegeliana* plants (individuals < 1.5m in height and < 20mm in stem diameter) were investigated at eight patches of kwongan, including four at Tutanning (1, 4, 5 and 7), two at Dongolocking (1 and 2) and two at Durokoppin (1 and 2) (see Section 2.2.2).

5.2.2 Environmental characteristics

At each patch, three parallel transects were located from the patch boundary into the kwongan. The patch boundary was defined by bordering *A. huegeliana* woodland or other vegetation community. At sites where there was no clear boundary and *A. huegeliana* plants were scattered throughout the patch transects were located at a selected point, e.g. a track or road. The three transects were evenly spaced across the patch and were 150 m in length.

From the beginning of each transect, paired 0.5 m × 0.5 m quadrats were located at 20 m intervals along each transect. *A. huegeliana* juveniles were absent from all quadrats located on all transects, therefore quadrats located on the transects were used to characterise environments in which *A. huegeliana* was absent. The paired quadrat was placed around a juvenile plant nearest to this point and these quadrats were used to characterise environments in which *A. huegeliana* was present. The total number of quadrats with *A. huegeliana* absent was 192 (8 patches × 3 transects × 8 quadrats) and for quadrats with *A. huegeliana* present was 189 (three juveniles could not be located along one transect at Durokoppin 2 within a reasonable distance of the paired quadrat located on the transect).

In October 2005, several environmental factors were assessed in each quadrat including visual estimates of perennial shrub cover (%), annual plant cover (%) and plant litter cover (%); and measurements of the dominant perennial plant height (m), distance to the base of the three nearest perennial plants (any species) (m) and distance to nearest fruit-bearing tree (m). The mean distance to neighbouring plants was then calculated. Very few of the nearest perennial plants were *A. huegeliana*; the vast majority were kwongan shrub species. A sample of the top 10cm of soil was also collected using an auger (diameter 5 cm), air dried and taken to the laboratory for analysis. The percentage of gravel and clay, and soil pH (measured in a 1:5 soil/water suspension) was measured for each soil sample in accordance with McDonald *et al.* (1990).

Univariate logistic regression was used to determine which environmental variables were significant in predicting presence/absence of juvenile *A. huegeliana* (Quinn & Keough 2002). The environmental variables were distance to parent tree, perennial, annual and litter cover, perennial plant height, distance to neighbouring plants, soil pH, and the gravel and clay content in the soil. Several variables had a significant relationship with juvenile presence/absence ($P \leq 0.15$); therefore, collinearity between these predictors was examined using Pearson's product moment correlation. If variables were highly correlated ($P < 0.05$, $r_s > 0.7$) the variable that had the strongest relationship with juvenile presence/absence was selected for subsequent use. Environmental factors interact to affect juvenile plants; therefore, multivariate logistic regression was used to determine which combination of variables best predicted juvenile presence/absence. This analysis was undertaken using the forward stepwise procedure and the Hosmer–Lemeshow goodness-of-fit statistic was calculated to assess the fit of the model (Quinn & Keough 2002). The Hosmer–Lemeshow statistic was not significant (HL = 7.79, d.f. = 8, $P = 0.454$), indicating no evidence for lack of fit of the model. All statistical analyses were undertaken using SPSS 15.0 (SPSS 2006).

5.3 Results

5.3.1 Effects of environmental factors on juvenile plant presence/absence

Several environmental variables had a significant relationship with juvenile presence/absence, including perennial cover, litter cover, distance to nearest neighbours and distance to parent tree (Table 5.1). None of these environmental predictors were highly inter-correlated (Table 5.2) and therefore all were included in the multivariate logistic regression model.

Results from the multivariate logistic regression model indicated that the combination of environmental factors that best predicted juvenile presence/absence was perennial shrubs cover, mean distance to three neighbouring plants and distance to nearest fruit-bearing tree (Table 5.3). This model accurately predicted 60.4% of present juveniles and 67.6% of absent juveniles, with an overall accuracy of predicting 63.9% juvenile presence/absence (−2 log likelihood = 488.43, d.f. = 3, $P < 0.05$).

The predicted probability of a juvenile *A. huegeliana* being present increased with a shorter distance to nearest parent tree, a shorter distance to neighbouring plants and increased perennial shrub cover (Figure 5.1 a–c). A juvenile *A. huegeliana* was more likely to occur (i.e. probability was greater than 50%) where the parent tree was less than 20 m away, perennial shrub cover was greater than 30% and neighbouring perennial plants were on average less than 20 cm from the juvenile plant.

Table 5.1: Results from univariate logistic regression analyses between the presence/absence of *Allocasuarina huegeliana* juveniles and the biotic and abiotic factors measured at each location. For significant relationships: $P < 0.01$**, $P < 0.05$*.

Variable	***B***	**SE**	**Wald statistic**	**d.f.**	***P***	***R***
Perennial shrub cover	0.033	0.008	15.635	1	0.001**	1.034
Annual cover	−0.005	0.039	0.014	1	0.905	0.995
Litter cover	0.013	0.006	4.800	1	0.028*	1.013
Perennial plant height	−0.184	0.151	1.493	1	0.222	0.832
Distance to neighbouring plants	−3.680	0.917	16.108	1	0.001**	0.025
Distance to parent tree	−0.016	0.006	7.44	1	0.006**	0.984
Gravel	0.004	0.009	0.212	1	0.645	1.004
Clay	0.008	0.026	0.106	1	0.745	1.008
pH	0.330	0.328	1.014	1	0.314	1.391

Table 5.2: Results from the Pearson correlation indicating significant inter-correlation between the predictive environmental variables. Variables were considered to be highly inter-correlated where $P < 0.05$ and $r \geq 0.70$*.

Environmental variables	**Perennial cover**	**Annual cover**	**Litter cover**	**Perennial height**	**Distance to neighbouring plants**	**Distance to parent tree**	**Gravel**	**Clay**	**pH**
Perennial cover	1								
Annual cover	−0.130*	1							
Litter cover	0.402*	−0.190*	1						
Perennial height	0.035	0.016	0.144*	1					
Distance to neighbouring plants	−0.242*	0.101*	0.01	0.249*	1				
Distance to parent tree	−0.045	−0.189*	0.022	−0.047	−0.057	1			
Gravel	0.084	0.049	0.044	−0.086	−0.076	−0.139*	1		
Clay	0.1	0.003	0.033	−0.06	−0.102*	−0.075	0.503*	1	
pH	0.086	0.141*	0.052	−0.059	−0.135*	−0.164*	0.255*	0.168*	1

Table 5.3: Results from the multiple logistic regression analysis between the presence/absence of *Allocasuarina huegeliana* juveniles and biotic and abiotic factors, including the factors significant to the model. For significant relationships: $P < 0.01$**, $P < 0.05$*.

Variable	***B***	**SE**	**Wald statistic**	**Degrees of freedom**	***P***	***R***
Perennial cover	0.027	0.009	9.682	1	0.002**	1.028
Distance to neighbouring plants	−3.264	0.943	11.976	1	0.001**	0.038
Distance to parent tree	−0.018	0.006	7.727	1	0.005**	0.982
Constant	0.154	0.385	0.159	1	0.690	1.166

B, Estimated regression coefficient; *R*, estimated odds ratio.

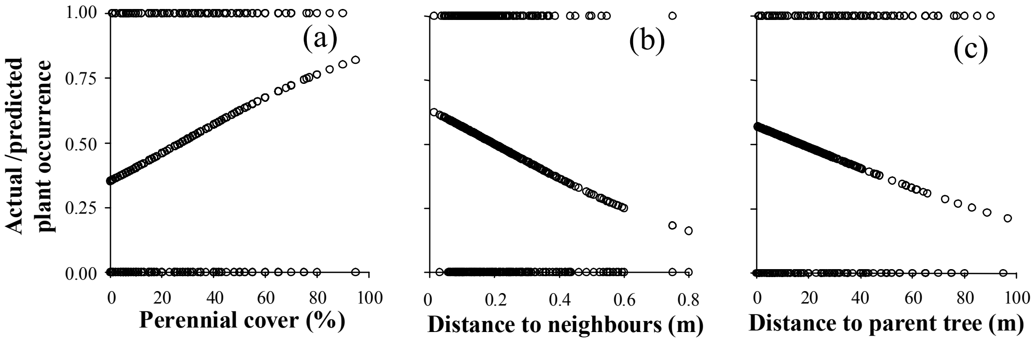


Figure 5.1: Scatter plots of the actual occurrence (y-axis: 0.00 = juvenile plant absent 1.00 = juvenile plant present) and predicted probability curves of *Allocasuarina huegeliana* juveniles in relation to: (a) perennial vegetation cover; (b) mean distance to three nearest perennial plants; and (c) distance to nearest fruit-bearing tree.

5.4 Discussion

The establishment of *A. huegeliana* plants within a patch of kwongan initially requires the presence of propagules. *A. huegeliana* has winged seeds that are wind dispersed and thus has a good dispersal capacity (Main 1993). The importance of dispersal in the establishment of *A. huegeliana* populations was indicated by the increased likelihood of a juvenile plant being present with a shorter distance to a fruit-bearing tree.

Wind dispersed propagules are generally dispersed close to the parent and seed density falls off steeply with distance (Howe & Wesley 1997). However the dispersal pattern from isolated plants differs strongly from that of plants in a closed stand. The densest seed rain from a stand of trees occurs at the margin, while the densest seed rain from isolated trees often occurs at a much greater distance from the source (Harper 1977). A similar pattern of dispersal was found in this study. The majority of juvenile *A. huegeliana* plants (93%) occurred within 45 m of a fruit-bearing tree; however, individuals were located up to 139 m from a fruit-bearing tree.

The presence or absence of a plant population and its density depends on the availability of a seed and on the frequency of 'safe sites' that provide the conditions required for seed germination and seedling establishment (Harper 1977). Perennial shrubs clearly provided 'safe sites' for *A. huegeliana* plants establishing in kwongan. This was indicated by the increased likelihood of a juvenile *A. huegeliana* being present at locations with higher levels of perennial shrub cover and shorter distance to neighbouring perennial plants. However, the occurrence of only 64% of juveniles could be accurately predicted. These results indicate that the occurrence of juveniles is probably affected by factors that affect plant survival at earlier stages and perhaps a degree of randomness.

Areas beyond shrub canopies were not heavily vegetated with annual plants. *A. huegeliana* seedlings that establish within shrubs would therefore be subjected to increased shade and competition from the surrounding vegetation. However, a number of *Casuarina* and *Allocasuarina* species have been found to be shade and drought tolerant and able to grow in established vegetation (Ladd 1989; Withers 1978, 1979). In this study, juveniles occurred in locations with up to 95% perennial cover. However, the perennial cover may have increased since the individual was a young seedling. Since more juvenile plants occurred within shrubs than in open areas, the benefits that perennial shrubs provide to the establishing *A. huegeliana* plants must outweigh the increased levels of inter-specific competition. *A. littoralis* seedlings have similarly been found to compete well with established vegetation due to their shade tolerance and drought resistance (Withers 1979).

The benefits that perennial shrubs provide to *A. huegeliana* plants may be protection from browsing herbivores, improved microhabitat conditions, or both. Shrubs in other ecosystems have been shown to improve microhabitat conditions for seedlings by increasing nutrient or soil water availability, and moderating air and soil temperatures by providing shade (Franco & Nobel 1989; Callaway *et al.* 1991; Caldwell *et al.* 1998; Carrillo-García *et al.* 2000; Shumway 2000). Shrubs have also been found to provide seedlings with protection from browsing animals (McAuliffe 1986; Callaway *et al.* 2000; Rebollo *et al.* 2002; Baraza *et al.* 2006).

Kwongan occurs on nutrient poor soils in a region that experiences a hot and dry climate during the summer months (Hopper *et al.* 1996). Herbivores such as kangaroos and rabbits are present at most reserves. Kwongan shrubs may improve microhabitat conditions for *A. huegeliana* plants by mitigating heat and drought stress during summer, increasing soil nutrients, or protect seedlings from browsing animals. However, this study was unable to differentiate between such processes. The benefits that perennial shrubs provide to seedlings are investigated in Chapter 6.

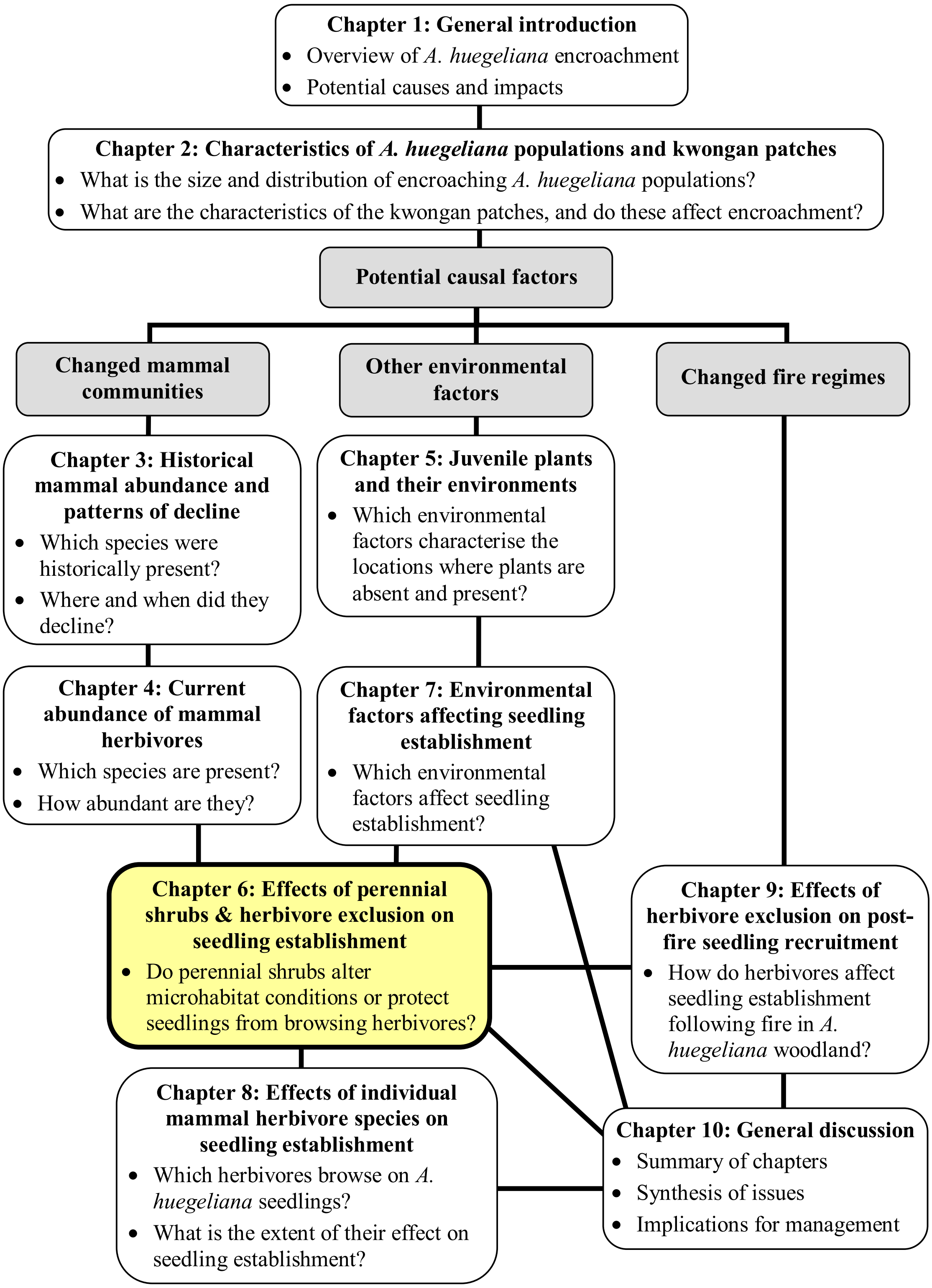
Other environmental factors, such as litter and annual plants, did not affect the occurrence of *A. huegeliana* juveniles. While these factors may not affect *A. huegeliana* establishment, the results may be due more to the size of the individual plants measured. The plants measured were < 1.5 m in height and < 20 mm in diameter and the largest of these plants were well established. The large plants had already passed through a range of 'environmental filters' and represented the surviving individuals. Litter, annual plants and other microhabitat conditions may affect *A. huegeliana* establishment, but at earlier germination and initial establishment stages of development. The effects of some of these environmental factors are investigated in Chapter 7.

Soil factors did not affect the occurrence of *A. huegeliana* juveniles, which indicates that *A. huegeliana* can readily establish on the same soil types as kwongan. These results provide further evidence that soil type does not exclusively determine *A. huegeliana* and kwongan community boundaries, as suggested in Chapter 2. Instead, the historical vegetation boundaries were probably maintained by interactions between soils and other factors such as disturbance regimes.

This chapter has demonstrated that *A. huegeliana* establishment primarily depends on a nearby seed source and is favoured by the presence of perennial shrubs. No other environmental factors measured in this study affected naturally occurring juveniles; however, these factors may affect emergence and establishing seedlings. It appears likely that few environmental factors will limit encroachment of *A. huegeliana* into kwongan, and if propagule pressure is high enough seedlings will establish. Subsequent chapters will investigate whether perennial vegetation provides establishing *A. huegeliana* seedlings with protection from browsing herbivores or improved microhabitats, and the environmental factors affecting emergence and younger seedlings.

Chapter 6

Effects of perennial shrubs and herbivore exclusion on seedling establishment during inter-fire intervals



6.1 Introduction

Chapter 5 demonstrated that the occurrence of *A. huegeliana* plants is favoured by perennial shrub cover. The benefits that the shrubs provided to *A. huegeliana* plants therefore appear to outweigh any increased levels of inter-specific competition. The benefits that perennial shrubs provide may be through protection from browsing herbivores, improved microhabitat conditions, or both.

Herbivores influence plants mainly through grazing or browsing (defoliation), trampling and excretion (Schulze *et al.* 2002). The impact of herbivory on plant performance depends on its timing, location, intensity and frequency (Crawley 1997). Although plants can tolerate defoliation to an extent, avoidance is a common mechanism by which plants cope with herbivory. Plants that protect other plants by physically impeding herbivores are known as biotic refuges (Milchunas & Noy-Meir 2002). Shrubs may provide protection from browsing, but they may also favourably or unfavourably alter the microhabitat conditions for seedlings establishing within them.

Shrubs can have a range of physical and chemical effects on their surrounding environments. For example, shrubs can moderate air and soil temperatures (Hunter & Aarssen 1988; Nolasco *et al.* 1997), create nutrient islands (Carrillo-García *et al.* 2000) and alter soil water availability (Caldwell *et al.* 1998; Wainwright *et al.* 1999; Shumway 2000). However, shrubs also can impede seedling establishment through increased competition for limited resources (Harper 1977). For a seedling to establish within a shrub the benefits that the shrub provides must therefore outweigh the potential increased levels of inter-specific competition.

This chapter examines the beneficial effect that perennial vegetation appears to have on *A. huegeliana* seedlings growing in long unburned (> 60 years) patches of kwongan. This chapter aims to determine: (1) the impact that mammal herbivores have on seedling establishment; (2) whether browsing activity varies among reserves with different herbivore communities; (3) whether perennial vegetation protects *A. huegeliana* seedlings from browsing herbivores; (4) whether perennial vegetation affects seedling establishment through improved microhabitat condition or increased competition; and (5) which of these facilitative processes are more important to the establishment of *A. huegeliana* seedlings.

If protection from herbivores was more important to the establishment of *A. huegeliana* seedlings than microhabitat favourability, excluding herbivores from seedlings in areas with no vegetation cover would result in a substantial increase in emergence, growth and survival. However, if microhabitat favourability was more important than protection from herbivores, seedling emergence, survival and growth would be higher within perennial shrubs than areas with no vegetation cover whether herbivores had access to seedlings or not.

6.2 Methods and materials

6.2.1 Study sites

The effects of perennial vegetation and excluding mammal herbivores on the emergence, growth and survival of *A. huegeliana* seedlings in unburned kwongan were investigated in three patches of kwongan, including one at each of Durokoppin (1), Dongolocking (1) and Tutanning (4) Nature Reserves (see Section 2.2.2). For the mammal herbivores present at the reserves and their abundance see Chapter 4 (Figure

4.1). Within each reserve, a patch of kwongan was chosen with a similar vegetation structure and time since fire in order to reduce the potential effect of site variations on seedling emergence, growth and survival. To gain an understanding of the effects of vegetation and herbivores at different stages of seedling development two experiments were carried out at each patch of kwongan. The first experiment involved planting *A. huegeliana* seeds (sown seed) and the second involved planting seedlings that had been grown at a nursery (green-stock).

6.2.2 Effects of herbivore exclusion and perennial shrubs on seedling emergence and survival (sown seed)

Eight areas within each patch were subjectively chosen, where a perennial shrub or several shrubs were present and covering an area of at least 1 m^2 and adjoined a bare area with no vegetation cover at least 2.5 m^2 in size (Figure 6.1). In the area of bare ground, an exclosure consisting of a 1 × 1 m pen covered in wire netting (30 mm diameter mesh) with a 30 cm mesh apron that continued along the ground, was erected to exclude mammal herbivores and to prevent rabbits from burrowing into the exclosure. An equivalent 1 × 1 m area was located in the same area with no vegetation cover, but was not fenced and allowed access to herbivores.

In each area with no vegetation cover, fenced area with no vegetation cover, and perennial shrubs, 100 *A. huegeliana* seeds were planted on a 50 × 50 cm grid in May 2005. The seed was collected from each reserve (20 infructescences from 10 trees at each reserve) in January 2005, air dried and stored in a paper bag until it was planted. Laboratory germination trials (10 Petri dishes with 20 seeds from each reserve placed on moistened Whatman's No. 1 filter paper) gave a mean germination rate of 67% at Durokoppin and Dongolocking and 77% at Tutanning.

Figure 6.1: Photographs of the three treatments (left to right): no vegetation cover, fenced area with no vegetation cover and perennial shrub cover. A grid of 100 *Allocasuarina huegeliana* seeds and 10 *A. huegeliana* seedlings were planted in each treatment.

Seedling emergence was recorded from June to July, and the fate of seedlings (dead/alive) was recorded at the end of winter (August), spring (November), summer (February) and autumn (May), until February 2007. Seedling emergence was adjusted for seed germinability (determined in the laboratory trial) by dividing the number of seedlings that emerged in each grid by the germinability of seed from that reserve. Seedling survival was calculated for each grid by dividing the number of seedlings that were alive at the end of each season by the total number of seedlings that emerged during June and July 2005. No further seedlings emerged after this time.

The effect of reserve (Durokoppin, Dongolocking and Tutanning), treatments (no vegetation cover, fenced area with no vegetation cover, and perennial shrubs) and their interaction on seedling emergence and survival at the end of the experiment were examined using ANOVA. Reserve and treatment were both treated as fixed factors. Post hoc comparisons of treatment and reserve means were made using

Tukey HSD tests (Quinn & Keough 2002). Percentage values were converted to proportions and arcsine square root transformed. These data met the assumptions of normality and homogeneity of variance, which were checked with residual plots, box-plots and using the Levene test. All analyses were undertaken using SPSS 15.0 (SPSS 2006). All results are given as mean ± standard error.

6.2.3 Effects of herbivore exclusion and perennial shrubs on survival, growth and browsing of planted seedlings (green-stock)

In each reserve, at five of the areas where seeds were planted on grids, 10 *A. huegeliana* seedlings were planted at least 20 cm apart within each area with no vegetation cover, fenced area with no vegetation cover, and perennial shrubs. The seedlings were grown at a *Phytophthora* accredited nursery (*Phytophthora* is a fungus that kills many native plant species) and planted in June 2005. The heights of seedlings were measured immediately after planting and the subsequent survival of seedlings, whether they had been browsed, and their heights were measured at the end of winter (August), spring (November), summer (February) and autumn (May), until February 2007. The height growth of each seedling over 21 months was calculated by deducting the height at planting from the height at the end of the study. Mean seedling growth, the percentage of seedlings that had survived, and the percentage that had been browsed by mammal herbivores was calculated for the 10 seedlings in each treatment at each location for each season.

The effect of reserve, treatments and their interaction on the growth, survival and browsing of planted seedlings (21 months old) were examined using the same method described for the analysis of seedling emergence and survival (sown seed).

Herbivores could not access seedlings in the no vegetation cover (fenced) treatment and no seedlings were browsed. These data were therefore excluded from the percentage of seedlings browsed ANOVA. These data met the assumptions of normality and homogeneity of variance, which were checked with residual plots, box-plots and using the Levene test. However a large number of seedlings died in the treatment with no vegetation cover and the sample sizes were uneven. Therefore, growth values were calculated for each seedling by deducting the height at planting from the last height recorded prior to the death of the seedling, except for seedlings that died in the first season after planting, and these values were used for the ANOVA. All results are given as mean ± standard error.

6.3 Results

6.3.1 Effects of herbivore exclusion and perennial shrubs on seedling emergence and survival (sown seed)

Seedling emergence was not affected by the exclusion of herbivores or by perennial vegetation, but differed among the reserves (Table 6.1). Mean seedling emergence was highest at Dongolocking (62% ± 2.34), followed by Tutanning (44% ± 2.63) and was lowest at Durokoppin (33% ± 2.82) (Figure 6.2).

There was a significant interaction between reserve and treatment on seedling survival (sown seeds) (Table 6.1). Only a small percentage of seedlings survived to the end of this study in all treatments at Durokoppin (4% ± 1.13) and Dongolocking (3% ± 0.90). Seedling survival was similarly low at Tutanning in areas with no vegetation cover (3% ± 1.63). However, survival was much higher in perennial shrubs (18% ± 5.97) and fenced areas with no vegetation cover (39% ± 5.97) at this reserve for these treatments (Figure 6.3), which accounts for the significant interaction. Seedling survival was also higher in perennial shrubs and fenced areas with no vegetation cover at Durokoppin and Dongolocking. However this effect was not significant due to the small number of seedlings that survived.

Seedling survival (sown seeds) declined rapidly following emergence at both Durokoppin and Dongolocking, and less than 30% of seedlings survived to the end of the first summer (2006) in all treatments (Figure 6.4 a–b). Although the decline in survival was more gradual at Tutanning than the other reserves, the greatest decline also occurred from emergence to the end of the first summer at this reserve (Figure 6.4 c).

Table 6.1: Results from the ANOVA investigating the effects of the reserves and treatments on *Allocasuarina huegeliana* seedling emergence and survival (sown seeds). For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	d.f.	**Emergence**			**Survival**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*
Reserve	2	1818.02	30.09	0.001**	1914.08	24.91	0.0018*
Treatment	2	156.90	2.60	0.082	1349.98	17.57	0.0018*
Reserve × Treatment	4	63.06	1.04	0.392	415.30	5.40	0.001*
Error	63	60.41			76.85		

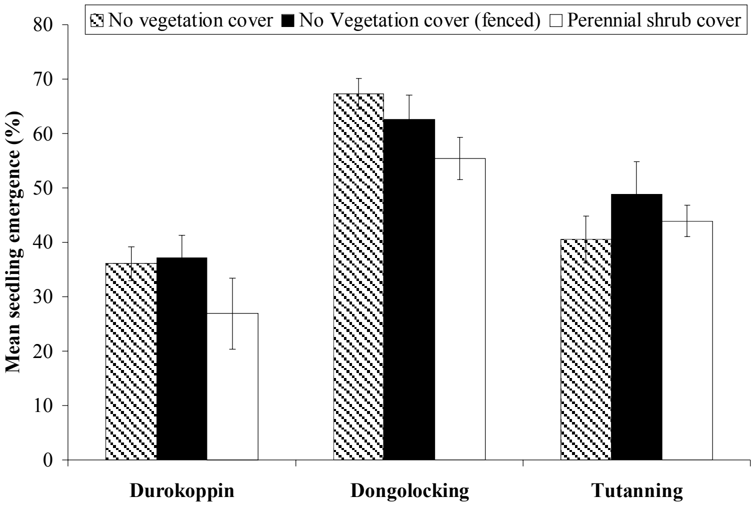


Figure 6.2: Mean percentage of *Allocasuarina huegeliana* seedlings emerged from seed sown in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at three Nature Reserves. Bars indicate standard errors.

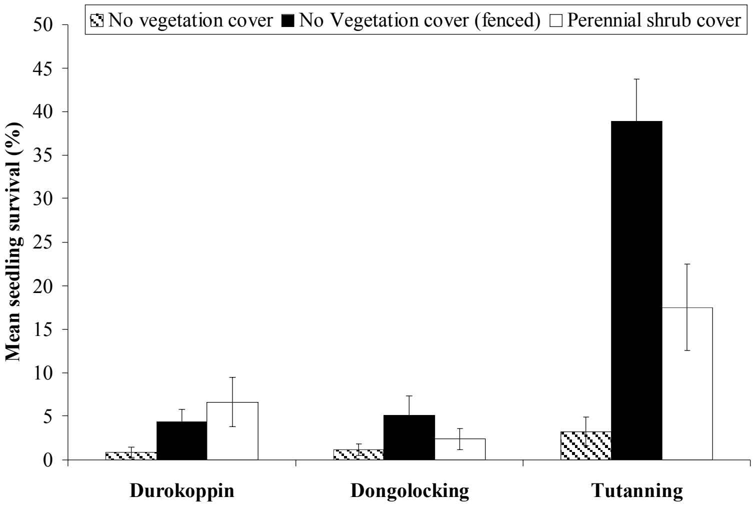


Figure 6.3: Mean survival of *Allocasuarina huegeliana* seedlings (sown seed) in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at three Nature Reserves. Bars indicate standard errors.

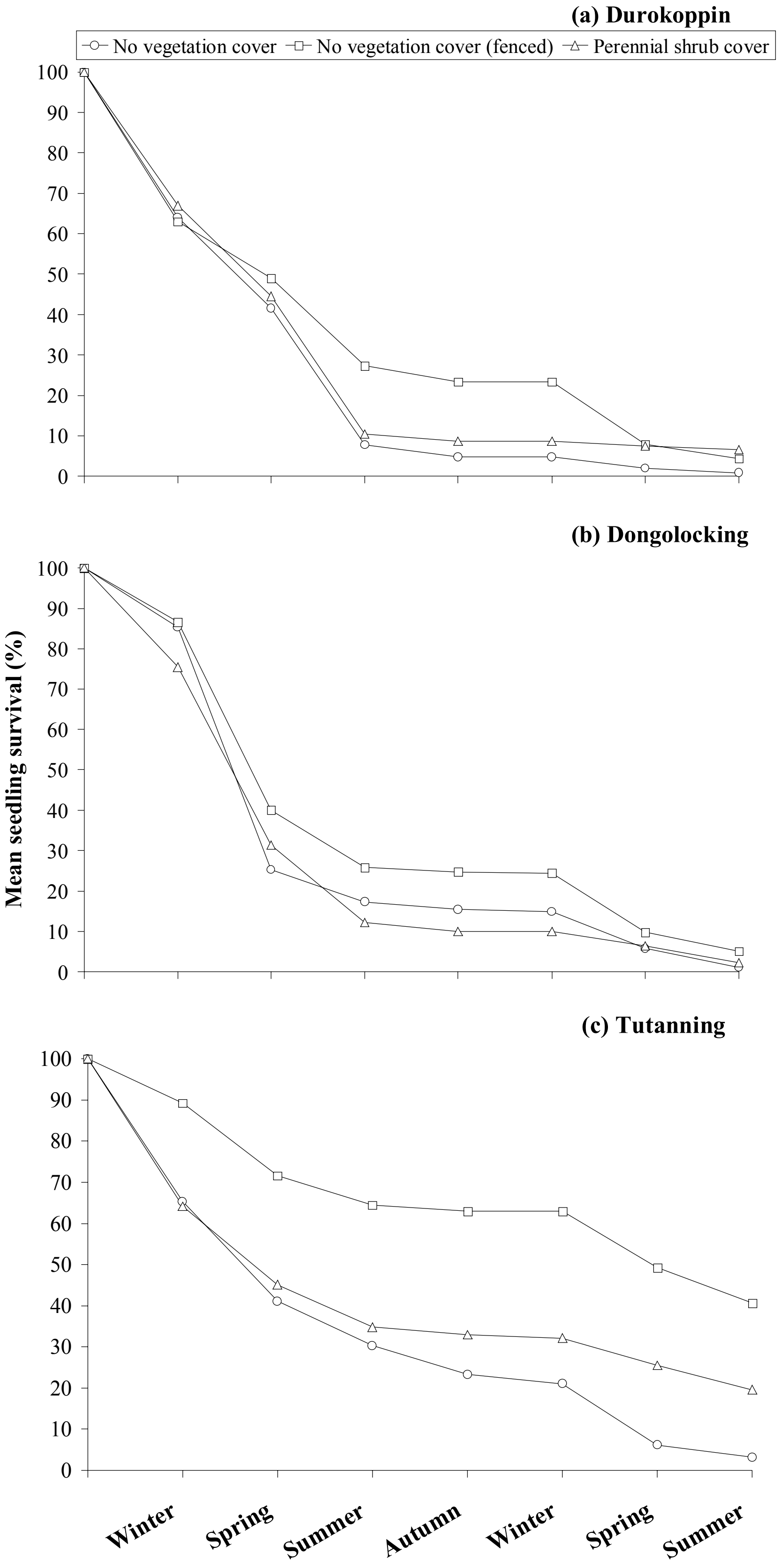


Figure 6.4: Mean *Allocasuarina huegeliana* seedling survival (sown seeds) from June–July 2005 and at the end of each season until March 2007, in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at (a) Durokoppin, (b) Dongolocking and (c) Tutanning Nature Reserves.

6.3.2 Effects of herbivore exclusion and perennial shrubs on survival, growth and browsing of planted seedlings (green-stock)

The exclusion of herbivores and the presence of perennial vegetation had a significant effect on the browsing, growth and survival of planted seedlings (green-stock) (Table 6.2). Mammal herbivores browsed most of the seedlings in areas with no vegetation cover soon after they were planted, and continued to browse extensively on these seedlings for the duration of the study (Figure 6.8 a–c). Perennial vegetation provided seedlings with protection from browsing herbivores and the percentage of seedlings browsed was much higher for seedlings in areas with no vegetation cover (76% ± 3.89) than for seedlings in perennial shrubs (10% ± 2.23) (Figure 6.5).

Mean seedling (green-stock) growth and survival was lowest in areas with no vegetation cover (growth −9.9 cm ± 0.83; survival 23% ± 6.79) (Figure 6.6 and 6.7). Mean seedling height at planting was 15.9 cm ± 0.35. Seedling heights declined soon after planting in areas with no vegetation cover, and remained at less than 10 cm for the duration of the study (Figure 6.9 a–c). Seedling growth and survival was much higher in fenced areas with no vegetation cover (growth 8.2 cm ± 1.44; survival 75% ± 7.23) and in perennial shrubs (growth 11.0 cm ± 1.77; survival 61% ± 7.29).

There was a significant interaction between reserve and treatments on seedling (green-stock) growth (Table 6.2). Seedling growth in fenced areas with no vegetation cover and in perennial shrubs was similar at Tutanning and Durokoppin. However, seedling growth was considerably higher in perennial shrubs than fenced areas with no vegetation cover at Dongolocking (Figure 6.6), which accounts for the significant interaction.

Herbivores and perennial shrubs generally had similar effects on seedlings (green-stock) at each reserve. These variables, however, differed significantly among the reserves (Table 6.2). The percentage of seedlings (green-stock) browsed was highest at Tutanning (49% ± 10.32), similarly high at Durokoppin (43% ± 12.81), but lower at Dongolocking (36% ± 11.69). Seedling survival was much higher at Tutanning (74% ± 7.02) than Dongolocking (51% ± 9.33), but seedling growth was similar at the two reserves (Tutanning 4.7 cm ± 2.68; Dongolocking 4.9 cm ± 3.21). Both growth and survival were lowest at Durokoppin (growth −0.2 cm ± 2.36; survival 40% ± 8.84) (Figure 6.6 and 6.7). The decline in survival of seedlings in areas with no vegetation cover was particularly rapid at Durokoppin (Figure 6.10 a).

Table 6.2: Results from the ANOVA investigating the effects of the reserves and treatments on browsing, height growth, and survival of planted *Allocasuarina huegeliana* seedlings (green-stock). For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source		**Browsed**				**Height growth**			**Survival**		
	d.f.	Mean Square	*F*	*P*	d.f.	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Reserve	2	373.16	5.01	0.015*	2	128.14	6.52	0.004*	3072.39	8.74	0.001*
Treatment	1	15908.56	213.68	0.001**	2	1927.14	98.12	0.001**	7211.87	20.52	0.001**
Reserve × Treatment	2	133.80	1.80	0.187	4	67.91	3.46	0.017*	119.41	0.34	0.849
Error	24	74.45			36	19.64			351.43		

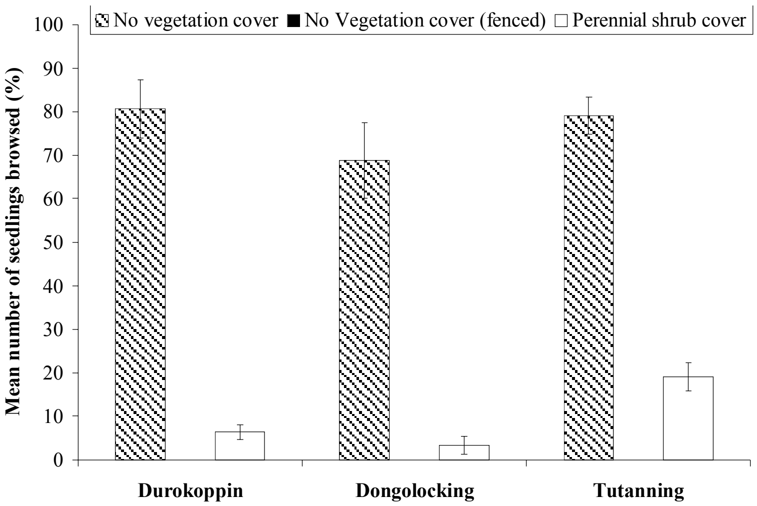


Figure 6.5: Mean percentage of *Allocasuarina huegeliana* seedlings browsed (green-stock) in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at three Nature Reserves. Bars indicate standard errors.

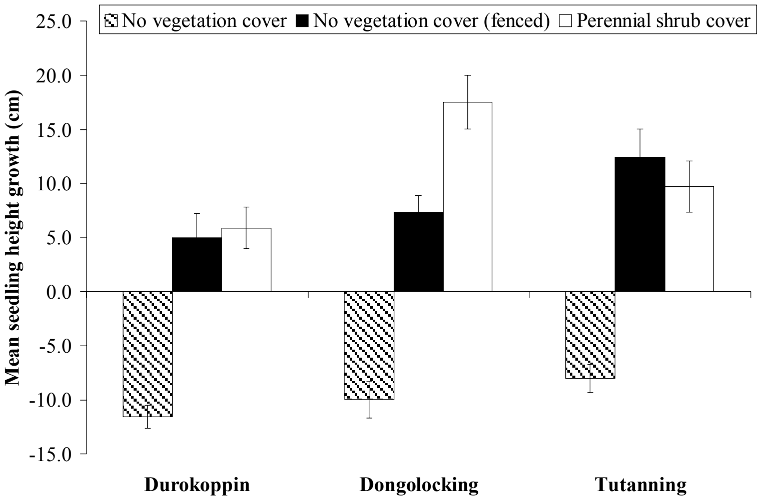


Figure 6.6: Mean *Allocasuarina huegeliana* seedling height growth (green-stock) in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at three Nature Reserves. Bars indicate standard errors.

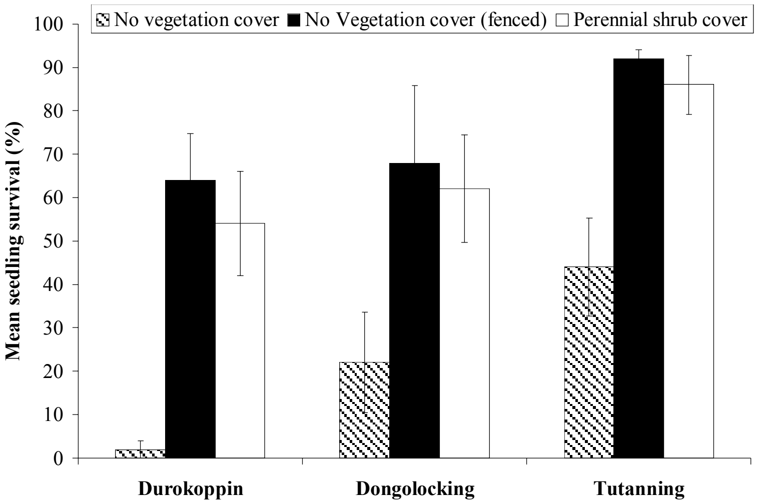


Figure 6.7: Mean *Allocasuarina huegeliana* seedling survival (green-stock) in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at three Nature Reserves. Bars indicate standard errors.

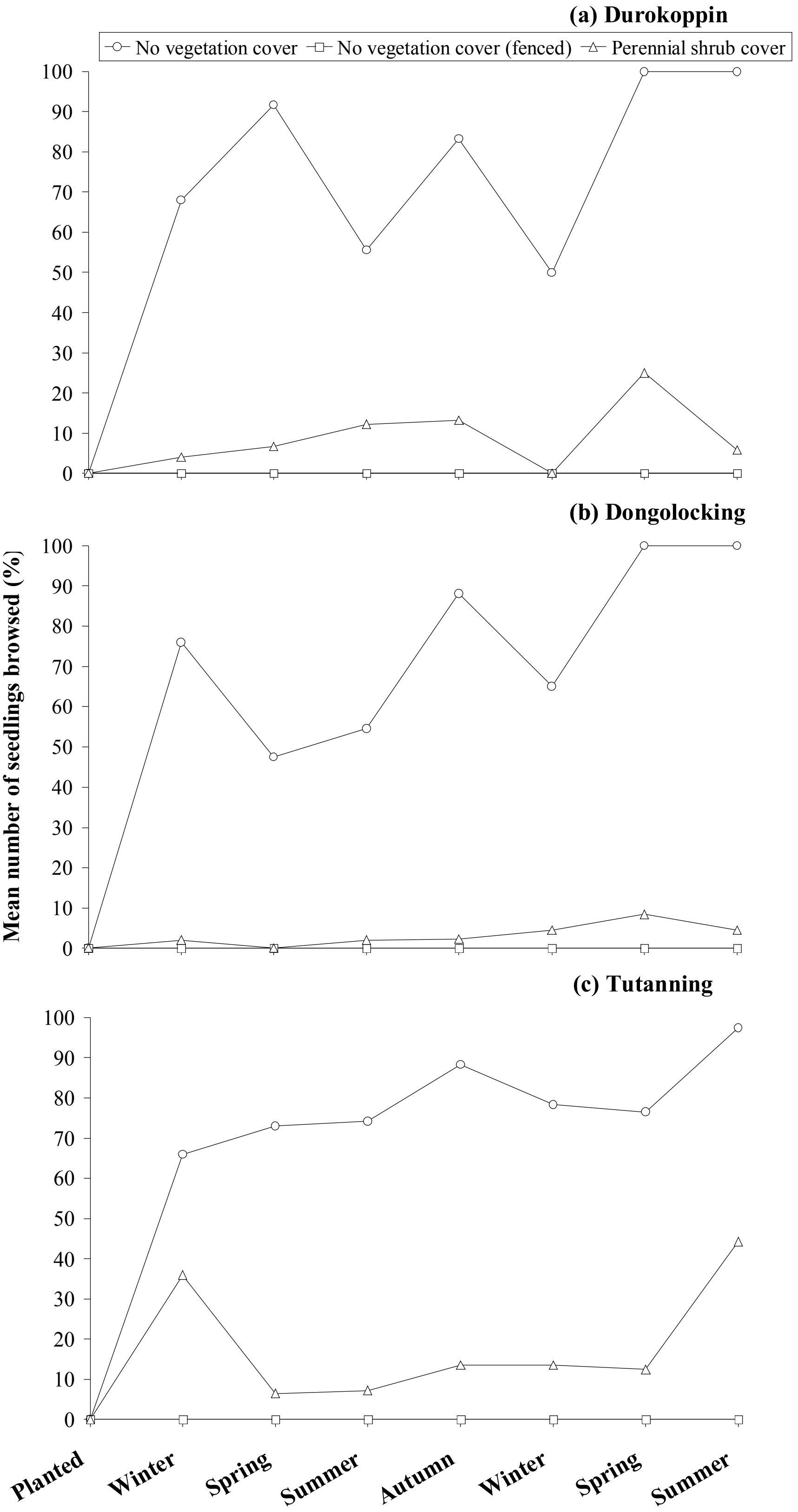
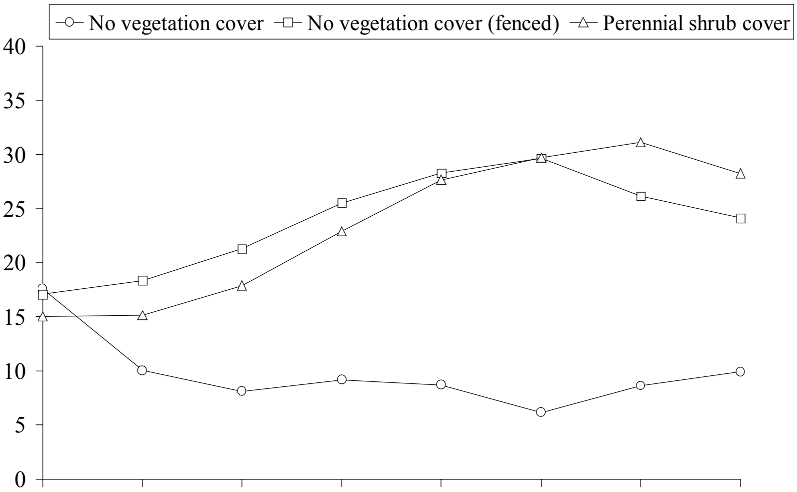
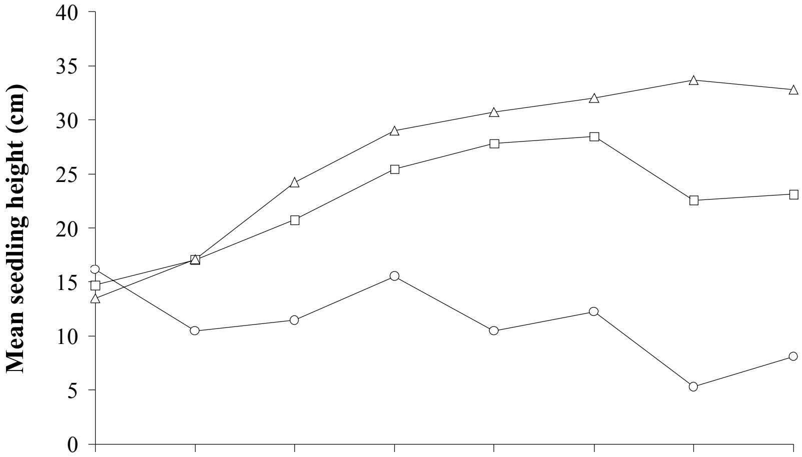


Figure 6.8: Mean percentage of *Allocasuarina huegeliana* seedlings browsed from planting (green-stock) in June 2005 and at the end of each season until March 2007, in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at (a) Durokoppin, (b) Dongolocking and (c) Tutanning Nature Reserves.

(a) Durokoppin



(b) Dongolocking



(c) Tutanning

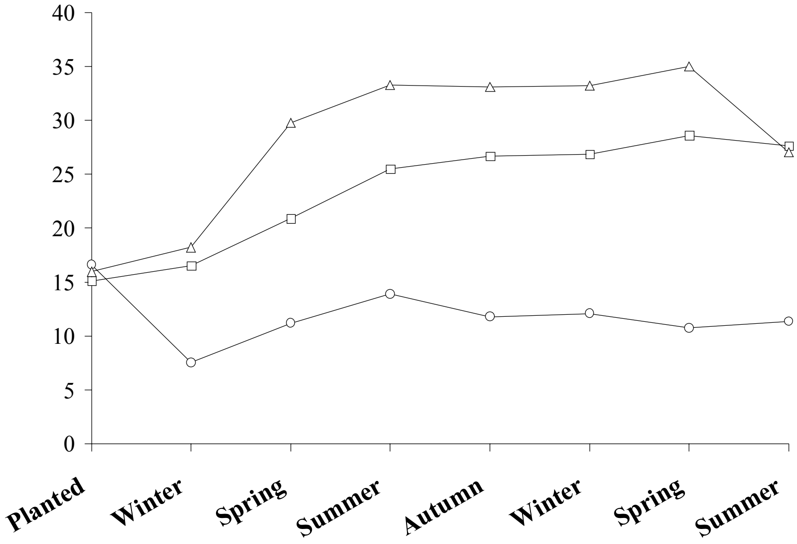


Figure 6.9: Mean *Allocasuarina huegeliana* seedling height from planting (green-stock) in June 2005 and at the end of each season until March 2007, in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at (a) Durokoppin, (b) Dongolocking and (c) Tutanning Nature Reserves.

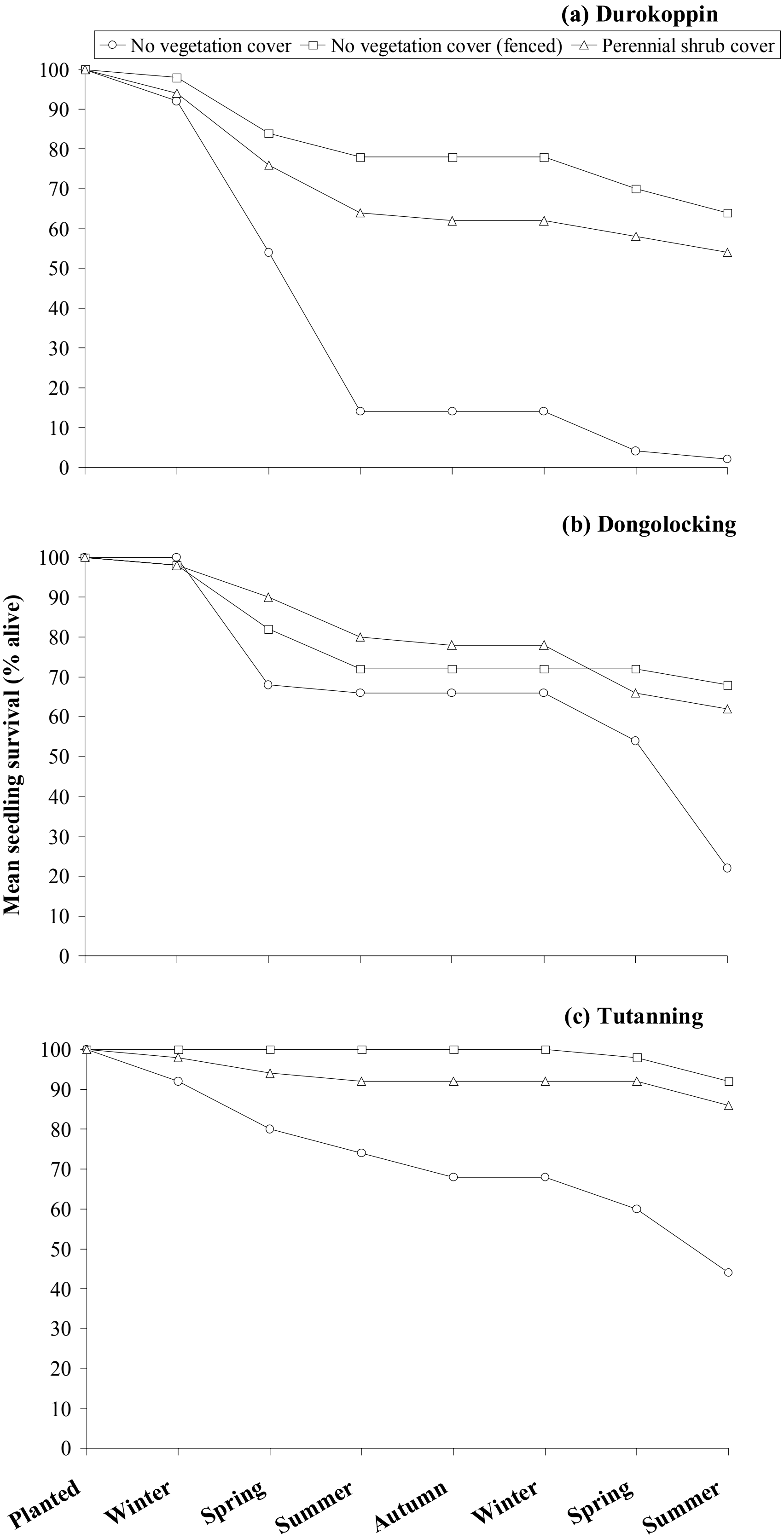


Figure 6.10: Mean *Allocasuarina huegeliana* seedling survival from planting (green-stock) in June 2005 and at the end of each season until March 2007, in areas with no vegetation cover, fenced areas with no vegetation cover, and areas with perennial shrub cover at (a) Durokoppin, (b) Dongolocking and (c) Tutanning Nature Reserves.

6.4 Discussion

Mammal herbivores did not affect seedling emergence; however, they did have a substantial negative effect on *A. huegeliana* growth and survival in areas with no vegetation cover soon after seedlings emerged. Koch *et al.* (2004) similarly found that protection from western grey kangaroos did not have a significant effect on initial germination of two *Xanthorrhoea* species, but had a significant effect on seedling growth and survival. The negative effect of herbivores on the survival of young *A. huegeliana* seedlings (sown seeds) in kwongan was particularly apparent at Tutanning. At this early stage of growth the seedlings were very small, i.e. only a few centimetres, and therefore unlikely to be browsed by mammals.

Field observations suggest that many areas where seeds were planted with no vegetation cover were paths created and maintained by kangaroos and wallabies. Trampling may therefore substantially reduce the number of *A. huegeliana* seedlings that establish in kwongan. Herbivores did not affect seedling survival (sown seeds) at Durokoppin or Dongolocking. However, survival rates were very low in all treatments at these reserves (1−5%) and thus few seedlings were available to be trampled or browsed by herbivores.

Muir (1985) found that only 6% of an *A. huegeliana* population in the Western Australian wheatbelt reached 20 cm or more in diameter, and that the greatest mortality occurred in the 0–2 cm diameter range. Ladd (1989) suggested that the size class structure of this population indicated that regeneration and survival were probably sporadic and that survival may depend on a sufficient number of wet years. Insufficient rainfall has been found to reduce survival of *A. huegeliana* seedlings in other parts of the wheatbelt (Ladd 1989; Yates *et al.* 2003), and survival of seedlings of other *Casuarina* and *Allocasuarina* species (Abbott 1984; Auld 1995). However, rainfall was much higher than average during the first summer (2005−06) after germination (Bureau of Meteorology 2007). During years of average summer rainfall, the survival of *A. huegeliana* seedlings may therefore be even lower than the levels recorded by this study.

Seedling growth and survival was generally higher in perennial shrubs than areas with no vegetation cover. The beneficial effects of shrubs to the growth and survival of young seedlings (sown seeds) and larger planted (green-stock) seedlings were obvious throughout the study at Tutanning. The effect of shrubs on young seedlings (sown seeds) was less pronounced at Durokoppin and Dongolocking, but the benefits to larger planted (green-stock) at these reserves were significant. Shrubs have been shown to facilitate growth and survival of seedlings through a number of mechanisms, primarily by altering the microhabitat conditions or reducing herbivory (Hunter & Aarssen 1988; Callaway 1995; Stachowicz 2001).

The effects of browsing by mammal herbivores were most noticeable on the larger planted *A. huegeliana* seedlings (green-stock). Although the levels of browsing varied among the reserves, seedlings in areas with no vegetation cover were browsed extensively by mammal herbivores at all reserves. Seedlings in these areas were continually browsed, which restricted their heights to around 10 cm and had a detrimental impact on survival. Leigh and Holgate (1979) also found that browsing and grazing by native mammals (kangaroos, wallabies and wombats) restricted the heights of regenerating plants to less than 11 cm at three different sites, compared with plants protected from herbivores which grew to an average height of 30 cm, 15-35 cm and 57 cm at each of the sites. Herbivory by these native mammals also significantly reduced seedling survival at these sites.

Perennial vegetation protected many *A. huegeliana* seedlings (green-stock) from browsing herbivores. Considerably fewer seedlings were browsed in perennial shrubs than in areas with no vegetation cover. A considerable number of studies have demonstrated that shrubs can protect other plants species growing under them from grazing or browsing herbivores (reviewed by Milchunas & Noy-Meir 2002). On the Patagonian steppe, Oesterheld & Oyarzábal (2004) showed that less palatable grasses provided protection from grazing by sheep to the highly palatable grass *Bromus pictus*. Jaksić and Fuentes (1980) found that native perennial herbs in the matorral scrub of central Chile were most abundant beneath shrubs, which protected the herbs from grazing by rabbits. In the North American Great Plains, Rebollo *et al.* (2002) showed that that the spiny cactus *Opuntia polyacantha* provided refuges for the dominant short-grass steppe species *Bouteloua gracilis* and other plants from grazing cattle. McAuliffe (1986) found that that the canopies of perennial plants protected seedlings of a common Sonoran Desert tree *Cercidium microphyllurn* with refuges from browsing cottontail rabbits and jackrabbits. Kwongan shrubs in this study appear to be providing similar biological refuges to *A. huegeliana* seedlings from browsing kangaroos and wallabies.

The similar growth and survival rates of seedlings in perennial shrubs and fenced areas with no vegetation cover indicated that in the absence of browsing, any positive or negative effects of the microhabitats counteracted each other, such that the impact on seedling growth and survival was minimal. Facilitation often operates simultaneously with competition and the net result of these interactions may range from positive to negative (Callaway & Walker 1997; Berkowitz *et al.* 1995; Holmgren *et al.* 1997). For example, nurse plants can improve some environmental conditions they can also have negative effects on other factors. A nurse plant can moderate air and soil temperatures (Hunter & Aarssen 1988; Nolasco *et al.* 1997), increase nutrient and organic carbon availability in the soil (Carrillo-García *et al.* 2000) and improve soil water availability (Caldwell *et al.* 1998). However, nurse plants can impede seedling growth and/or survival by increasing litter accumulation (Facelli & Pickett 1991), reducing the availability of light and soil water (Franco & Nobel 1989), or by excreting allelopathic substances (Callaway *et al.* 1991).

The balance of facilitative and competitive interactions on *A. huegeliana* generally had a neutral (i.e. little or no) effect. However, kwongan shrubs in some areas appeared to have negative or positive affects on seedling growth and/or survival. Shrubs benefited planted seedlings (green-stock) at Dongolocking, where seedling heights were taller in perennial shrubs than fenced areas with no vegetation cover. Conversely, perennial vegetation had a negative effect on seedling survival (sown seed) at Tutanning, where survival was lower in perennial shrubs than fenced areas with no vegetation cover.

Similar growth and survival rates of seedlings in perennial shrubs and fenced areas with no vegetation cover indicate that *A. huegeliana* seedlings are tolerant of competition from the existing vegetation. Withers (1979) found that *A. littoralis* and *A. verticillata* seedlings were able to establish in dense grass swards and attributed this to shade tolerance and drought resistance. *A. huegeliana* has also been observed regenerating sporadically in grassy swards in the wheatbelt, which has been attributed to drought resistance (Ladd 1989). However, competition with annual grasses has found to reduce the survival of *A. campestris* seedlings (Hobbs & Atkins 1991).

Any effects of increased competition from perennial shrubs were far outweighed by the benefits that the shrubs provided to establishing *A. huegeliana* seedlings through protection from browsing herbivores. Similar patterns have been found in other systems subjected to grazing and browsing. Rousset & Lepart (2000) showed that the protection offered by shrubs to downy oak *Quercus humilis* seedlings from grazers offset the negative effects on growth so that plants could survive to overtop the shrub canopy and reach maturity. Similarly, Oesterheld & Oyarzábal (2004) found that protection from grazing by sheep to the highly palatable grass *Bromus pictus* outweighed the competitive effects of the less palatable grasses that provided protection. McAuliffe (1986) also identified that due to herbivore pressure, seedling distributions of a Sonoran Desert tree *Cercidium microphyllum* were largely limited to areas beneath other perennial plants, despite the likely competitive effects.

The negative effects of browsing on seedling growth and survival were obvious; however, it should be noted that the seedling growth measurements and subsequent analysis were influenced by mortality. The growth of surviving seedlings was calculated over a longer period of time than the seedlings that did not survive, which probably grew less. Mortality may skew data e.g. taller plants may be those more likely to survive. However, the results from this study indicate that herbivory reduced seedling growth and hence increased mortality (Fig 6.6). This highly significant result occurs irrespective of mortality levels; if mortality alone were important, a zero increase in height would be expected.

The ability of seedlings to escape browsing by establishing in perennial shrubs suggests that the herbivore communities at the reserves studied are unable to prevent *A. huegeliana* encroachment in long unburned patches of kwongan. Although herbivore communities have declined at many reserves, populations at Tutanning have largely recovered (Chapter 3). Since large numbers of seedlings were also able to escape browsing and establish in perennial shrubs at this reserve, it seems unlikely that herbivores could have prevented *A. huegeliana* encroachment in the past. However, herbivores may play an important role in post-fire conditions through selective browsing on *A. huegeliana* seedlings (Chapter 9).

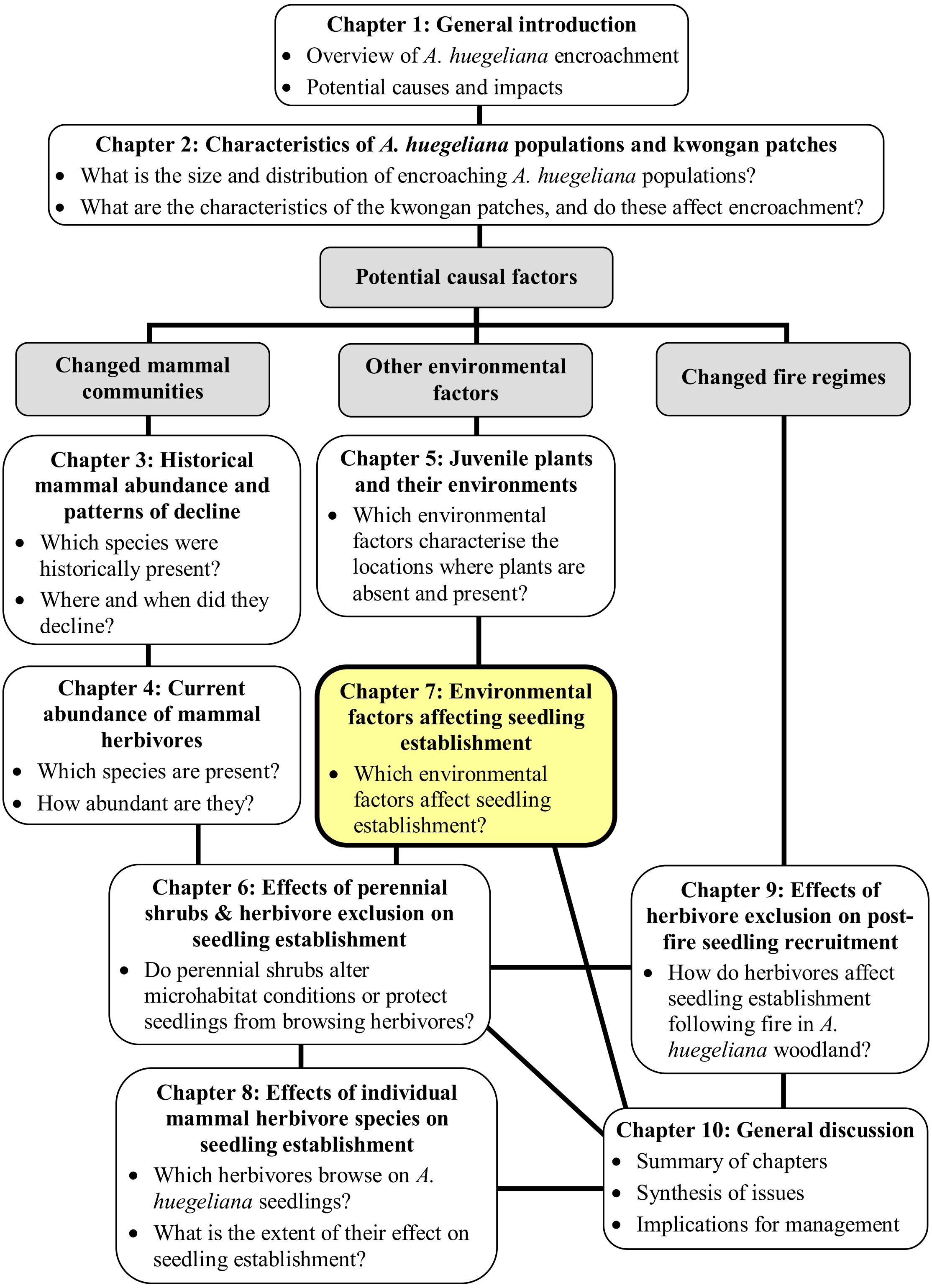
Although the effect of perennial shrubs and herbivore exclusion explained most of the variation in the growth, survival and browsing of *A. huegeliana* seedlings, these seedling response variables also differed substantially among the reserves. Seedlings emergence was higher at Dongolocking, which indicates that germination conditions were more favourable at this reserve. However, the conditions for seedling survival (sown seed and green-stock) were much more favourable at Tutanning. The high survival rates at Tutanning were particularly interesting given that browsing levels were also highest at this reserve. These results further suggest that environmental conditions were more favourable at Tutanning, which offset the impacts of browsing. Such variation in seedling emergence and survival is likely to be due to variation in the environmental conditions among the reserves.

The reserves were located across a geographical range and were subject to different climatic conditions. Abiotic factors such as temperature and rainfall have an important effect on germination (Mott & Groves 1981) and plant establishment (Harper 1977). These factors have been found to affect establishment of several *Casuarina* and *Allocasuarina* species in Australia (discussed in Section 5.1). Seedling survival (sown seed) was much higher at Tutanning than Durokoppin and Dongolocking, where survival rates were very low. This pattern is not explicable by climatic variation. Total rainfall and average temperatures were similar at Tutanning and Dongolocking. However, Durokoppin received about 100 mm less rainfall over the duration of the study and had slightly higher temperatures (Bureau of Meteorology 2007). Survival may therefore be expected to be lower at Durokoppin than the other reserves, but these factors do not explain the differences in emergence and survival at Tutanning and Dongolocking. Instead, these differences may be due to other environmental factors such as soil properties or annual plant cover, some of which are investigated in Chapter 7.

In conclusion this chapter has shown that mammal herbivores browse extensively on seedlings in areas with no vegetation cover and significantly reduce the number of *A. huegeliana* seedlings that establish in kwongan. However, this study could not identify which herbivore species were browsing on seedlings. Although the levels of browsing varied to some extent among the reserves, this did not result in increased growth or survival where browsing levels were lower. Perennial shrubs provided refuge to seedlings from browsing herbivores and as a consequence many seedlings were able to grow and survive. In the absence of browsing, the effects of possible microhabitat differences between shrubs and areas with no vegetation cover appeared to counteract each other. Therefore, any benefits which may have been provided by differences in microhabitat conditions were of less importance than protection from browsing. Environmental conditions appeared to vary among the reserves and had an important effect on seedling establishment and will be investigated in the next chapter.

Chapter 7

Environmental factors affecting seedling establishment



Chapter 1: General introduction
- Overview of *A. huegeliana* encroachment
- Potential causes and impacts

Chapter 2: Characteristics of *A. huegeliana* populations and kwongan patches
- What is the size and distribution of encroaching *A. huegeliana* populations?
- What are the characteristics of the kwongan patches, and do these affect encroachment?

Chapter 3: Historical mammal abundance and patterns of decline
- Which species were historically present?
- Where and when did they decline?

Chapter 4: Current abundance of mammal herbivores
- Which species are present?
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Chapter 5: Juvenile plants and their environments
- Which environmental factors characterise the locations where plants are absent and present?

Chapter 7: Environmental factors affecting seedling establishment
- Which environmental factors affect seedling establishment?

Chapter 6: Effects of perennial shrubs & herbivore exclusion on seedling establishment
- Do perennial shrubs alter microhabitat conditions or protect seedlings from browsing herbivores?

Chapter 9: Effects of herbivore exclusion on post-fire seedling recruitment
- How do herbivores affect seedling establishment following fire in *A. huegeliana* woodland?

Chapter 8: Effects of individual mammal herbivore species on seedling establishment
- Which herbivores browse on *A. huegeliana* seedlings?
- What is the extent of their effect on seedling establishment?

Chapter 10: General discussion
- Summary of chapters
- Synthesis of issues
- Implications for management

7.1 Introduction

Chapter 6 demonstrated that perennial shrubs benefit the establishment of *A. huegeliana* seedlings by protecting them from browsing herbivores. However, there was substantial variation in seedling survival and growth among the treatments (presence or absence of perennial vegetation) and the reserves that could not be explained by herbivore browsing alone. Such variation is likely to be due to other environmental factors that affect establishment.

There is a range of potential physical and chemical differences between areas with no vegetation cover and perennial shrub cover. Differences such as temperature, water availability, soil nutrients and organic matter may exist between areas with no vegetation cover and shrubs (Hunter & Aarssen 1988; Callaway 1995; Stachowicz 2001; Bruno *et al.* 2003). These factors may also affect seedling emergence and establishment. Additionally, 'perennial shrub cover' consists of a composite of many variables such as the density of the canopy, amount of plant litter and allelopathic effects of particular plant species, which may affect the conditions and resources available to seedlings that establish within a shrub.

Seedlings of many *Casuarina* and *Allocasuarina* are able to recruit in established vegetation, which has been attributed to their shade tolerance and drought resistance (Ladd 1989). However, seedling establishment of some species has been affected by soil conditions and reduced by annual plant competition and high levels of leaf litter (see Section 5.1). Few environmental factors affected the occurrence of juvenile *A. huegeliana* plants (Chapter 5). However, the causal events that determine whether a seedling establishes are usually untraceable when the plant has developed and mature vegetation is studied (Harper 1977). The juvenile plants measured in the previous study (Chapter 5) were relatively large (up to 1.5 m) and had already survived a range of environmental factors and were therefore no longer affected by these factors. Additionally, the conditions surrounding these plants have most likely changed from when the seedlings first emerged. To accurately determine which environmental factors affect *A. huegeliana* establishment it is important that young seedlings are studied.

This chapter examines the environmental factors affecting the establishment of *A. huegeliana* seedlings in long unburned (> 60 years) patches of kwongan and aims to determine which environmental factors affect emergence, growth, survival and browsing of *A. huegeliana* seedlings. The effects of environmental factors were investigated into seedlings in two of the three treatments used in the previous study (Section 6.2); areas with no vegetation cover and perennial shrub cover. Only seedlings in these treatments were investigated in this study because they were exposed to similar conditions that naturally establishing seedlings would experience i.e. they were not fenced from browsing herbivores. The environmental factors that affect these seedlings would best indicate the factors that affect naturally establishing *A. huegeliana* seedlings. Because this study did not include the fenced treatment, the findings of this study were considered separately from the previous chapter.

7.2 Methods and materials

7.2.1 Study sites

The environmental factors affecting emergence, growth, survival and browsing of *A. huegeliana* seedlings in unburned kwongan were investigated in three patches of kwongan including one at each of Durokoppin (1), Dongolocking (1) and Tutanning (4) Nature Reserves (see Section 2.2.2). The *A. huegeliana* seedlings (sown seed and green-stock) examined in this study were planted for the experiments described in Chapter 6 (Section 6.2). Only seedlings in areas with no vegetation cover and perennial shrub cover were used in this study. The selection of locations where seeds and seedlings were planted, replication and seedling measurements are described in Section 6.2.

7.2.2 Environmental characteristics of locations where seeds and seedling were planted

In October 2005, 0.5m × 0.5m quadrats were located around each grid of planted seeds (sown seeds) and each planted seedling (green-stock) and several environmental factors were assessed, including visual estimates of perennial shrub cover (%), annual plant cover (%) and plant litter cover (%), and the distances from the seedlings to the base of the three nearest perennial plants (any species) (m) were measured. The mean distance to neighbouring plants was then calculated. The environmental factors were selected as surrogates of microhabitat conditions such as soil moisture, organic carbon, light availability, and soil and air temperatures, which were not measured due to time and financial constraints. This study assumes that the surrogates modify the environment in some way e.g. percentage shrub cover affects light availability and temperature; and that leaf litter affects organic carbon, nutrients and moisture availability. However, it should be noted that we cannot be sure of the exact effects of the surrogates on the environment or the magnitude of these effects.

A sample of the top 10cm of soil was collected adjacent to each grid and in the middle of each group of 10 seedlings planted in each treatment using an auger (diameter 5 cm), and subsequently air dried. The percentage of gravel and clay, and soil pH (measured in a 1:5 soil/water suspension) was measured in the laboratory for each soil sample in accordance with McDonald *et al.* (1990).

7.2.3 Factors affecting seedling emergence and survival (sown seeds)

The effect of reserves (Durokoppin, Dongolocking and Tutanning), treatments (no vegetation cover and perennial shrubs) and their interaction on seedling emergence, and survival at 22 months were examined using ANOVA. Reserve and treatment were both treated as fixed factors. Percentage values were converted to proportions and arcsine square root transformed. Post hoc comparisons of the reserve means were made using Tukey HSD tests (Quinn & Keough 2002). Assumptions of homogeneity of variance and normality were checked with residual plots, box-plots using the Levene test. These data met the assumptions.

The effect of the predictive environmental variables (percentage perennial, annual and litter cover, soil pH, percentage gravel and clay) on seedling emergence and survival was examined using Pearson's product moment correlation and ANCOVA models (Quinn & Keough 2002). Each environmental variable was entered as a covariate into the model with the fixed design factors (reserve and treatment). The assumption of homogeneous regression slopes was checked by examining the interaction between the environmental covariates and treatment. None of the interactions were significant, and therefore homogeneity of the regression slopes was assumed. Collinearity of the environmental variables was examined using the Pearson correlations. No variables were highly inter-correlated ($P < 0.05$ and $r_s \geq 0.70$).

Several outliers were identified in the environmental covariates which could not be corrected through transformation, including one outlier for perennial cover, annual cover, litter cover, pH and gravel. Outliers can have undue influence on estimates of group effects and the conclusions from the ANOVA (Quinn & Keough 2002). Therefore ANCOVA was carried out with the outliers included and omitted. There was little difference between the results of the two analyses, which suggests that the outliers were not influential. The outliers were therefore included in the analyses. All analyses were undertaken using SPSS 15.0 (SPSS 2006).

7.2.4 Factors affecting the growth, survival and browsing of planted seedlings (green-stock)

The effect of reserves (Durokoppin, Dongolocking and Tutanning), treatments (no vegetation cover and perennial shrubs) and their interaction on the growth, survival and browsing of planted seedlings at 22 months were examined using the same method described for the analysis of seedlings emergence and survival (sown seed). The distance to neighbouring plants was also included as a covariate. A large number of seedlings died in the treatment with no vegetation cover and the sample sizes were uneven. Therefore, growth was calculated for each seedling by deducting the height at planting from the last height recorded prior to the death of the seedling, except for seedlings that died during the season of planting (June–August), and these values were used for the ANOVA. These data met the assumptions.

The effect of the predictive environmental variables (perennial, annual and litter cover, distance to neighbouring plants, soil pH, gravel and clay) on the growth, survival and browsing of planted seedlings was examined using the same method described for analysis of seedling emergence and survival. None of the interactions between the environmental covariates and treatment were significant, and therefore homogeneity of the regression slopes was assumed. Variables were highly inter-correlated where $P < 0.05$ and $r_s \geq 0.70$. Perennial cover and plant litter were highly inter-correlated ($r_s = 0.797$) and this was considered in the interpretation of the results.

Several outliers were identified in the environmental covariates, including two outliers for perennial cover, annual cover and gravel. ANCOVA was carried out with the outliers included and omitted. There was a substantial difference between the two analyses for perennial cover and annual cover, which suggests that the outliers were influential. However, the results of the two analyses for gravel were similar, thus the outliers had little effect. Results from both tests are presented for the environmental variables that were affected by outliers (perennial and annual cover), and the reasons for the outliers and their influence on the results are discussed. All analyses were undertaken using SPSS 15.0 (SPSS 2006).

ANCOVA also assumes that the continuous covariate values do not depend on the categorical predictors in the model (Quinn & Keough 2002). However, several environmental covariates varied among the treatments, reserves, or both (Figure 7.1 and 7.2). If the covariate is influenced by the categorical independents, some of the indirect effects of the independents will be removed from the dependent when ANCOVA adjusts for the covariate (Tabachnick & Fidell 1996). However, the environmental variables are a more detailed quantitative assessment of the treatments and reserves, and are therefore expected to explain some of the effects of these fixed factors.

7.3 Results

7.3.1 Factors affecting seedling emergence and survival (sown seed)

The treatments did not affect seedling emergence, but emergence was significantly different among the reserves (see Table 6.1). Plant litter significantly affected seedling emergence (Table 7.1), which declined as litter cover increased. However, litter cover only explained a small amount of variation in emergence. When litter cover was included in the ANCOVA the effect of reserve remained significant and explained much more variation in emergence. The effect of the reserves on seedling emergence was not explained by any of the environmental variables, and remained significant for all ANCOVAs (Table 7.1).

The reserves and treatments had a significant effect on seedling survival (sown seeds) (see Table 6.1). No environmental variables had a direct, significant affect on seedling survival (sown seed) (Table 7.2). Perennial cover explained much, but not all, of the treatment effect on seedling survival. The variation in seedling survival accounted for by the treatments reduced substantially when perennial cover was included in the ANCOVA, but the treatment effect remained significant (Table 7.2).

The effect of the reserves on seedling survival was not explained by any of the environmental variables, and remained significant for all ANCOVAs (Table 7.2).

Table 7.1: Results from ANCOVA models investigating the effects of the environmental variables, reserves and treatments on *Allocasuarina huegeliana* seedling emergence (sown seed). For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	d.f.	**Perennial cover**			**Litter cover**			**Annual cover**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Covariate	1	8.01	0.16	0.695	261.71	5.81	0.021*	11.78	0.23	0.634
Reserve	2	1355.78	26.45	0.001**	1457.03	32.33	0.001**	1251.76	24.46	0.001**
Treatment	1	6.81	0.13	0.717	0.58	0.01	0.911	159.10	3.11	0.085
Reserve × Treatment	2	108.59	2.12	0.133	132.76	2.95	0.064	110.53	2.16	0.128
Error	41	51.26			45.07			51.17		

Table 7.1 (cont.):

Source	d.f.	**pH**			**Gravel**			**Clay**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Covariate	1	24.77	0.49	0.489	126.94	2.62	0.113	1.07	0.02	0.886
Reserve	2	1236.98	24.33	0.001**	1191.09	24.63	0.001**	955.17	18.57	0.001**
Treatment	1	171.17	3.37	0.074	186.37	3.85	0.056	162.29	3.16	0.083
Reserve × Treatment	2	100.68	1.98	0.151	106.93	2.21	0.122	105.41	2.05	0.142
Error	41	50.85			48.36			51.43		

Table 7.2: Results from ANCOVA models investigating the effects of the environmental variables, reserves and treatments on *Allocasuarina huegeliana* seedling survival (sown seed). For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	d.f.	**Perennial cover**			**Litter cover**			**Annual cover**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Covariate	1	123.21	1.70	0.199	0.11	0.00	0.969	16.51	0.22	0.642
Reserve	2	489.39	6.76	0.003**	454.74	6.03	0.005**	355.16	4.73	0.014*
Treatment	1	500.25	6.91	0.012*	548.37	7.27	0.010*	900.33	12.00	0.001**
Reserve × Treatment	2	206.04	2.84	0.070	177.77	2.36	0.107	164.76	2.20	0.124
Error	41	72.44			75.45			75.05		

Table 7.2 (cont.):

Source	d.f.	**pH**			**Gravel**			**Clay**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Covariate	1	69.88	0.95	0.336	62.60	0.85	0.363	53.18	0.72	0.402
Reserve	2	468.64	6.36	0.004**	263.65	3.57	0.037*	478.90	6.46	0.004**
Treatment	1	938.48	12.73	0.001**	972.71	13.16	0.001**	823.97	11.11	0.002**
Reserve × Treatment	2	177.79	2.41	0.102	181.95	2.46	0.098	159.34	2.15	0.130
Error	41	73.74			73.92			74.15		

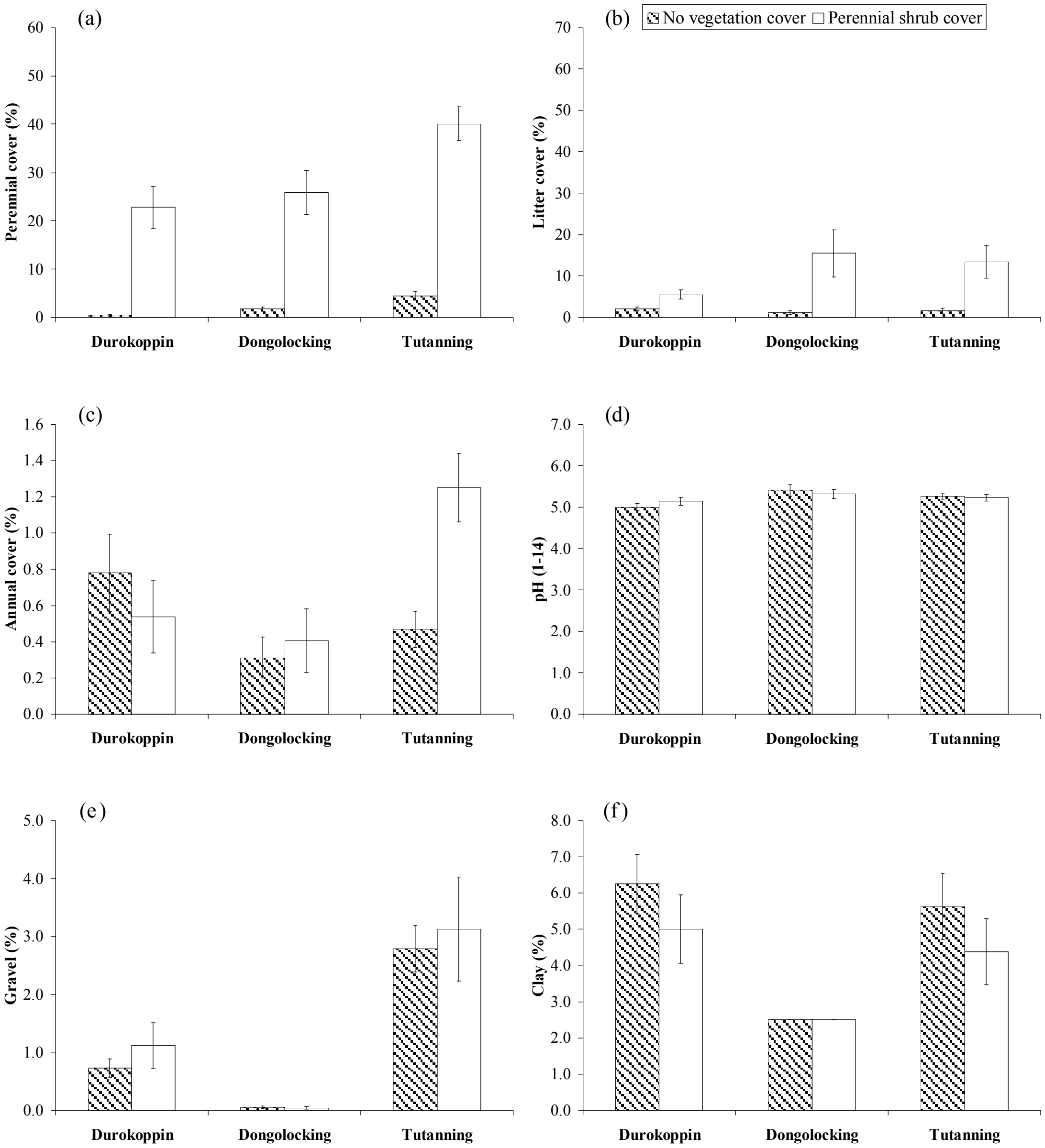


Figure 7.1: Environmental variables recorded within 0.5 × 0.5 m quadrats located around grids where *Allocasuarina huegeliana* seeds were sown in areas with no vegetation cover and perennial shrub cover at three Nature Reserves. The environmental variables included (a) perennial cover, (b) litter cover, (c) annual cover, (d) pH, (e) gravel and (f) clay. Bars indicate standard errors.

7.3.2 Factors affecting the growth, survival and browsing of planted seedlings (green-stock)

The treatments significantly affected seedling height growth, survival and the proportion of seedlings browsed (see Table 6.2). Seedlings planted in perennial shrubs were taller, had higher survival rates and fewer were browsed than seedlings planted in areas with no vegetation cover (see Figures 6.5−6.7).

The effect of the treatments on seedlings was largely explained by perennial cover. Perennial cover and litter cover were strongly correlated with seedling growth, survival and browsing (Table 7.3). However, the relationship between perennial cover and seedling growth, survival and browsing was stronger than litter cover (Table 7.3). The variation in seedling growth, survival and browsing accounted for by the treatments reduced substantially when perennial cover was included in the ANCOVA models (Tables 7.4−7.6). When the two perennial cover outliers were omitted, the effect of this variable increased and explained all of the treatment effect because the inter-correlation between treatments and perennial cover also increased.

While the treatments accounted for most of the variation in seedling growth, survival and browsing (Tables 7.4−7.6), the reserves also significantly affected seedlings. There was a significant interaction between reserve and treatment on seedling growth (Table 7.5), and two environmental variables (distance to neighbouring plants, annual plant cover) had a direct, significant effect on the seedlings (Tables 7.4−7.6).

Fewer seedlings were browsed at Dongolocking than the other reserves (Table 6.2). The reserve effect was explained by annual cover (outliers omitted) and gravel (Table

7.4). However, annual cover was very low in all cases (< 2%), and these factors could not realistically affect the browsing activity of herbivores on seedlings. These factors removed the effect of browsing because they varied among the reserves in a similar pattern to browsing, i.e. were lower at Dongolocking than the other reserves. These variables were therefore confounded with the reserves, and the differences in browsing between reserves clearly cannot be attributed to annual cover and gravel.

The distance to neighbouring plants had a direct, significant effect on the percentage of seedlings browsed (Table 7.4). More seedlings were browsed as the distance to neighbouring plants increased. However, this variable only explained a small amount of variation in the percentage of seedlings browsed when included in the ANCOVA, and the effect of reserve and treatment remained significant and explained much more of the variation.

Seedling growth was greater at Dongolocking than the other reserves, which accounted for the reserve effect (Figure 6.6). Growth was much higher in perennial shrubs at Dongolocking than the other treatments and reserves, which explained the significant interaction. Plant litter cover explained the reserve and interaction effect and clay explained the reserve effect (Table 7.5). The variation in plant litter and seedling growth between treatments and reserves was very similar. Plant litter was greater at Dongolocking, particularly in perennial shrubs, than the other treatments and reserves (Figure 7.2 c). This variable therefore contributed to both the reserve effect and the interaction between reserve and treatment. Clay levels were lower at Dongolocking than the other reserves (Figure 7.2 g), and this variable apparently contributed to the greater seedling growth at this reserve.

Seedling survival was higher at Tutanning than the other reserves (Figure 6.7). However, none of the environmental variables explained this effect, and reserve remained significant for all ANCOVAs (Table 7.6). When the outlier values for annual plant cover were included in the analysis (Table 7.6), this variable was significantly associated with seedling survival. However, annual cover was very low in all cases (< 2%), and is therefore unlikely to have had an important effect on seedling survival.

However, annual cover was very low in all locations (< 2%; Figure 7.2 d), including the outliers, and only explained a small amount of variation in survival. The effect of reserve and treatment remained significant and explained much more variation in survival when this variable was included in the ANCOVA (Table 7.6). Annual cover did not have a significant effect on seedling survival when the outliers were omitted. Few definite conclusions can therefore be drawn from the effect of annual cover on seedling survival.

Table 7.3: Results from the Pearson correlation between *Allocasuarina huegeliana* seedling height growth, survival and the percentage of seedlings browsed (green-stock) and the predictive environmental variables. Variables were considered to be highly inter-correlated where $P < 0.05$ and $r \geq 0.70$*.

Variable	**Browsing**	**Growth**	**Survival**
Browsing	1		
Growth	−0.891*	1	
Survival	−0.687*	0.576*	1
Perennial cover	−0.843*	0.877*	0.721*
Distance to neighbouring plants	0.031	−0.192	−0.401*
Litter cover	−0.723*	0.844*	0.533*
Annual cover	−0.018	−0.013	−0.117
pH	−0.12	0.102	0.094
Gravel	0.141	−0.128	0.232
Clay	0.113	−0.273	−0.161

Table 7.4: Results from the ANCOVA models investigating the effects of the environmental variables, reserves and treatments on the percentage of *Allocasuarina huegeliana* seedlings browsed (green-stock). For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	d.f.	**Perennial cover**			**Annual cover**			**Distance to neighbours**			**Litter cover**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
With outliers								*No outliers*					
Covariate	1	12.51	0.16	0.691	1.24	0.02	0.901	285.62	4.38	0.048*	24.80	0.32	0.575
Reserve	2	354.87	4.60	0.021*	302.57	3.90	0.035*	316.06	4.84	0.018*	269.45	3.52	0.046*
Treatment	1	969.23	12.56	0.002**	15764.35	203.06	0.001**	16025.06	245.53	0.001**	1348.45	17.60	0.001**
Reserve×Treatment	2	139.05	1.80	0.187	132.75	1.71	0.203	159.27	2.44	0.109	141.86	1.85	0.180
Error	23	77.14			77.63			65.27			76.61		
Without outliers													
Covariate	1	106.46	1.40	0.250	0.10	0.00	0.972						
Reserve	2	346.62	4.56	0.023*	276.96	3.26	0.059						
Treatment	1	322.10	4.23	0.052	12680.62	149.18	0.001**						
Reserve×Treatment	2	154.18	2.03	0.157	116.34	1.37	0.276						
Error	21	76.07			85.00								

Table 7.4 (cont.):

Source	d.f.	**pH**			**Gravel**			**Clay**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Covariate	1	0.35	0.00	0.947	0.34	0.00	0.948	4.22	0.05	0.818
Reserve	2	331.37	4.27	0.027*	71.17	0.92	0.414	318.11	4.10	0.030*
Treatment	1	15874.32	204.38	0.001**	15870.44	204.33	0.001**	15744.22	203.14	0.001**
Reserve×Treatment	2	133.95	1.72	0.201	132.24	1.70	0.204	135.90	1.75	0.196
Error	23	77.67			77.67			77.50		

Table 7.5: Results from the ANCOVA models investigating the effects of the environmental variables, reserves and treatments on *Allocasuarina huegeliana* seedling growth (green-stock). For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	d.f.	**Perennial cover**			**Annual cover**			**Distance to neighbours**			**Litter cover**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
With outliers								*No outliers*					
Covariate	1	17.77	1.02	0.323	2.52	0.14	0.712	0.32	0.02	0.895	0.30	0.02	0.900
Reserve	2	82.31	4.73	0.019*	106.75	5.91	0.008**	91.11	5.02	0.016*	28.83	1.59	0.226
Treatment	1	134.66	7.74	0.011*	3230.08	178.83	0.001**	3077.56	169.49	0.001**	372.33	20.50	0.001**
Reserve×Treatment	2	73.47	4.22	0.027*	82.32	4.56	0.022*	77.52	4.27	0.027*	30.20	1.66	0.212
Error	23	17.40			18.06			18.16			18.16		
Without outliers													
Covariate	1	82.61	5.92	0.024*	5.00	0.25	0.619						
Reserve	2	53.89	3.86	0.037*	91.68	4.67	0.021*						
Treatment	1	15.09	1.08	0.310	2512.07	128.02	0.001**						
Reserve×Treatment	2	27.70	1.98	0.162	74.10	3.78	0.040*						
Error	21	13.96			19.62								

Table 7.5 (cont.):

Source	d.f.	**pH**			**Gravel**			**Clay**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Covariate	1	3.54	0.20	0.662	2.16	0.12	0.733	51.93	3.26	0.084
Reserve	2	80.03	4.44	0.023*	84.14	4.65	0.020*	36.91	2.32	0.121
Treatment	1	3272.86	181.64	0.001**	3256.47	180.13	0.001**	3175.04	199.51	0.001**
Reserve×Treatment	2	65.16	3.62	0.043*	82.34	4.55	0.022*	87.36	5.49	0.011*
Error	23	18.02			18.08			15.91		

Table 7.6: Results from the ANCOVA models investigating the effects of the environmental variables, reserves and treatments on *Allocasuarina huegeliana* seedling survival (green-stock). For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source	d.f.	**Perennial cover**			**Annual cover**			**Distance to neighbours**			**Litter cover**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
With outliers								*No outliers*					
Covariate	1	103.16	0.35	0.557	1641.31	7.33	0.013*	43.05	0.15	0.705	88.23	0.30	0.588
Reserve	2	1403.39	4.82	0.018*	3157.98	14.10	0.001**	1366.15	4.65	0.020*	2290.60	7.86	0.003**
Treatment	1	1337.10	4.60	0.043*	10204.92	45.55	0.001**	9350.81	31.86	0.001**	1682.34	5.77	0.025*
Reserve×Treatment	2	80.25	0.28	0.761	299.09	1.33	0.283	137.49	0.47	0.632	49.73	0.17	0.844
Error	23	290.92			224.04			293.53			291.57		
Without outliers													
Covariate	1	0.65	0.00	0.964	688.68	2.81	0.108						
Reserve	2	918.51	3.03	0.070	3115.35	12.72	0.001**						
Treatment	1	400.80	1.32	0.263	7949.01	32.46	0.001**						
Reserve×Treatment	2	127.56	0.42	0.662	233.23	0.95	0.402						
Error	21	302.77			244.87								

Table 7.6 (cont.):

Source	d.f.	**pH**			**Gravel**			**Clay**		
		Mean Square	*F*	*P*	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Covariate	1	1455.15	6.27	0.020*	7.44	0.03	0.875	13.90	0.05	0.830
Reserve	2	2059.27	8.87	0.001**	1937.33	6.57	0.006**	2385.90	8.09	0.002**
Treatment	1	9174.54	39.52	0.001**	9536.04	32.32	0.001**	9443.84	32.03	0.001**
Reserve×Treatment	2	40.51	0.17	0.841	121.28	0.41	0.668	121.09	0.41	0.668
Error	23	232.14			295.08			294.80		

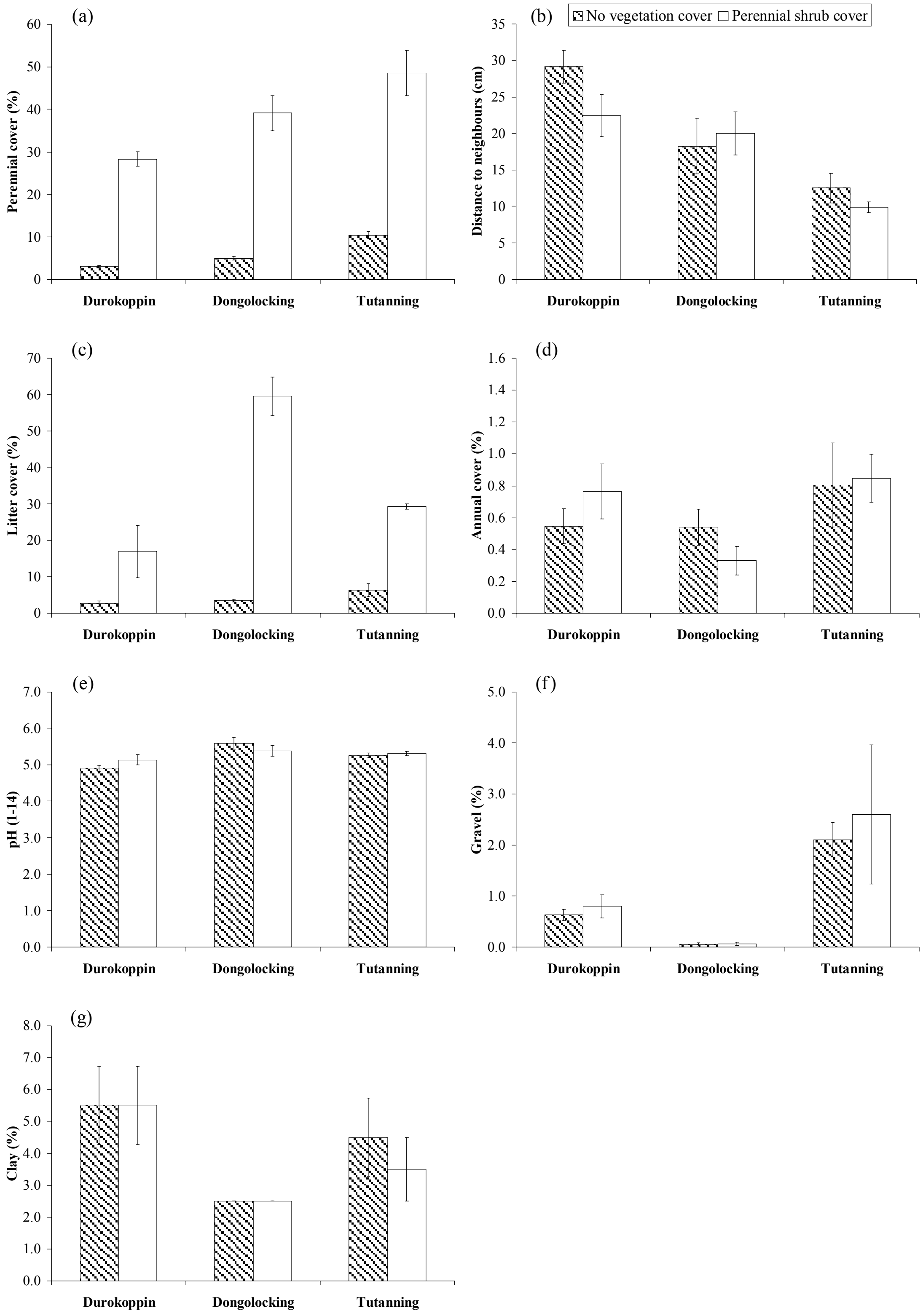


Figure 7.2: Environmental variables recorded within 0.5 × 0.5 m quadrats located around *Allocasuarina huegeliana* seedlings (green-stock) planted in areas with no vegetation cover and perennial shrub cover at three Nature Reserves. The environmental variables included (a) perennial cover, (b) distance to neighbours, (c) litter cover, (d) annual cover, (e) pH, (f) gravel and (g) clay. Bars indicate standard errors.

7.4 Discussion

Few factors were associated with the emergence of *A. huegeliana* seedlings. Increased levels of plant litter caused a slight decline in seedling emergence. Increased levels of plant litter caused a slight decline in seedling emergence. Many studies have reported the effects of plant litter on seed germination and seedling establishment (reviewed by Facelli & Pickett 1991). Litter can alter the physical and chemical environment through releasing nutrients and phytotoxic substances into the soil; shading seeds and seedlings; reducing the thermal amplitude in the soil; and reducing evaporation from the soil. However, litter may also diminish water availability when it retains a large proportion of rainfall (Facelli & Pickett 1991).

Plant litter has been found to favour germination and establishment, for example by conserving water during dry conditions (Fowler 1986) and adding nutrients (Facelli & Pickett 1991). However, in a meta-analysis of 35 independently published studies on the effects of plant litter on vegetation, Xiong & Nilsson (1999) found that litter generally had an overall negative effect on germination and establishment. Litter generally has a negative effect on germination because it creates a physical barrier which can prevent seeds and germinant roots from reaching the soil or bury seeds and prevent sprouts from emerging (Facelli & Pickett 1991). Litter from kwongan shrubs may have inhibited seedling emergence through such mechanisms. Litter cover was much greater within perennial shrubs than areas with no vegetation cover; however, the treatments did not affect emergence. The effect of litter on seedling emergence was therefore somewhat limited.

Soon after seedlings emerged, protection from browsing and trampling by herbivores appeared essential for *A. huegeliana* seedlings to establish. This was indicated by the dominant effect of the treatments, i.e. absence or presence of perennial vegetation, on the growth, survival and browsing of seedlings. Shrubs have been shown to protect seedlings from a range of small and large mammal herbivores, such as elk and ibex (Baraza *et al.* 2006), rabbits (Jaksić & Fuentes 1980; McAuliffe 1986) and sheep and cattle (Callaway *et al.* 2000; Rebollo *et al.* 2002; Oesterheld & Oyarzábal 2004). Details of some of these studies are discussed in Section 6.4.

The importance of kwongan shrubs in protecting seedlings from browsing herbivores was reiterated by the effect of shrubs that neighboured the seedlings. Fewer seedlings were browsed where the distance to neighbouring shrubs was smaller. Herbivores presumably had easy access to the seedlings in areas with little to no vegetation, which were subsequently suppressed by constant browsing and survival rates were generally low. Conversely, perennial shrubs presumably obstructed herbivores from reaching seedlings growing within them. Few seedlings were browsed and subsequently most grew taller and survived.

Fewer seedlings were browsed at Dongolocking than the other reserves. Although seedlings in perennial shrubs grew taller at this reserve, seedling survival was not greater. The lower levels of browsing at Dongolocking were not explained by any of the environmental variables or by differences in herbivore abundance (Chapter 4). Herbivores including kangaroos, brush wallabies and rabbits were generally more abundant at Dongolocking than Durokoppin (Chapter 4), but browsing levels were lower at Dongolocking. Therefore, herbivore presence does not necessarily correspond directly with browsing pressure.

Perennial cover accounted for most, but not all of the effects of the treatments on *A. huegeliana* seedlings. Although omitting the perennial cover outliers increased the amount of variation explained by this variable, the outliers indicated natural variation in kwongan shrubs. Perennial cover was not expected to explain all of the treatment effects on seedling establishment because the treatments represented a range of potential physical and chemical differences. Additionally, many different species shrubs of were involved, and species of some shrubs may have more of an effect (either positive or negative) than others. Increased replication of exclosure locations may have removed these outliers and the problems associated with analysing and interpreting these data.

Results from this study reveal an interesting difference in the characteristics of the kwongan among the reserves. Shrub cover, density (indicated by distance to neighbouring plants) and litter all varied among the reserves. These inter-site differences may be due to a productivity gradient associated with the geographical locations of the reserves. For example, the production of litter depends primarily on the site productivity (Facelli & Pickett 1991). Litter results from this study indicate that Dongolocking had the highest productivity, followed by Tutanning, and Durokoppin had the lowest site productivity. While Dongolocking and Tutanning experience more similar climatic conditions, Durokoppin experiences higher temperatures and lower levels of rainfall, which may contribute to lower site productivity. Inter-site differences may also be due to differences in dominant shrub species. The high degree of floristic heterogeneity in kwongan across geographical gradients is well known (Hopper 1979; Brown 1989; Hopper 1992; Hopper *et al.* 1996; Hopper & Gioia 2004) and is likely to have contributed to the differences in the characteristics such as shrub cover and height. In addition to naturally occurring environmental variations, differences in disturbance histories may also influence the composition of remnant vegetation (Lunt 1998b), and thus the characteristics of the kwongan among the reserves.

Although the treatments were the main factor affecting seedling establishment, the reserves also had an important effect on seedling growth and survival, which is discussed in Section 6.4. Seedling emergence and growth were higher at Dongolocking than the other reserves, but seedling survival was much higher at Tutanning. The benefits that these reserves provided to seedling emergence and survival could not be explained by climatic differences or the environmental variables measured in this study, and therefore remain unknown. However, the higher levels of growth at Dongolocking, particularly in perennial shrubs, were explained by several environmental factors.

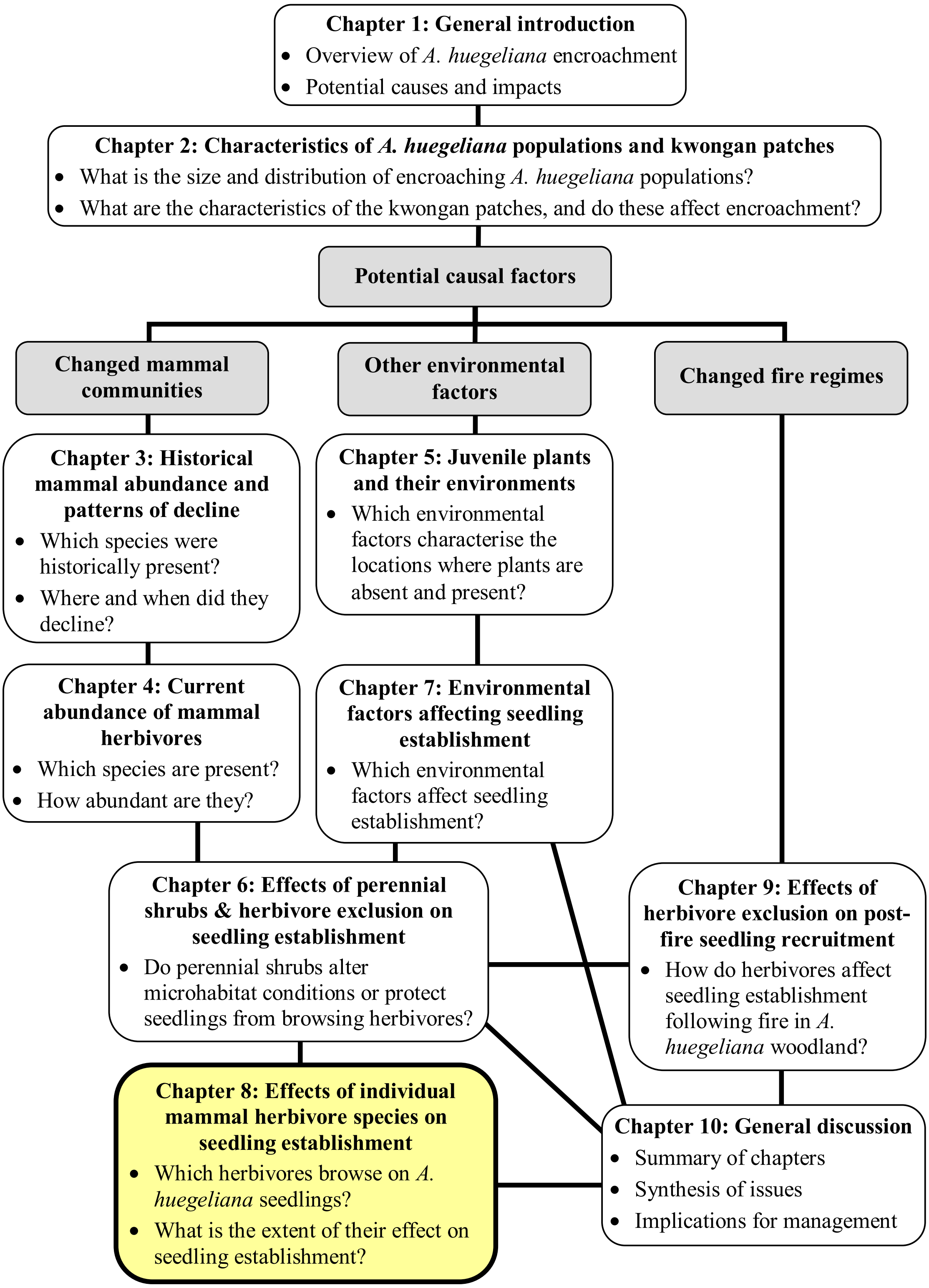
Seedlings may have grown taller at Dongolocking because fewer were browsed. However, the greater growth was also partially explained by higher litter cover and lower levels of clay at this reserve. As discussed previously, litter can favour vegetation development by conserving water during dry conditions (Fowler 1986) and adding nutrients (Facelli & Pickett 1991). In arid areas, clay reduces water availability for plants by keeping water near the surface which is rapidly lost though evaporation (Barchuk *et al.* 2005). Seedlings at Dongolocking may have benefited through such processes. However, the effects of clay and litter cover were confounded by the effects of the reserves. It is not possible to separate the effects of these variables from the differences among the reserves. Replication of the exclosure experiments in multiple patches of kwongan within each reserve is required to address the issue of collinearity between the reserves and environmental variables, but was not possible due to logistical limitations.

The only environmental factor that was directly associated with seedling establishment was annual cover. Seedling survival (green-stock) declined as annual cover increased. However, the levels of annual cover were very low in kwongan where seeds and seedlings were planted in this study (< 2%), and the effect of annual cover was only significant when the outliers (also less than 2%) were included in the analysis. In addition, emergence of *A. huegeliana* seedlings in this study was not affected by annual plants. Such low levels of annual cover probably did not affect seedling establishment. However, Hobbs and Atkins (1991) found that annual plants reduced the germination of seeds and survival of seedlings of *Allocasuarina campestris*. The establishment of other woody species is often inhibited by annual species, generally through competition for water and nutrients (Schultz *et al.* 1955; Griffin 1971; da Silva & Bartolome 1984; Eliason & Allen 1997).

In conclusion, *A. huegeliana* can establish in a range of environmental conditions in unburned kwongan. The findings from this chapter support those found in other chapters, and reiterate the importance of perennial shrubs in providing protection from browsing herbivores for *A. huegeliana* seedlings to establish. However, these findings did not provide much additional clarification about other environmental factors that may be important to *A. huegeliana* seedling establishment. Plant litter was associated with seedling emergence and annual cover was associated with seedling survival, but these effects were minor. The reserves were also associated with seedling establishment, but the factors responsible for this effect could not be determined. However, many factors that may affect seedling establishment were not measured in this study (largely due to financial and time constraints) such as soil nutrients and organic matter, soil water availability, soil temperature, allelopathic effects of particular shrub species and light levels.

Chapter 8

Effects of individual mammal herbivore species on seedling establishment during inter-fire intervals



8.1 Introduction

Chapter 6 showed that mammal herbivores have an important effect on *A. huegeliana* seedlings establishing in kwongan, but was not able to determine which species were responsible for browsing the seedlings.

A number of herbivores are present within Nature Reserves in the Western Australian wheatbelt that may affect the establishment of *A. huegeliana* seedlings, including western grey kangaroos (*Macropus fuliginosus*), tammar wallabies (*Macropus eugenii*), western brush wallabies (*Macropus irma*), rabbits (*Oryctolagus cuniculus*) and invertebrates. Main (1993) proposed that *Allocasuarina* encroachment was due the absence or decline of a grazing or browsing herbivore. Specifically, he suggested that the decline of tammars at Tutanning during the 1970s was responsible for the encroachment of *A. huegeliana* into kwongan at this reserve.

The loss of mammal herbivores from a range of systems has been found to have a significant impact on vegetation dynamics, including the loss of diversity in understorey plant communities in forests in Mexico (Dirzo & Miranda 1990), woodland encroachment and subsequent loss of heathlands in Britain (Bullock & Pakeman 1997), tree encroachment into grassy woodlands in Tasmania (Kirkpatrick 2004) and encroachment of several woody shrubs into semi-arid pastoral lands in eastern Australia (Noble & Grice 2002; Noble *et al.* 2007).

Many studies investigating the effects of mammal herbivores on plant communities have used fenced exclosure experiments (Smart *et al.* 1985; Hulme 1994; Ritchie *et al.* 1998; Brookshire *et al.* 2002; Turkington *et al.* 2002; Augustine & McNaughton

2004). Such experiments attempt to exclude several herbivores, or ideally a single herbivore, from a small area of a natural ecosystem. The responses of individual plants or plant communities to the release or reduction of herbivory can indicate the extent to which various herbivores influence factors such as recruitment, species composition and cover of the community.

The opportunity to investigate the effect of tammar wallabies on *A. huegeliana* seedlings has recently become possible due to the recovery of this species at Tutanning Nature Reserve. The density of the current population of tammars at Tutanning is similar to levels that are thought to have occurred historically (Chapter 3). This chapter examines the effect that different herbivores, including the tammar wallaby, have on *A. huegeliana* seedlings in a patch of kwongan at Tutanning Nature Reserve in the Western Australian wheatbelt.

This chapter aims to determine: (1) the separate effects of kangaroos, wallabies and rabbits on the emergence, growth and survival of *A. huegeliana* seedlings in an unburned (38 years) patch of kwongan; and (2) whether perennial shrubs protect seedlings from all herbivores. If tammars were able to limit the establishment of *A. huegeliana* seedlings in kwongan in the past, and their decline in the 1970s enabled numerous plants to establish, tammars should have a significant impact on seedling growth and survival at Tutanning now that their populations have recovered.

8.2 Methods and materials

8.2.1 Study site

The effects of four mammal herbivores (kangaroos, tammars, brush wallabies and rabbits) on the emergence, growth and survival of *A. huegeliana* seedlings in kwongan were investigated at one patch of kwongan at Tutanning Nature Reserve (6) (see Section 2.2.2).

8.2.2 Exclosure design

Three locations were subjectively chosen 30–40 m apart and evenly spaced across the site. At each location three adjoining 5 × 5 m pens and an adjoining 5 × 5 m open area were erected in a random direction. The three pens had 1.8 m fences to prevent kangaroos jumping in and were designed to selectively exclude other herbivores (Figure 8.1). The first pen excluded kangaroos, wallabies and rabbits (−K −W −R) using wire netting (30 mm diameter mesh) with a 30 cm mesh apron that continued along the surface of the ground. The second pen excluded kangaroos and wallabies, but allowed rabbits to enter (−K −W +R) through larger sized mesh (0.1 × 0.1 m). The third pen allowed wallabies and rabbits to enter under a mesh fence that was raised 30cm above the ground, but not kangaroos (−K +W +R). The unfenced area allowed access to these mammals (+K +W +R).

In practice, the herbivores that occurred at this site were tammar wallabies and kangaroos. The only herbivore scats found throughout this study in all exclosure locations and across the remainder of the site (see Chapter 4) were from these species. Although brush wallabies are known to occur in small numbers at the reserve and rabbits are assumed to be present, no scats from these species were found.

Additionally, no rabbit warrens were observed around the site and no seedlings were browsed in the −K −W +R areas. The −K −W −R and −K −W +R treatments were therefore effectively the same, and exclosures that included or excluded wallabies only affected tammars.

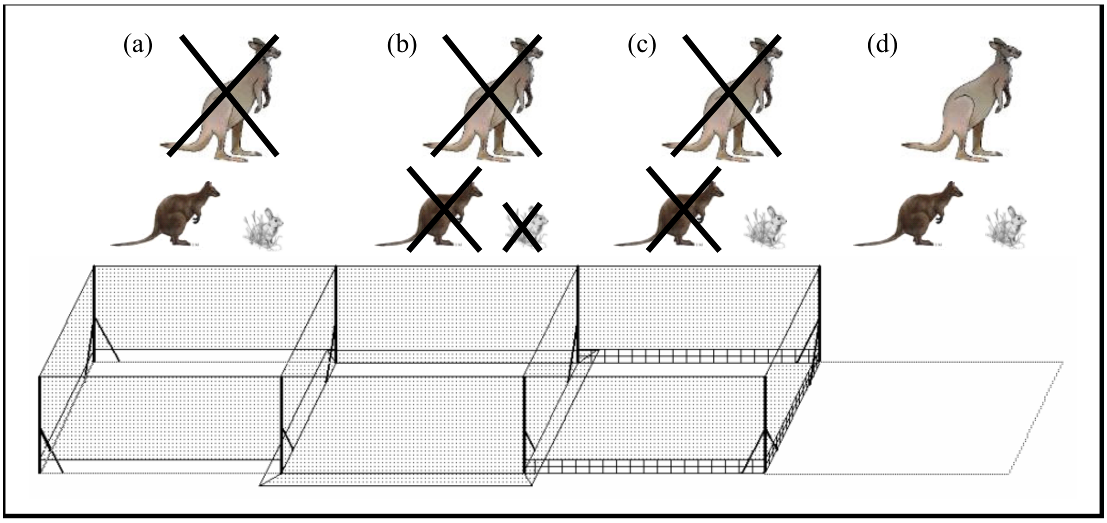


Figure 8.1: Diagram of a set of exclosures and adjacent unfenced area, indicating the mammal herbivores that were excluded from, or had access to, each treatment area including (a) −K +W +R, (b) −K −W −R, (c) −K +W +R and (d) +K +W +R (n = 3 sets).

To determine whether kangaroos were effectively excluded from the −K +W +R exclosure, double-sided tape was attached to the base of the raised fence to collect hair in the event they entered and departed the exclosure. The tape was collected and replaced every 4−6 weeks and the mammal species belonging to each hair sample was identified according to Brunner *et al.* (2002).

The design of the −K +W +R exclosure was mostly successful in keeping kangaroos out. Kangaroo scats and hair were recorded in −K +W +R at location 2 on one occasion, however no seedlings were browsed. Kangaroo hair was collected on three occasions (from 12 collection periods over 21 months) from −K +W +R at location 3. Two hair samples were found on the tape on each occasion, which indicates that most likely an individual kangaroo entered and left the area during the sample period. Kangaroos are locally known to be able to crawl under low fences to access crops in paddocks adjacent to bushland. It is possible that the kangaroo did not fully enter the exclosure and just put their head under the fence. However, there were substantial quantities of hair on the tape, which suggests that the kangaroo went right under the fence. As the exclosure wire was not bent, the kangaroo that entered the exclosure may have been a young or small one. A number of tammars also entered −K +W +R during the sample period. Therefore, the browsing activity that occurred in this area during these periods cannot be unequivocally attributed to tammars. Browsing activity at other times and browsing in −K +W +R at the other locations can be attributed to tammars.

8.2.3 Herbivore presence

The presence of herbivores within −K −W +R, −K +W +R and +K +W +R at the three locations across the site was monitored by removing scats from all areas in June 2005, and scats subsequently deposited in these areas were collected at intervals of 4−6 weeks, identified and counted. The total number of scats deposited by each herbivore species over the duration of the study was calculated for each treatment and location.

8.2.4 Effects of herbivore exclusion on seedling emergence and survival (sown seed)

In each treatment (−K −W −R, −K −W +R, −K +W +R, +K +W +R), 100 *A. huegeliana* seeds were planted on a 50 × 50 cm grid at two locations subjectively selected where a perennial shrub was present and a bare area with no vegetation cover at the beginning of June 2005 (100 seeds/grid × 1 grid/type of vegetation cover × 2 types of vegetation cover/treatment × 4 treatments/location × 3 locations = 2400 seeds). The seeds were collected from Tutanning (20 infructescences from 10 trees) in January 2005, air dried and stored in a paper bag until sowing.

Seedling emergence was recorded from June to July and the fate of seedlings (dead/alive) was recorded at the end of the study in February 2007. Seedling survival was calculated for each grid by dividing the number of seedlings that were alive at the end of the study by the total number of seeds that emerged.

The effect of the location (1−3), treatments (−K −W −R, −K −W +R, −K +W +R, +K +W +R), vegetation cover (no vegetation cover and perennial shrub cover), and their interactions on seedling emergence and survival were examined using ANOVA. The treatments and vegetation cover were treated as fixed factors, and location as a random factor. Post hoc comparisons of treatment and vegetation cover means were made using Tukey HSD tests (Quinn & Keough 2002). Percentage values were converted to proportions and arcsine square root transformed. Assumptions of homogeneity of variance and normality were checked with residual plots and box-plots. These data met the assumptions. All analyses were undertaken using SPSS 15.0 (SPSS 2006). All results are given as mean ± standard error.

8.2.5 Effects of herbivore exclusion on the survival, growth and browsing of planted seedlings (green-stock)

In each treatment, 10 *A. huegeliana* seedlings were planted at least 20 cm apart in areas with no vegetation cover, and the same number in perennial shrubs (10 seedlings/type of vegetation cover × 2 types of vegetation cover/treatment × 4 treatments/location × 3 locations = 240 seedlings). The seedlings were grown at a *Phytophthora* accredited nursery and planted in June 2005.

The heights of seedlings were measured immediately after planting and subsequent survival of seedlings, whether they had been browsed, and their heights were measured at the end of winter (August), spring (November), summer (February) and autumn (May), until February 2007. A number of seedlings died in some locations and treatments, which made the sample sizes uneven for analysis. Seedling growth was therefore calculated by deducting the height at planting from the height recorded prior to the death of the seedling. Mean seedling growth, the percentage of seedlings that survived to the end of the study, and the mean percentage that had been browsed by mammal herbivores (averaged across the seasons) was calculated for the 10 seedlings in the areas with no vegetation cover and in perennial shrubs within the four treatments at each location.

The effect of the location, treatments, vegetation cover and their interactions on the growth, survival and browsing of planted seedlings were examined using the same method described for the analysis of seedlings emergence and survival (sown seed). These data met the assumptions. All results are given as mean ± standard error.

8.3 Results

8.3.1 Herbivore presence

Herbivore presence varied across the site. The largest numbers of kangaroo and tammar scats were found at location 3 (Figure 8.2). The number of kangaroo scats was similar at locations 2 and 3, but there were many tammar scats at location 2 and only a few at location 1. Tammars were not exclosure-shy, and readily entered −K +W +R. The number of tammar scats was low in both +K +W +R and −K +W +R at location 1, and scats were more abundant within −K +W +R than +K +W +R at locations 2 and 3 (Figure 8.2).

8.3.2 Seedling emergence and survival (sown seed)

There was a significant interaction between location and treatment on emergence (Table 8.1). Seedling emergence varied among the treatments particularly at locations 1 and 3, but there was no consistent treatment effect. Emergence was much higher in −K −W +R at location 3 (67% ± 3.00) than all other treatments at the three locations, which accounted for the significant interaction (Figure 8.3).

Seedling survival (sown seeds) was not affected by the treatments or vegetation cover, but was significantly affected by the locations (Table 8.1). Seedling survival was lowest at location 1 (0% ± 0.30), also low but slightly higher at location 2 (2% ± 1.09) and highest at location 3 (8% ± 3.10) (Figure 8.4).

8.3.3 Growth, survival and browsing of planted seedlings (green-stock)

Vegetation cover significantly affected the percentage of seedlings browsed, and there was a significant interaction between the treatments and vegetation cover on browsing (Table 8.2). Perennial shrubs protected many seedlings from browsing. Fewer seedlings were browsed within shrubs (12% ± 4.20) than seedlings in areas with no vegetation cover (46% ± 14.80). However, many more seedlings were browsed in areas without vegetation cover in +K +W +R than seedlings in areas within perennial shrubs and in areas with no vegetation cover in −K +W +R (Figure 8.5), which accounts for the significant interaction. The treatments also had a strong effect on the percentage of seedlings browsed (Table 8.2). Large numbers of seedlings were browsed in +K +W +R (48% ± 5.18), while only a few seedlings were browsed in −K +W +R (10% ± 5.18) even at locations where numerous tammar scats were present (Figure 8.2). However, the treatment effect on the percentage of seedlings browsed was not significant at the $P < 0.05$ level (Table 8.2).

Mean seedling growth was significantly affected by the locations and treatments, and there was a significant interaction between treatment and vegetation cover on growth (Table 8.2). There was substantial variation in conditions across the site and seedlings grew much taller at location 2 (15.6 cm ± 5.25) than location 1 (−0.9 cm ± 3.16) and location 3 (−4.6 cm ± 2.70) over the duration of the study. Seedlings declined in height over the duration of the study in treatments where kangaroos had access (+K +W +R), but increased in height in all other treatments. Seedlings in areas with no vegetation cover grew taller than seedlings in perennial shrubs in all treatments except +K +W +R. In this treatment, seedlings in areas with no vegetation cover declined to a much greater extent than seedlings in perennial shrubs (Figure 8.6), which accounted for the significant interaction.

There were significant interactions between location and treatment, and treatment and vegetation cover on seedling survival (Table 8.2). Despite heavy browsing on seedlings in +K +W +R the treatments did not affect survival at locations 1 and 2 (Figure 8.7). However, seedling survival was much higher in −K −W −R than the other treatments at location 3 (Figure 8.7), which accounts for the significant interaction between location and treatment. This large difference in survival occurred even though no herbivores accessed −K −W −R or −K −W +R and the treatments were effectively the same.

Seedling survival was not affected by vegetation cover where herbivores did not have access to the seedlings (−K −W −R and −K −W +R), and perennial shrubs had a slightly negative effect on survival where only tammars had access to the seedlings (−K +W +R). However, seedling survival was much lower in areas with no vegetation cover where all herbivores had access to the seedlings (+K +W +R) than seedlings in all other treatments (Figure 8.7), which accounted for the significant interaction between treatment and vegetation cover.

Table 8.1: Results from the ANOVA investigating the effects of the locations, treatments, vegetation cover and their interactions on *Allocasuarina huegeliana* seedling emergence and survival (sown seeds) in a patch of kwongan at Tutanning Nature Reserve. For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source		**Emergence**			**Survival**		
	d.f.	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Location	2	45.63	0.53	0.614	346.79	7.73	0.022*
Treatment	3	22.02	0.26	0.855	39.61	0.88	0.501
Location × Treatment	6	86.17	4.46	0.028*	44.87	0.67	0.679
Vegetation cover	1	28.90	1.50	0.256	0.08	0.00	0.974
Treatment × Vegetation cover	3	7.14	0.37	0.777	61.19	0.91	0.477
Error	8	19.31			67.09		

Table 8.2: Results from the ANOVA investigating the effects of the locations, treatments, vegetation cover and their interactions on browsing, height growth and survival of planted *Allocasuarina huegeliana* seedlings (green-stock) in a patch of kwongan at Tutanning Nature Reserve. For significant relationships: $P < 0.01$**, $P < 0.05$*.

Source		**Browsed**				**Height growth**			**Survival**		
	d.f.	Mean Square	*F*	*P*	d.f.	Mean Square	*F*	*P*	Mean Square	*F*	*P*
Location	2	208.00	1.60	0.384	2	927.33	19.97	0.002**	951.32	2.19	0.193
Treatment	1	2204.62	16.97	0.054	3	519.32	11.19	0.007**	718.45	1.66	0.274
Treatment × Location	2	129.89	4.15	0.106	6	46.43	2.94	0.080	433.82	6.73	0.008**
Vegetation cover	1	1544.10	49.34	0.002**	1	35.53	2.25	0.172	112.67	1.75	0.223
Treatment × Vegetation cover	1	446.57	14.27	0.019*	3	171.97	10.89	0.003**	286.76	4.45	0.041*
Error	4	31.30			8	15.78			64.46		

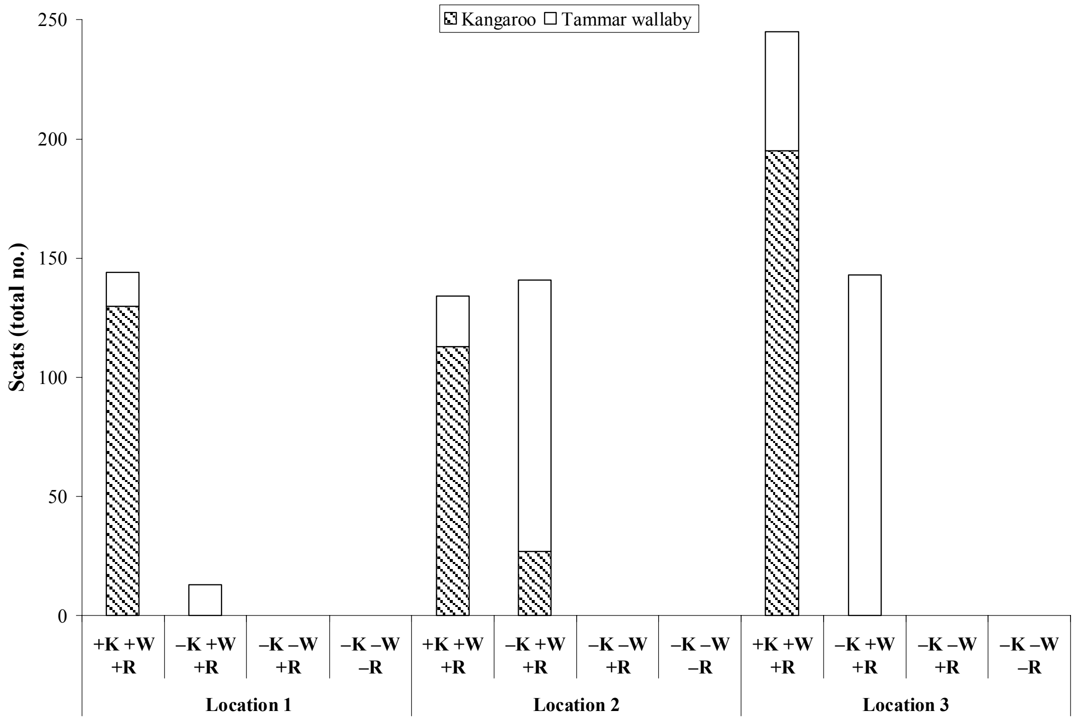


Figure 8.2: Total number of kangaroo and tammar wallaby scats found from June 2005 to February 2007, in four treatments at three locations in a patch of kwongan at Tutanning Nature Reserve. K = kangaroo, W = tammar wallaby and R = rabbit, and +/− indicates where herbivores are included or excluded from the treatment.

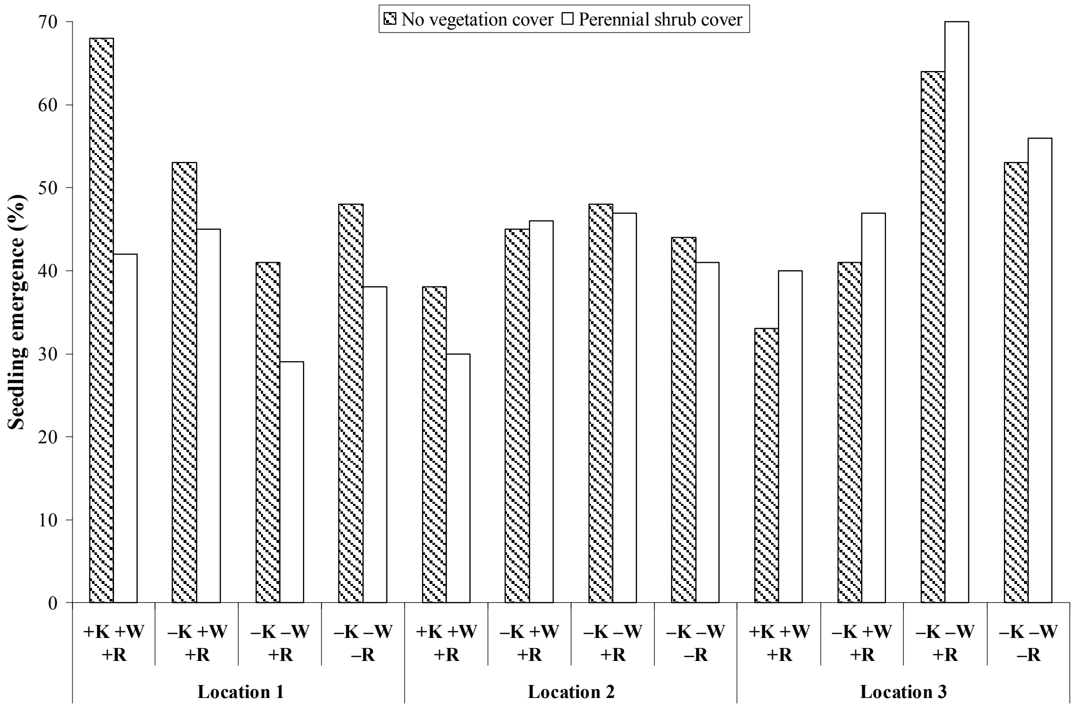


Figure 8.3: Percentage of *Allocasuarina huegeliana* seedlings emerged from seed sown in areas with no vegetation cover and perennial shrub cover, within four treatments at three locations in a patch of kwongan at Tutanning Nature Reserve. K = kangaroo, W = tammar wallaby and R = rabbit, and +/− indicates where herbivores are included or excluded from the treatment.

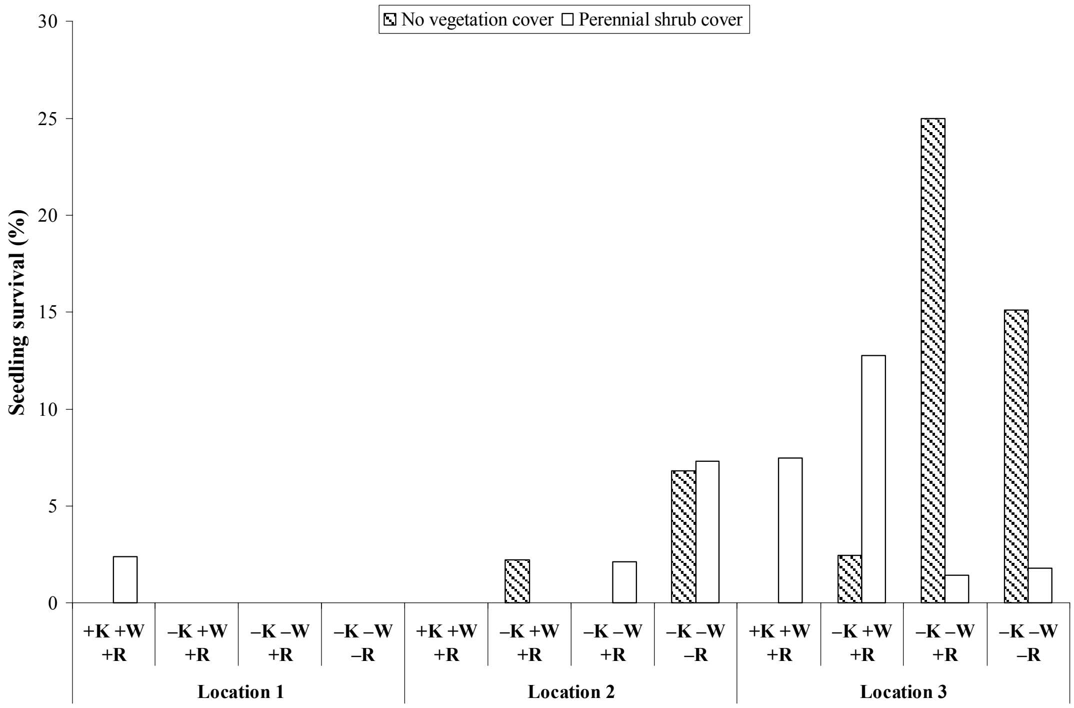


Figure 8.4: Percentage survival of *Allocasuarina huegeliana* seedlings (sown seed) in areas with no vegetation cover and perennial shrub cover, within four treatments at three locations in a patch of kwongan at Tutanning Nature Reserve. K = kangaroo, W = tammar wallaby and R = rabbit, and +/– indicates where herbivores are included or excluded from the treatment.

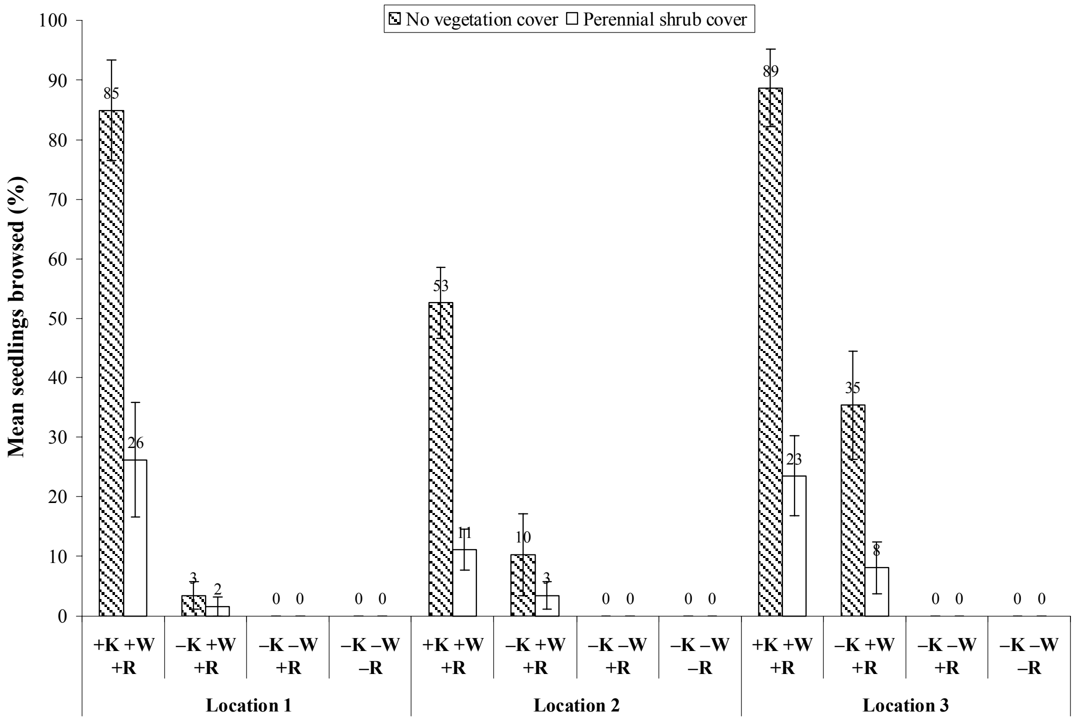


Figure 8.5: Mean percentage of *Allocasuarina huegeliana* seedlings browsed (green-stock) in areas with no vegetation cover and perennial shrub cover, within four treatments at three locations in a patch of kwongan at Tutanning Nature Reserve. K = kangaroo, W = tammar wallaby and R = rabbit, and +/– indicates where herbivores are included or excluded from the treatment. Bars indicate standard errors.

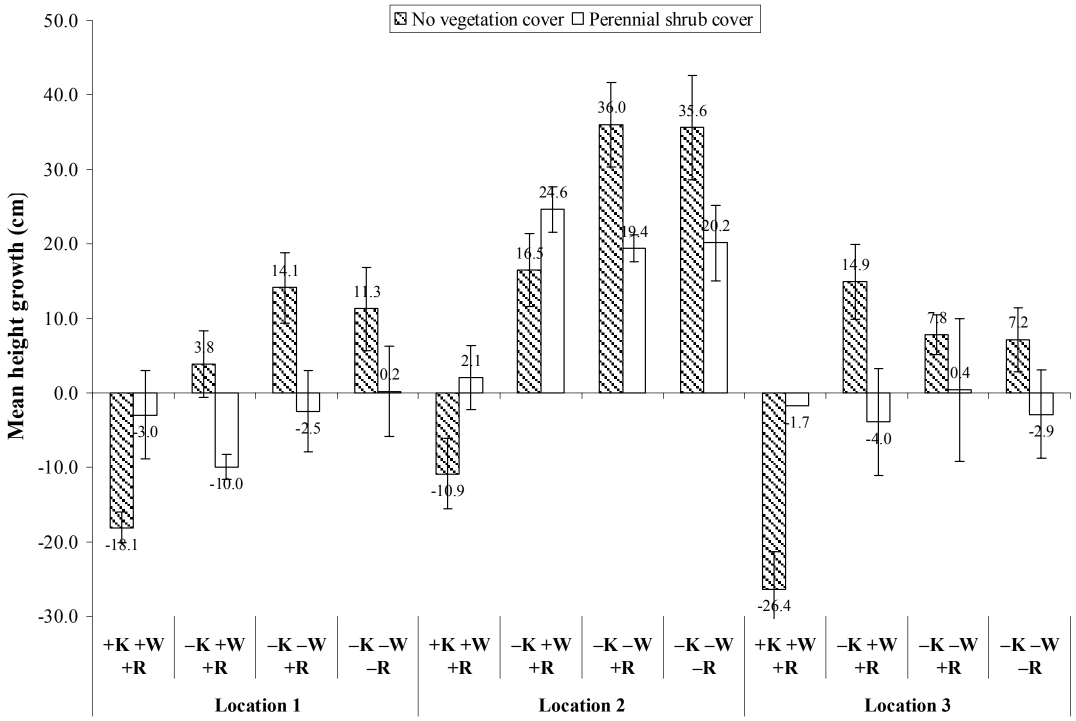


Figure 8.6: Mean *Allocasuarina huegeliana* seedling height growth (green-stock) in areas with no vegetation cover and perennial shrub cover, within four treatments at three locations in a patch of kwongan at Tutanning Nature Reserve. K = kangaroo, W = tammar wallaby and R = rabbit, and +/– indicates where herbivores are included or excluded from the treatment. Bars indicate standard errors.

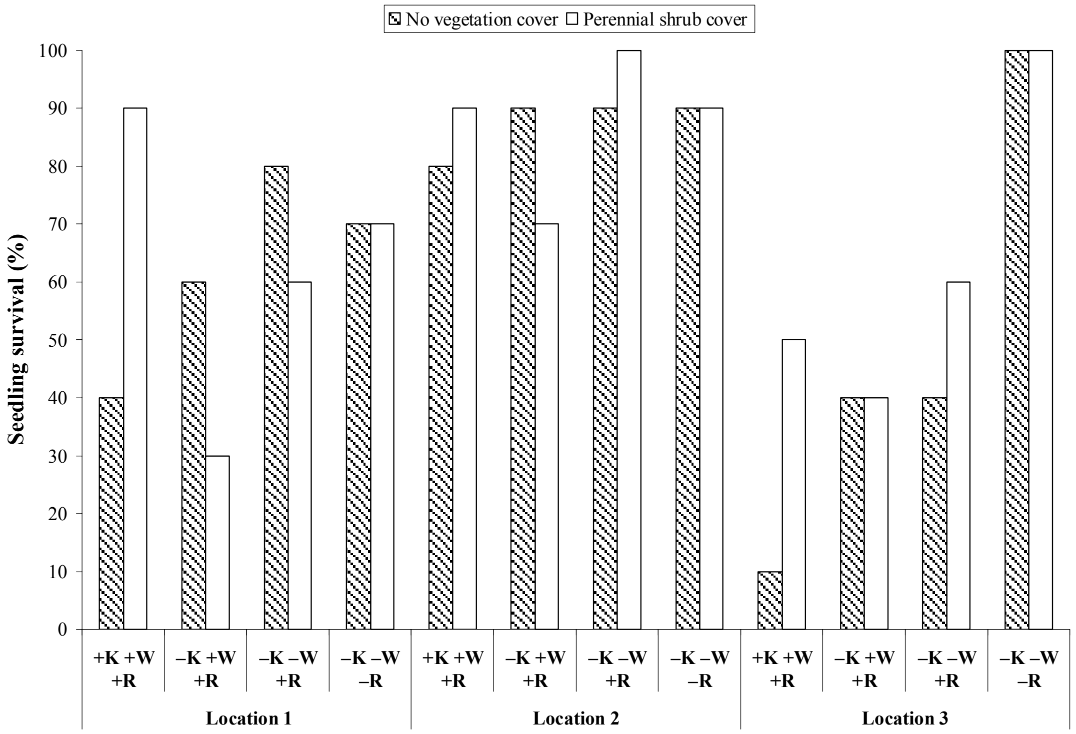


Figure 8.7: Mean *Allocasuarina huegeliana* seedling survival (green-stock) in areas with no vegetation cover and perennial shrub cover, within four treatments at three locations in a patch of kwongan at Tutanning Nature Reserve. K = kangaroo, W = tammar wallaby and R = rabbit, and +/– indicates where herbivores are included or excluded from the treatment. Bars indicate standard errors.

8.4 Discussion

The absence of rabbits and brush wallabies from the study site was ultimately beneficial for the purposes of this study because only two mammal herbivores were responsible for browsing – kangaroos and tammar wallabies. The effects of each herbivore on *A. huegeliana* seedlings could therefore be more accurately determined. The interpretation of the results of this study is somewhat limited by not having a treatment that only kangaroos were able to enter and not tammars, thus exhibiting the effect of kangaroos alone: this was logistically impossible to achieve. However, the effects of kangaroos can be inferred by examining the difference between the area where both tammars and kangaroos could access, and the exclosure where only tammars had access to seedlings.

Large numbers of *A. huegeliana* seedlings were browsed in unfenced areas where both kangaroos and tammars had access to seedlings. Although seedlings were able to tolerate heavy browsing, the height growth of most seedlings in areas with no vegetation cover was effectively suppressed. In the exclosures where only tammars could access seedlings, these mammals browsed only a few seedlings and had little impact on emergence, growth and survival. Fewer tammar scats were deposited in the unfenced areas than the exclosures, and assuming that scats are correlated with browsing activity (Chapter 4), tammars were most likely less abundant than kangaroos and browsed less in the unfenced areas. Even if tammars had a similar impact on seedlings in the two areas they could access, most browsing and subsequent effects on seedling growth and survival in unfenced areas can be attributed to kangaroos.

Although western grey kangaroos are often considered to consume primarily grasses, they have been found to frequently consume *Casuarina* spp. in a *Eucalyptus* wandoo-grass pasture landscape near Bakers Hill (east of Perth) (Halford *et al.* 1984) and a variety of shrub and tree species in *Eucalyptus* forest at Perup Nature Reserve in southwest Western Australia (Shepherd *et al.* 1997). Results from this study provide increasing evidence that western grey kangaroos consume shrub and tree seedlings as well as grasses. The large extent of browsing carried out by kangaroos indicates that this herbivore plays an important role in slowing *A. huegeliana* encroachment into kwongan. The higher growth and survival rate of seedlings where kangaroos were excluded indicates that the abundance of *A. huegeliana* seedlings would be remarkably greater if kangaroos were absent or if browsing activity was lower.

The limited impact of tammars on seedling emergence, growth and survival suggests that these wallabies have little impact on *A. huegeliana* encroachment into kwongan even where their densities are high. These results cast doubt on Main's (1993) theory that the decline of tammar wallabies during the 1970s caused the encroachment of *A. huegeliana* into kwongan at Tutanning. The low levels of browsing by tammars in this study are consistent with results obtained in Chapter 6, which found that similar numbers of *A. huegeliana* seedlings were browsed at three Nature Reserves in the wheatbelt even though tammars were absent from two of these reserves. Additionally, large numbers of seedlings are currently establishing in many kwongan patches at Tutanning (Chapter 2) despite the tammar population having recovered to high densities since the early 1990s (Chapter 3). Reintroduction of tammars to other reserves is therefore unlikely to affect *A. huegeliana* encroachment.

Brush wallaby scats were absent from the study site and few scats were found at other sites at Tutanning (Chapter 4). There are no records of a massive decline in brush wallaby populations similar to that experienced by tammars during the 1970s at this reserve. Therefore, brush wallaby populations may be naturally low at this reserve or the decline of this species was not noted. Brush wallabies appear to be much more abundant at a site at Dongolocking Nature Reserve, where their scats were found to be as abundant as kangaroos (Chapter 4). However, huge numbers of seedlings are also present at the site (Chapter 2). Therefore, it appears unlikely that the low population densities or possible decline of this species at Tutanning caused *A. huegeliana* to encroach into kwongan.

The loss of mammal herbivores from other parts of Australia has been suggested as causing increased recruitment of particular species. Kirkpatrick (2004) considered that the loss of wallabies and wombats from an urban remnant in Tasmania contributed to increased densities of *Eucalyptus* and *Allocasuarina* trees in areas of grassy woodland. The loss of the burrowing bettong (*Bettongia lesueur*), brush-tailed bettong (*B. penicillata*) and bridled nailtail wallaby (*Onychogalea fraenata*) has similarly been identified as enabling several woody shrub species to encroach into semi-arid pastoral lands in eastern Australia (Noble & Grice 2002; Noble *et al.* 2007). The loss of selective browsing following fire was considered to be particularly important in causing changes to vegetation in both of these systems, and is examined in the context of this study in Chapter 9.

While herbivores had a major impact on *A. huegeliana* seedlings, microhabitat conditions also appear to have a substantial impact on the seedling establishment.

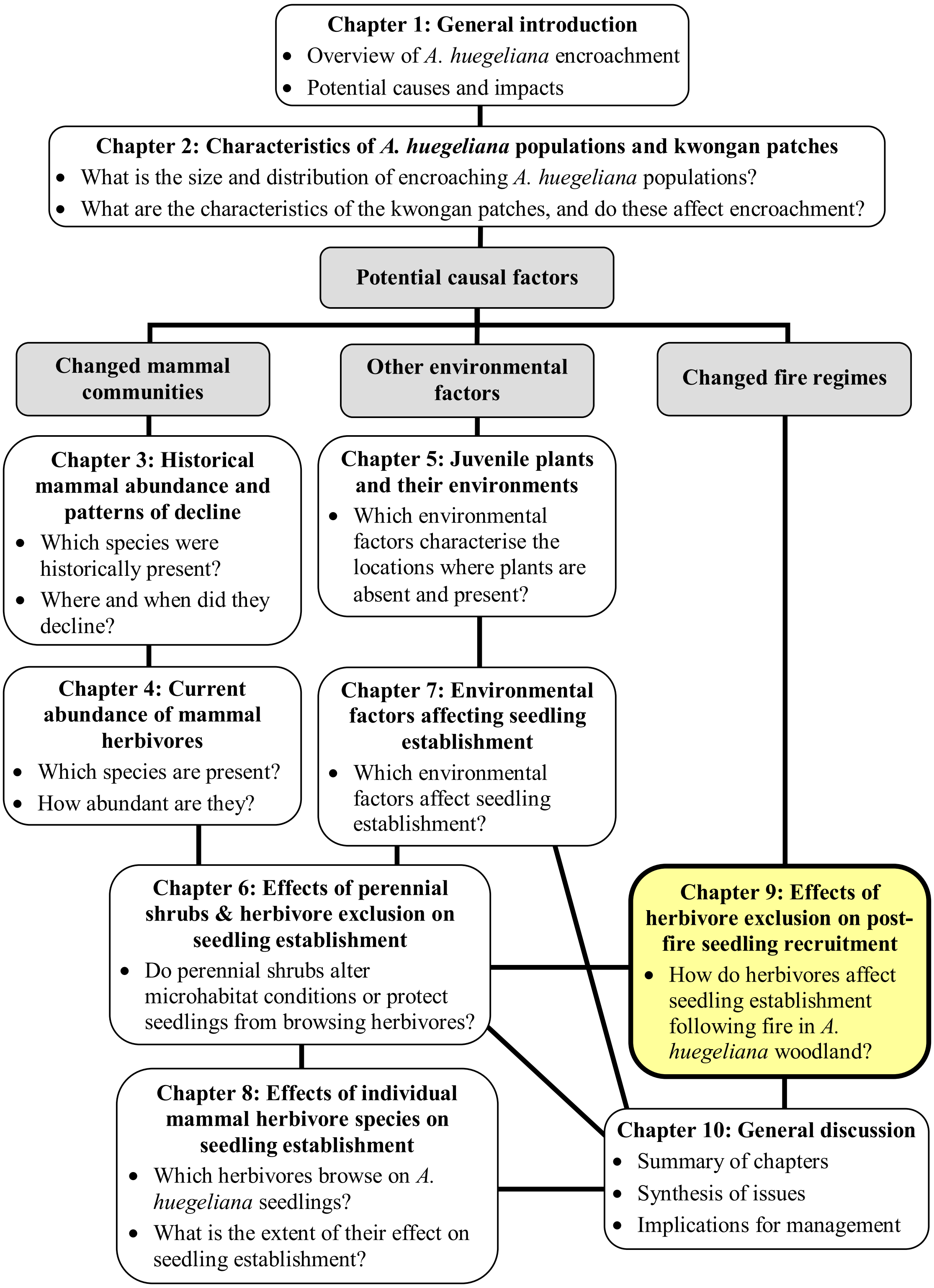
Seedling survival (sown seeds) appeared to be more favourable at location 3, but growth and survival of planted seedlings (green-stock) was more favourable at Location 2. These differences are most likely due to variations in biotic or abiotic conditions across the site which affects the favourability of the locations for establishment (Chapter 7).

Establishment also appears to vary substantially between sites within Tutanning. Seedlings survival (sown seeds) was much lower in this study than at another site at Tutanning where emergence and survival studies were conducted at the same time (Chapter 6). These differences are also likely to be due to variation in environmental conditions between the sites. The process of *A. huegeliana* invasion into kwongan is therefore complicated, and the rate of encroachment is affected by a number of factors that can vary between sites that at first glance appear to be relatively similar.

This chapter has shown that kangaroos are responsible for most of the browsing that occurs on *A. huegeliana* seedlings in kwongan. Seedlings are only able to establish in kwongan because they can escape browsing by establishing in perennial shrubs. However, without kangaroos the encroachment of *A. huegeliana* into kwongan would be much more extensive and rapid. Tammars have a limited effect on the establishment of *A. huegeliana* seedlings even where tammar densities are relatively high. It is therefore unlikely that the decline of tammars during the 1970s at Tutanning was responsible for *A. huegeliana* encroachment into kwongan at this reserve. The decline of mammal herbivores does not appear to be the main cause of *A. huegeliana* encroachment into kwongan in the Western Australian wheatbelt.

Chapter 9

Effects of herbivore exclusion on seedling recruitment following fire



9.1 Introduction

Chapters 6 and 8 showed that herbivores were unable to entirely prevent the establishment of *A. huegeliana* seedlings during long fire-free periods because the kwongan is dominated by woody shrubs that protect seedlings browsing herbivores. However, selective browsing by herbivores after fire, when the kwongan shrubs that previously protected seedlings from herbivores have been removed, may be important in limiting *A. huegeliana* seedlings that recruit in kwongan.

Browsing and grazing by native mammals has been shown to have a considerable effect on seedling survival in recently burned areas in a number of vegetation communities in Australia. Leigh and Holgate (1979) found that post-fire herbivory by eastern grey kangaroos, red-necked wallabies (*Macropus rufogriseus*) and wombats (*Vombatus ursinus*) caused a large decline in the survival of seedlings, and resprouting trees and shrubs. Meers & Adams (2003) illustrated how grazing by eastern grey kangaroos in areas of burnt Eucalypt open forest can significantly affect seedling density and survival. Three shrubs species were entirely eliminated from areas that were grazed. Following a fire in mallee vegetation, grazing by eastern grey and red kangaroos has been shown to reduce the survival of *Acacia* seedlings where the area burned was relatively small (20–50 ha) (Cohn & Bradstock 2000).

Browsing by smaller herbivores following fire has also been shown to limit seedling recruitment. Wykes & McArthur (1995) found that grazing by tammar wallabies on Garden Island following a small fire (9 ha) eliminated seedlings of the tree species *C. preissii* and *Melaleuca hueglii*. On nearby Rottnest Island, grazing by Quokkas (*Setonix brachyurus*) has been implicated in the failure of the tree species *Melaleuca* *lanceolata* and *Callitris preissii* to regenerate following fire (Rippey & Hobbs 2003). In addition to native mammal herbivores, grazing by rabbits (Leigh *et al.* 1987; Wimbush & Forrester 1988; Cohn & Bradstock 2000) and invertebrates such as grasshoppers (*Goniaea* spp.) has also been found to have a significant effect on seedling survivorship following fire (Whelan & Main 1979).

It was beyond the scope of this study to undertake experimental fires in kwongan where *Allocasuarina huegeliana* encroachment had occurred to determine the effects of post-fire browsing. However, an opportunity to observe the effects of herbivores on *A. huegeliana* recruitment following fire arose at Boyagin Nature Reserve when the Department of Environment and Conservation (DEC) carried out a prescribed burn covering 176 hectares of the reserve in early May 2004. A number of 10 × 10 m wire exclosures were erected after the fire in several different vegetation types, including two exclosures within *A. huegeliana* woodland. The exclosures excluded all vertebrate herbivores, including rabbits, and no herbivore scats were observed inside the fenced area.

This chapter aims to determine the effects of mammal herbivore browsing on the density and height of *A. huegeliana* seedlings after a fire in an area of woodland at Boyagin Nature Reserve in the Western Australian wheatbelt.

9.2 Methods and materials

9.2.1 Study site

Boyagin Nature Reserve is a remnant of natural bushland on the western edge of the Central Wheatbelt, located about 24 km north east of Pingelly (about 45 km northwest of Tutanning Nature Reserve). The 4780 ha reserve is comprised of two blocks (west and east) separated by a gap of approximately 500 m of farmland. The vegetation consists of *Eucalyptus wandoo*, *E. accedens* and *Allocasuarina huegeliana* woodland and areas of kwongan (Nevill 2001).

9.2.2 Effects of herbivore exclusion on seedling density and height

The effects of browsing and grazing on plant communities after fire have been assessed using used a range of measurements including survival, height, density, percentage cover, number of leaves, leaf area, and species richness, abundance and frequency (Leigh & Holgate 1979; Tozer & Bradstock 1997; Cohn & Bradstock 2000; Meers & Adams 2003; Rippey & Hobbs 2003; Hill & French 2004). Plant height and density are two measurements that can be measured are easily and rapidly and were therefore selected for use in this study. The above studies have ranged from 12 months to 8 years in duration; however, most have showed significant effects of herbivores on the plant community within the first two years after fire. Plant measurements for this study were recorded 30 months after fire and are therefore likely to show herbivore impacts on the regeneration of *A. huegeliana*.

A. huegeliana seedling heights and densities were recorded inside and outside the two exclosures in November 2006. Within each exclosure, sixteen 1 m × 1 m quadrats were located across an evenly spaced grid, and the number of seedlings within each quadrat was recorded. Outside each exclosure, four 1 m^2 quadrats were located within the 10 × 10 m areas adjacent to the four sides of the exclosure (total of 16 quadrats), and the number of seedlings was also counted. Seedlings heights were recorded from 32 randomly selected seedlings inside the exclosures, and from the same number of seedlings in the area surrounding the exclosure, up to 10 m away from the fence.

The effect of excluding herbivores on seedling height and density were examined using paired t-tests with the average seedling height and density for inside and outside each exclosure. Only two replicates were therefore available for analysis.

9.3 Results

9.3.1 Effects of herbivore exclusion on seedling density and height

Seedlings were taller inside the exclosures than outside the exclosures, where they were exposed to mammal herbivores. Seedlings were similar heights outside both exclosures, but were taller within Exclosure 1 than Exclosure 2 (Figure 9.1). Seedling densities were very high within Exclosure 2. Stem densities were low in comparison within Exclosure 1 and outside both exclosures (Figure 9.2). Results from the t-tests indicated that there was no significant difference in seedling height ($t_1 = 3.40$, $P = 0.182$) and density ($t_1 = 1.13$, $P = 0.462$) inside and outside the exclosures. It should be noted that the sample size was very small and seedling density variances were not equal, which limited the analysis.

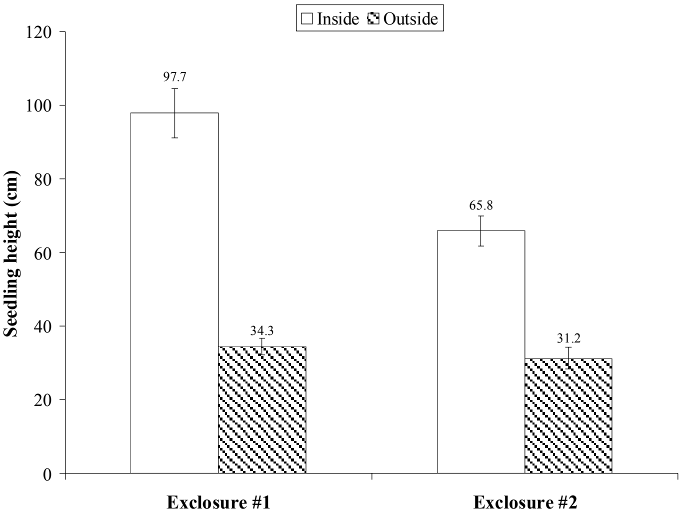


Figure 9.1: Mean seedling height (at two and a half years), inside and outside two exclosures located in an *Allocasuarina huegeliana* woodland burned in April 2004 at Boyagin Nature Reserve.

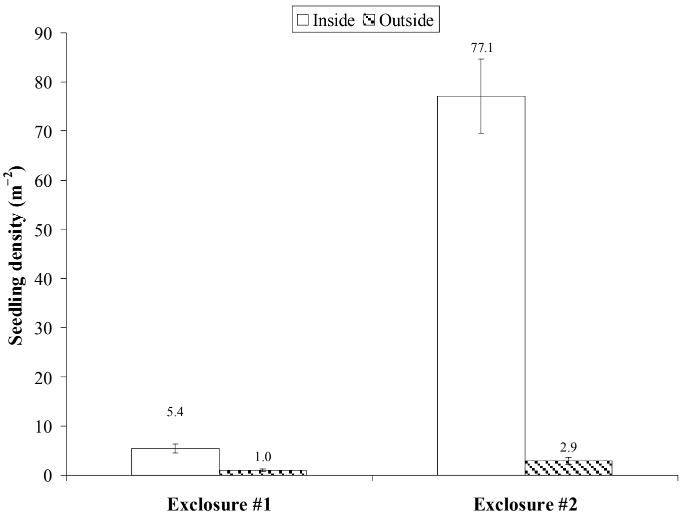


Figure 9.2: Mean seedling density (at two and a half years), inside and outside two exclosures located in an *Allocasuarina huegeliana* woodland burned in April 2004 at Boyagin Nature Reserve.

9.4 Discussion

Results from this study showed that *A. huegeliana* is a fast-growing species following fire, and browsing by herbivores has a significant impact on seedling height. Without herbivory, seedlings grew to heights of almost 1 m during the two and a half years following fire. At current levels of browsing pressure at this reserve seedlings were restricted to heights of less than 40 cm.

The suppression of seedling height growth by herbivores indicates that these trees would take longer to reach reproductive maturity. Propagule supply from the *A. huegeliana* woodland into neighbouring vegetation communities such as kwongan would therefore be lower for a longer period of time. Such a reduction in propagule pressure would potentially delay encroachment of *A. huegeliana* into kwongan, but how long this effect lasts is unknown.

A. huegeliana appears able to establish at high densities following fire. Seedlings established at densities ranging from 10 000 to 770 000 stems per hectare at Boyagin. Other studies have also shown prolific recruitment of *A. huegeliana* seedlings following fire. After a fire in the nearby Dryandra Nature Reserve the density of two-year-old *A. huegeliana* saplings varied from 16 800 to 103 600 plants per hectare (Ladd 1989). At Chiddarcooping Nature Reserve, located *ca.* 360 km northeast of Perth near the eastern margin of the wheatbelt, *A. huegeliana* seedlings established at densities of 548 000 plants per hectare following a fire in 1987 and around 300 000 plants per hectare following a fire in 2000 (Yates *et al.* 2003).

The limitations of the experimental design and the large differences in seedling densities between the two exclosures make it difficult to be conclusive about the effect of browsing on seedling density. The difference in seedling density between the two locations where herbivores were excluded may be due to natural patchiness in seedling density. Alternatively, factors such as the size of the seed bank, soil type or erosion may have varied between the two locations and affected the density of seedlings recruited. However, field observations indicated that herbivore exclusion had a substantial impact on recruitment at both exclosures (Figure 9.3).

The mammal community at Boyagin has undergone a similar decline in diversity and abundance to that experienced in remnants throughout southwest of Western Australia (Kinnear *et al.* 2002). During a survey in 1972 only one tammar was sighted and after intensive trapping in 1982 only one brushtail possum was captured (Kinnear *et al.* 2002). Fox baiting was implemented at Boyagin from 1985 to 1989 and most species have to some extent recovered. Woylies, numbats and quendas have been successfully reintroduced (Orell 2004). Tammar and brush wallabies are also present but only occur in small numbers (Kinnear *et al.* 2002; Orell 2004). The kangaroo population most likely remains similar to historical levels (see Chapter 3).

Field observations of herbivore scats around the exclosures at Boyagin indicated that kangaroos were the most abundant herbivore at the site and tammar wallabies were also present in low numbers. Although rabbits are assumed to be present at the reserve, no scats or warrens were observed at the site. Since rabbits rarely graze more than 300–400 m away from their warrens (Leigh *et al.* 1989), most of the post-fire browsing effects can be attributed to kangaroos and tammars.

The current herbivore community at Boyagin is comparable to the other wheatbelt Nature Reserves (Durokoppin, Dongolocking and Tutanning) studied in this project. Therefore, the herbivore communities present at these reserves are likely to have a similar effect on *A. huegeliana* recruitment if a fire was to occur. However, post-fire browsing may be more intense at reserves where mammal populations are more abundant, such as tammars at Tutanning or brush wallabies at Dongolocking. The effect of herbivores after fire can also be greater in smaller or patchy burns (Christensen & Maisey 1987; Cohn & Bradstock 2000).

The decline of herbivores and the loss of their ecological function in selective post-fire browsing have been implicated in vegetation change in other parts of Australia. Noble and Grice (2002) and Noble *et al.* (2007) suggested that in the semi-arid pastoral lands in eastern Australia, episodic fire and selective browsing by medium-sized marsupials including the burrowing bettong (*Bettongia lesueur*), brush-tailed bettong (*B. penicillata*) and bridled nailtail wallaby (*Onychogalea fraenata*), which are now regionally extinct or rare, contributed to regulating populations of native shrub species that are now regarded as ‘woody weeds’.

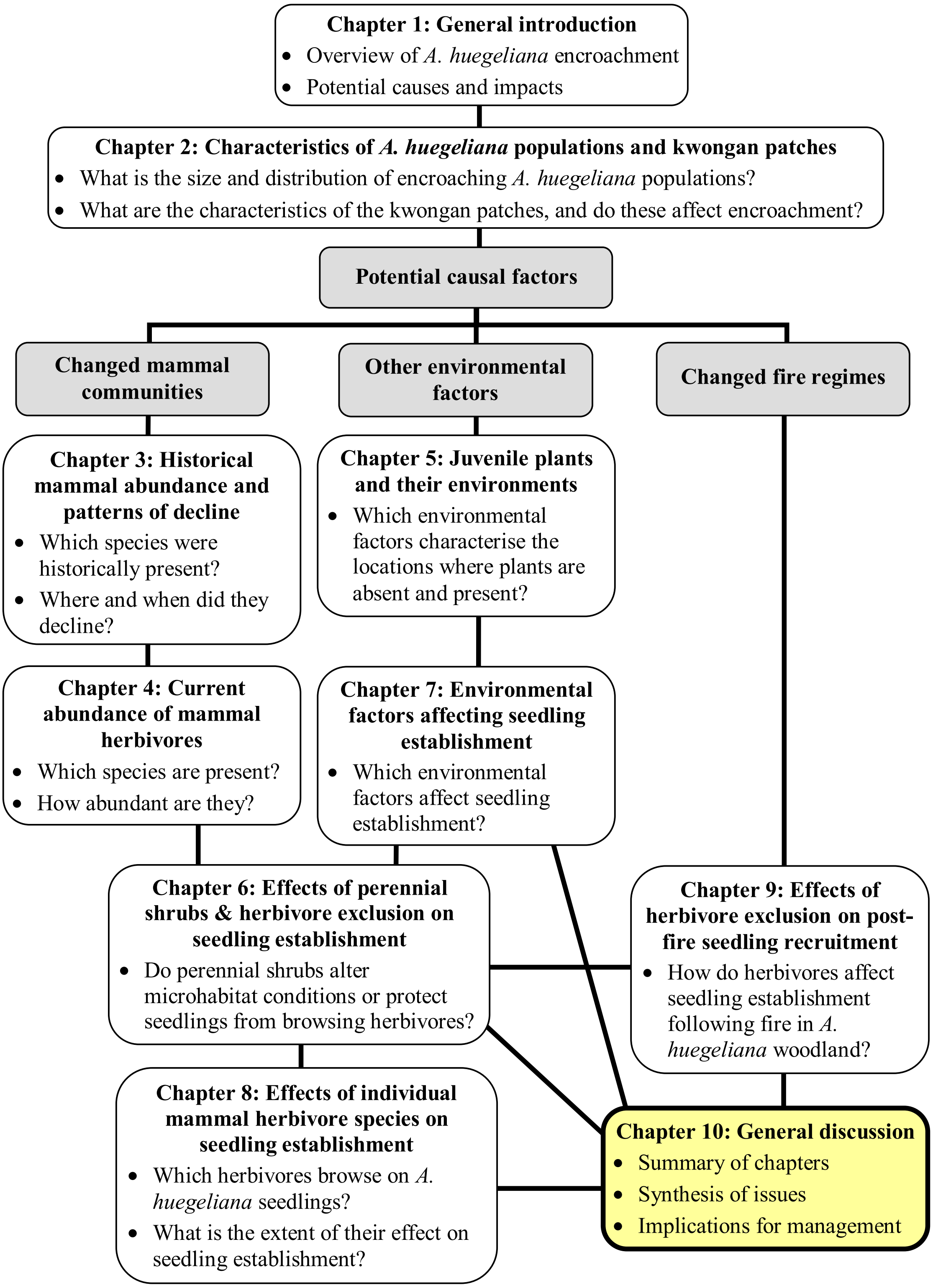
The burrowing bettong and brush-tailed bettong (or woylie) were historically present at all of the reserves studied (Chapter 3). The burrowing bettong is now locally extinct at all of these reserves and the brush-tailed bettong is only present in small numbers at Boyagin and Tutanning. The decline or absence of these species may also contribute to *A. huegeliana* encroachment into kwongan throughout the wheatbelt. However, if *A. huegeliana* populations are regulated through selective browsing following fire, the results from this study indicate that there are other mammal herbivores remaining at most reserves that would fulfil this function.

This chapter has shown that native herbivores, particularly kangaroos, can have a large impact on the recruitment of *A. huegeliana* seedlings following fire in woodland areas. However, the impact of browsing on *A. huegeliana* seedlings in kwongan after fire and whether current herbivore populations can eliminate *A. huegeliana* seedlings from kwongan remains to be seen. Results from this study suggest that recruitment of *A. huegeliana* seedlings following fire is likely to be very dense in patches of kwongan that are heavily invaded with many fruit-bearing trees. However, fire and post-fire herbivory may be able to eliminate most *A. huegeliana* seedlings within kwongan patches that have been less encroached upon. This can only be determined by undertaking experimental investigations after burning patches of kwongan of different sizes with different levels of *A. huegeliana* encroachment, ideally at several reserves. Unfortunately this could not be carried out during this study.

Figure 9.3: Photographs of Exclosure 1 (October 2005) in an area of *Allocasuarina huegeliana* woodland at Boyagin Nature Reserve burned in April 2004. Top: the exclosure fence line. Middle: *A. huegeliana* seedlings inside the exclosure. Bottom: (directly adjacent to the exclosure) limited *A. huegeliana* recruitment outside the exclosure.

Chapter 10

General discussion



Prior to this study, little was known about *A. huegeliana* encroachment into kwongan in the Western Australian wheatbelt. This lack of knowledge posed a problem for the conservation of remaining areas of kwongan in the region (Chapter 1). This study attempted to address these issues by determining whether the encroaching populations were likely to persist and increase, which factors affect the rate and extent of encroachment, and whether altered fire and browsing regimes were driving this process. This chapter will describe the findings of the study, propose a conceptual model of the encroachment process, discuss the limitations of the study and identify further research directions and explain other factors (than those investigated in this study) that may cause or contribute to encroachment. It will then describe the problems associated with conserving dynamic ecosystems and explain the need for urgent management and restoration strategies.

10.1 Summary of chapters

This study confirms that *A. huegeliana* has encroached into patches of kwongan in the central and southern wheatbelt, both where *A. huegeliana* woodland was an adjacent community and where it was not (Chapter 2). *A. huegeliana* has dispersed widely throughout these patches of kwongan and recruitment appears likely to continue in most areas. Although most sites were dominated by seedlings and juvenile plants, a few sites were dominated by large trees that had formed a dense canopy over the kwongan understorey (Chapter 2).

Few of the environmental factors measured in this study affected the extent of encroachment in unburned patches of kwongan (Chapter 2), the location of juvenile *A. huegeliana* plants (Chapter 5) or seedling establishment (Chapter 7). The primary requirements for *A. huegeliana* to establish in kwongan were a seed source (Chapters 2 and 5) and the presence of perennial shrubs (Chapters 5 and 6). In contrast to the commonly held understanding that vegetation communities in southwestern Australia are largely controlled by soil factors, these did not appear to limit *A. huegeliana* encroachment (Chapter 2). However, soil sampling was limited in both profile depth and in the range of properties analysed.

Perennial shrubs were important for seedling establishment because they provided a refuge from browsing mammal herbivores, rather than by improving microhabitat conditions (Chapter 6). Western grey kangaroos browsed extensively on *A. huegeliana* seedlings in areas with no vegetation cover (Chapter 8) and significantly reduced the number of seedlings that established in kwongan (Chapters 6 and 8). Mammal herbivores were unable to entirely prevent the establishment of *A. huegeliana* seedlings in kwongan because numerous seedlings escaped browsing by establishing in perennial shrubs (Chapter 6).

Although the mammal communities varied among the reserves, the abundance of western grey kangaroos was similar (Chapter 4) and browsing pressure on *A. huegeliana* seedlings in kwongan was also similar (Chapter 6). This is likely to be the case with other reserves of a similar or larger size throughout the wheatbelt. However, in smaller vegetation remnants kangaroos may be absent or their populations less abundant (Arnold *et al.* 1995). In these areas browsing pressure would be lower and encroachment of *A. huegeliana* into kwongan is therefore likely to be more rapid and extensive (Chapter 8).

Main (1993) proposed that the decline of native mammal herbivores was responsible for *Allocasuarina* encroachment. In particular, the decline of tammar wallabies during the 1970s at Tutanning enabled *A. huegeliana* to encroach into kwongan. Mammal communities are less diverse and most species less abundant now than they were at the time of European settlement (Chapter 3). However, the patterns of decline from the 1900s onwards were very different among the reserves studied and there was no native mammal common to all three reserves that declined around the time many *A. huegeliana* plants began to establish in kwongan in 1970s (Chapter 3).

Although the population of tammars declined massively at Tutanning during the 1970s, they have since recovered to levels where they are locally considered to be pests (Chapter 3). Tammars had a limited effect on the establishment of *A. huegeliana* seedlings at Tutanning even where their densities were relatively high (Chapter 8). In addition, brush wallaby populations appear to have recovered at a site at Dongolocking (Chapter 4), but huge numbers of seedlings are establishing in kwongan it this remnant (Chapter 2). It therefore appears unlikely that the decline of a single mammal species, including tammars, is the main cause of *A. huegeliana* encroachment.

10.2 Conceptual model of *Allocasuarina huegeliana* encroachment

A. huegeliana encroachment into kwongan appears to be driven primarily by increasing propagule pressure from adjacent or nearby *A. huegeliana* woodland and exacerbated by the availability of safe sites within mature woody shrubs. If sufficient amounts of seed enter a site to allow a species to overcome recruitment limitation many native or naturalised plant species can become established and persist in sites from which they were previously absent (Tilman 2004). Propagule pressure and woody shrub development are both driven by increased inter-fire intervals.

As time since fire increases, *A. huegeliana* trees grow taller and canopy sizes increase. Consequently, the supply of propagules and dispersal distance into nearby kwongan also increases (Figure 10.1). Kwongan shrubs grow larger as time progresses and provide safe sites for *A. huegeliana* seedlings to establish where they are inaccessible to browsing herbivores. If no fires occur, the kwongan shrubs eventually senesce and inter-specific competition is reduced. However, field observations suggest that senescent shrubs would continue to provide a physical barrier that prevents herbivores from browsing on seedlings that establish within them. As the *A. huegeliana* plants that have established in kwongan grow and reproduce, they further increase propagule pressure. Seedlings continue to establish increase until the carrying capacity of the site has been reached.

Fire appears to be the only mechanism that could prevent encroachment by killing the source supply of propagules from *A. huegeliana* trees in neighbouring woodland areas, removing kwongan shrubs that protect seedlings from herbivores and killing any *A. huegeliana* seedlings that have established in kwongan. Selective browsing by native mammal herbivores following fire may also be important in removing *A. huegeliana* seedlings that establish in kwongan following fire (Chapter 9).

Fire regimes have been dramatically altered throughout the wheatbelt and many kwongan remnants that were historically burned at frequencies of between 1 and 20 years have not been burned for more than 60 years (Chapter 1). To inhibit *A.*

huegeliana encroachment in the past, fires would have had to occur at intervals frequent enough so that few *A. huegeliana* plants established in kwongan and matured to produce fruit. *A. huegeliana* may shed seed throughout the year, but there is always carry-over of propagules in the canopy (Ladd 1989). This species is therefore able to regenerate prolifically after fire because a heavy seed rain is released from the cones stored in the canopy (Ladd 1989). When encroaching populations are producing fruit, fire may therefore promote regeneration of *A. huegeliana* rather than inhibiting it. However, if patches are subjected to successive fires at short intervals *A. huegeliana* may also be removed.

10.3 Study limitations and further research directions

The research in this thesis focussed on the effects of browsing by mammal herbivores and a range of environmental factors on *A. huegeliana* establishment in unburned kwongan. While the effects of these factors have been clarified to an extent, there are a number of limitations to the findings of this study. These limitations arise from both the studies that were carried out and from the areas that were not investigated and include incomplete knowledge about the effects of encroachment on kwongan, the effect of interactions among patch-scale characteristics on the extent of encroachment, the role of soil in determining the vegetation communities it supports, and the effects of fire and post-fire herbivory on kwongan and encroaching *A. huegeliana* populations. These factors may have an important effect on *A. huegeliana* encroachment. Research into these areas would provide a greater understanding of the processes driving *A. huegeliana* encroachment and benefit the development of appropriate and effective management strategies.

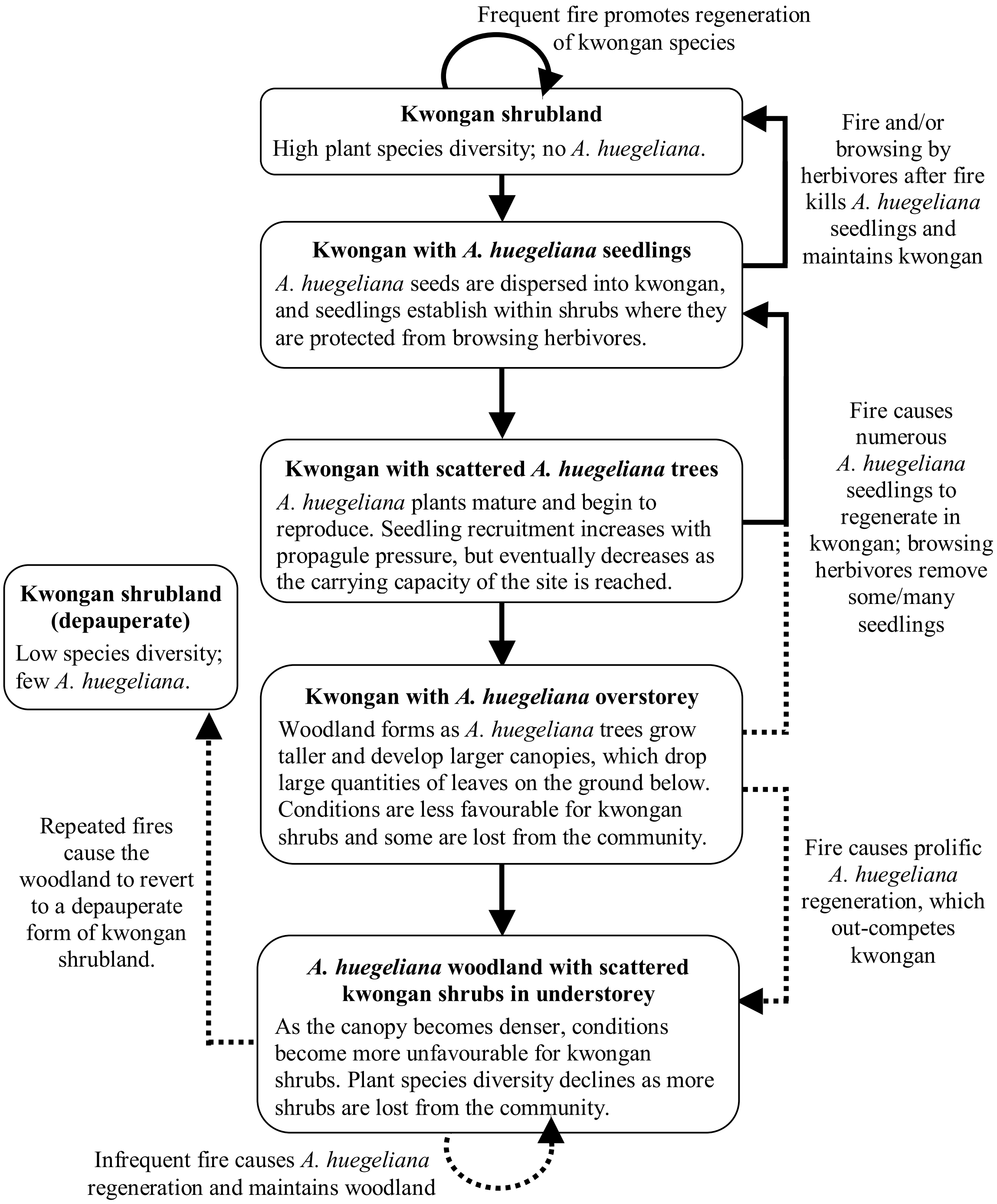


Figure 10.1: Conceptual diagram of *Allocasuarina huegeliana* encroachment into kwongan and the changes in structure and composition that is likely to occur over time as the community progresses from kwongan shrubland to *A. huegeliana* woodland in the absence of fire. The first three boxes encompass the transitions covered in this thesis. The solid arrows indicate possible changes to the community if fire and selective browsing by herbivores (following fire) were to occur at the different stages of development. The lower two boxes are largely speculative and the dashed arrows indicate totally speculative transitions.

10.3.1 Impacts of encroachment on kwongan

This study did not examine the impact of *A. huegeliana* encroachment on species richness and composition of kwongan, or on other factors such as soil properties and fire regimes. Due to the high degree of heterogeneity among patches of kwongan (Chapter 2), a comparison of sites where *A. huegeliana* had and had not colonized would not provide reliable analysis of the effects of encroachment. Historical data sets of species richness and abundance in patches of kwongan at Tutanning exist (Brown & Hopkins 1983), and some of patches have since been encroached upon while others have not. Re-surveying these sites may provide a valuable insight into the effects of encroachment on kwongan.

The impacts of *A. huegeliana* encroachment in a heterogeneous system such as kwongan may alternatively be assessed at smaller scales by undertaking chronosequence studies within particular sites, for example Costello *et al.* (2000). However, such studies require the accurate identification of tree growth ring markers. This study found that reliable growth rings could not be identified for *A. huegeliana.* If further studies are also unsuccessful in establishing dendrochronological sequences for *A. huegeliana* surrogate characteristics for age, such as height, stem diameter and canopy size, may be useful in determining the effects of encroachment on species richness as time progresses. Such information is essential to better understand the potential loss of species from this high conservation value community and thus clarify the urgency of this issue.

The impact of *A. huegeliana* encroachment on soil properties may have a significant effect on the persistence of kwongan. Main (1993) suggested that the increased densities of *Allocasuarina* cause greater quantities of nitrogen to be fixed in the soil and contributes to soil acidity. He further proposed that *Allocasuarina* can grow in acid conditions to its advantage relative to other shrubs and so contributes to their decline in abundance. An assessment of the impacts of *A. huegeliana* on soil properties should indicate whether mature stands of this species can raise soil nutrient or acidity levels to an extent that the sites can not support kwongan again i.e. they form alternative stable states, even if repeated fires were implemented.

Mature *A. huegeliana* stands may alter fire regimes and, in turn, have an important effect on the regeneration potential of kwongan. Mature stands of *A. huegeliana* may inhibit fires and thereby help perpetuate the encroachment process. This issue, and the others described above, is likely to become of increasing importance as the current, recently invaded sites become dominated by mature *A. huegeliana* stands.

10.3.2 Patch-scale characteristics

The effect of interactions among patch-scale characteristics (e.g. time-since-fire, propagule pressure, and soil type) on the extent of encroachment at each patch could not be analysed because there were not enough patches to fit multiple regression models. A broader survey of kwongan throughout the wheatbelt to include patches that have and have not been colonized by *A. huegeliana*, and characteristics such as herbivore abundance, may provide a greater understanding of the interactive effects of these patch-scale characteristics on the extent and rate of encroachment that were not detected in this study. A greater understanding of these effects may identify particular characteristics that indicate the susceptibility of a kwongan patch to encroachment, which would assist in prioritising remnants for management.

10.3.3 Soil analyses

Results from this study found that *A. huegeliana* encroachment is occurring in a range of soil types, and that this factor did not appear to exclusively determine vegetation community boundaries (Chapter 2). However, soil sampling was limited in depth (only the top 10 cm was sampled) and the analysis did not include factors such as compaction, organic matter, nutrients or a range of other chemical properties that may affect *A. huegeliana* establishment. Additionally, soil sampling was limited to kwongan. Sampling areas of *A. huegeliana* woodland through the boundary transition areas and into kwongan may reveal more about the differences in soil characteristics between the two vegetation communities.

10.3.4 Effects of fire and post-fire browsing in kwongan

No experimental fires were carried out in this study and therefore a number of uncertainties remain about the role of fire and post-fire browsing in preventing *A. huegeliana* encroachment in the past, and whether these can be used as tools to eliminate *A. huegeliana* from patches of kwongan that have been encroached upon. Key questions that remain include:

- Can shorter fire intervals can prevent encroachment by *A. huegeliana*. If so, what fire interval length is appropriate?
- Do *A. huegeliana* seedlings commonly recruit in kwongan that has not been encroached upon after fire, particularly in areas bordering *A. huegeliana* woodland? If so, what eliminates these seedlings (e.g. browsing or interspecific competition) after fire to maintain the kwongan structure?
- What are the effects of fire in kwongan that has been encroached upon to a varying extent on *A. huegeliana* recruitment?

- Can successive fires within a short interval (e.g. 5 years) eliminate *A. huegeliana* from kwongan that has been encroached upon without adversely affecting the kwongan community?
- Can post-fire browsing by vertebrate and invertebrate herbivores eliminate *A. huegeliana* seedlings from kwongan that has been encroached upon? If so, what extent of encroachment is reversible by fire and post-fire browsing?

10.4 Other potential causal factors of encroachment

Altered fire and browsing regimes are commonly identified as factors causing encroachment and were the focus of this study. However, a range of other factors have also been implicated as causing encroachment in other systems including increased seed dispersal, climate change, increased atmospheric carbon dioxide (CO_2) concentrations and combinations of these factors (Neilson 1986; MacDonald *et al.* 1993; Polley *et al.* 1994; Savage *et al.* 1996; Weltzin *et al.* 1997; Allen & Breshears 1998; Soulé *et al.* 2003).

10.4.1 Climate change

Studies of vegetation history using pollen analysis have suggested that *Casuarina* [*Allocasuarina*] was much more abundant in the past (> 1000 years) in some parts of Australia (Singh *et al.* 1981; Singh & Geissler 1985; D'Costa *et al.* 1989; Ladd *et al.* 1992; Martin & McMinn 1994; Harle *et al.* 2002; Hope *et al.* 2004). In many areas *Casuarina* has since been replaced by eucalypt and heath vegetation (Kershaw *et al.* 2002). The causes of *Casuarina* decline is much debated and has been attributed to climate change causing increased rainfall and leaching of soils that would favour other vegetation types (Ladd *et al.* 1992); increased fire frequencies as a consequence of either increased biomass production due to increased rainfall (Ladd 1989), or the arrival of Aboriginal people to Australia (Singh *et al.* 1981; Singh & Geissler 1985); and increased soil salinity and/or rising groundwater levels (Crowley 1994).

More recent changes in climate have also been cited as a major factor driving woody plant encroachment, but evidence in support of this contention is mixed. Williams *et al.* (1987) and Hobbs & Norton (2004) found that the rate of transition from annual grassland to shrubland in northern California, USA, was greatest during 1982–83 when the highest levels of rainfall ever were recorded in the area. Shrub encroachment into *Eucalyptus* semi-arid savanna in north-western New South Wales, Australia, is also considered to occur during wet periods when soil moisture is sufficient for shrub seedlings to establish (Hodgkinson 1991). However, other studies have found no clear trends in increases in woody plant cover with changes in climate (e.g. Veblen & Lorenz 1988; Bahre & Shelton 1993; Knapp & Soule 1998; Dullinger *et al.* 2004; Briggs *et al.* 2005; Norman & Taylor 2005).

Winter rainfall has decreased in the southwest of Western Australia since the mid 1970s by about 15–20%, which has been attributed to natural variability and the enhanced greenhouse effect (IOCI 2002). While such changes would inevitably impact on ecosystem dynamics, encroachment has been primarily associated with periods of increased rainfall when conditions are more favourable for seedling recruitment (Savage *et al.* 1996; Mast *et al.* 1998; Ansley *et al.* 2001; League & Veblen 2006). Periods of drought, on the other hand, have been associated with widespread shrub and tree mortality and a consequential reduction in woody cover (Archer *et al.* 1988; Allen & Breshears 1998; Fensham *et al.* 2005). Although drought may reduce the competitive effects of kwongan shrubs, it would appear unlikely that the decline in rainfall across the wheatbelt would cause *A. huegeliana* seedlings to establish.

10.4.2 Altered hydrology

The Western Australian wheatbelt had undergone significant hydrological change over the past 100 years. The broad scale clearing of perennial native vegetation and its replacement with annual crop plants has led to increased deep drainage of soil water and increased groundwater recharge. This has caused the development of shallow water tables and land surface salinisation (Peck & Williamson 1987; George 1992; McFarlane *et al.* 1993). It may be possible that higher water tables levels are benefiting trees such as *A. huegeliana*, as the (generally) deeper root systems of trees come into contact with a rising water table earlier than understorey species (Cramer *et al.* 2004). Species of *Casuarina* [*Allocasuarina*] are among the most tolerant of Australia species to waterlogging and salinity (Bell 1999). Therefore, kwongan shrubs may be less able to tolerate increased levels of salinity than *A. huegeliana*, thereby decreasing plant vigour and competition with establishing seedlings.

Many areas in the wheatbelt are affected by salinisation and waterlogging, and at most immediate risk are those systems that occur in the lowest landscape positions (Cramer & Hobbs 2002). A major topographical division exists between the valley floors and the uplands that support kwongan (Beard 1990). Rising water tables will affect the valley floors and some of the lower slopes, while systems located higher in the landscape (including kwongan) will be more protected from rising groundwater (Cramer & Hobbs 2002). Since kwongan is located high in the landscape the water table most likely remains relatively deep in these areas and would subsequently have little impact on vegetation in these systems. If a rising water table benefited *A. huegeliana* it would only benefit mature trees with deep root systems that could access the water, not seedlings with shallow root systems. These changes are therefore unlikely to cause increased seedling establishment in kwongan.

10.4.3 Increased atmospheric carbon dioxide (CO_2)

Increased atmospheric CO_2 concentrations have recently been implicated in causing shrub and tree encroachment (Polley *et al.* 1994; Bond & Midgley 2000; Bond *et al.* 2003; Soulé *et al.* 2003) through increasing biomass production and water use efficiency, and improving the ability of plants to cope with environmental stresses (see Knapp & Soule 1998). However, the mechanisms linking increased levels of CO_2 and encroachment are disputed in other studies (e.g. Archer *et al.* 1995; Wand *et al.* 1996; Van Auken 2000). In their study on the effects of increased CO_2 and land use on Australian vegetation over the past 200 years, Berry & Roderick (2002) concluded that encroachment may have been exacerbated by the increase in CO_2, but other changes associated with European settlement were important.

The effects of elevated atmospheric CO_2 are thought to preferentially benefit woody as opposed to herbaceous species (Idso & Kimball 1993). Increased CO_2 may therefore explain woody plant encroachment in grasslands or savannas (e.g. Bond & Midgley 2000; Bond *et al.* 2003). However, kwongan is dominated by woody shrubs. Elevated levels of atmospheric CO_2 should therefore benefit both *A. huegeliana* and kwongan shrubs. However, it may be possible that certain species such as *Allocasuarina* are able to respond disproportionately to increasing CO_2 through some as yet unexamined differential effect. For example, increasing CO_2 may affect the symbiotic relationship between *Allocasuarina* species and the nitrogen fixing bacteria *Frankia* or mycorrhizal fungi to enable greater nitrogen or nutrient uptake and thus benefit *A. huegeliana* over kwongan species.

10.4.4 Reduced abundance of seed predators

Another factor that may be contributing to *A. huegeliana* encroachment is the reduction of seed predators. Carnaby's Black-Cockatoo (*Calyptorhynchus latirostris*) is endemic to the southwest of Western Australia. These cockatoos feed primarily in woodland and kwongan and their main food is seeds from species of *Banksia*, *Dryandra*, *Hakea*, *Grevillea*, *Allocasuarina* and *Eucalyptus* (Saunders 1980). Carnaby's cockatoo has undergone a major decline particularly in the drier areas of its range and the central wheatbelt (Saunders 1990). Between 1968 and 1987 this species disappeared from over one third of its range, with both reduced density and local extinctions (Saunders & Ingram 1995). It is unknown whether Carnaby's cockatoos consume *A. huegeliana* seed. However, other Black-Cockatoo species are known to consume large quantities of *Allocasuarina* seed and for some species it is their primary food source (Joseph 1982; Pepper *et al.* 2000; Crowley & Garnett 2001). It is therefore possible that the decline of Carnaby's cockatoos may have caused a decline in *A. huegeliana* seed predation and subsequently increased propagule supply into kwongan.

A range of factors may be responsible for *A. huegeliana* encroachment. These factors may act alone or synergistically with each other and/or with altered disturbance regimes to cause or exacerbate encroachment. In complex systems such as these, it is unsurprising that *A. huegeliana* encroachment may be the result of multiple interacting causal factors. This study investigated a subset of factors that were thought to be causing *A. huegeliana* encroachment and was of most proximal relevance to management.

10.5 Problems associated with conserving dynamic ecosystems

This study of *A. huegeliana* encroachment highlights the problems inherent in conserving dynamic ecosystems, not only in the Western Australian wheatbelt, but elsewhere in Australia and around the world. This study adds to the growing number of observations of ecosystems that are changing due to encroachment by species that were formerly more restricted in range or abundance (Veblen & Lorenz 1988; Cheal 1996; Lunt 1998b; Rose *et al.* 2000; Roques *et al.* 2001; Kirkpatrick 2004; Briggs *et al.* 2005; Franco & Morgan 2007). These studies emphasise the need for active management to conserve vegetation communities in a particular desired state, rather than assuming that species assemblages would be maintained by 'natural processes'.

In systems where rapid change is occurring, decisions need to be made relating to what management goals should be. Should remnant vegetation be actively managed to maintain what is (or was) there? Or should these areas be left alone to enable current ecosystem processes to reach a new equilibrium even if this means a loss of plant species? Franco & Morgan (2007) suggest that one way to resolve this question is to ask what vegetation structure conserves the greatest overall biodiversity (including plants, invertebrates and vertebrates) and what management regimes are required to maintain this structure.

In the context of this study, conserving kwongan is particularly important due to its floristic diversity and high levels of endemism. However, conserving both kwongan and *A. huegeliana* woodland communities would most likely provide the greatest value to overall biodiversity. However, the reality of complex systems is that vegetation of the future will probably differ from the vegetation state chosen for conservation regardless of the management inputs imposed (Lunt 1998b).

10.6 Need for management of remnant vegetation in the wheatbelt

Conservation in fragmented ecosystems such as the Western Australian wheatbelt aims to maintain viable and representative species assemblages. Recently, much attention has been focused on conservation of areas threatened by processes such as salinity and grazing by livestock. There are also large areas that are not at risk from these processes, yet these areas are essentially unmanaged since there is a perception of lower levels of threat. This study has shown that in the absence of human intervention, 'natural processes' will not maintain *A. huegeliana* woodland–kwongan boundaries in remnant vegetation in the wheatbelt. These communities may be under increasing levels of threat if encroachment results in the loss of plant diversity as *A. huegeliana* forms dense stands that prevent kwongan species from regenerating.

In order to conserve both kwongan and *A. huegeliana* woodland communities, restoration strategies are required to control or eliminate *A. huegeliana* populations that have already invaded heathlands. Management strategies also need to be implemented to prevent invasion occurring at other locations. Actions to eliminate or control *A. huegeliana* populations in patches of kwongan that have been encroached upon need to occur urgently while most sites are dominated by seedlings and juvenile plants (Chapter 2), and thus fewer resources are required for management, and restoration outcomes are more likely to be successful.

This study has shown that a range of potential factors may cause *A. huegeliana* to encroach into kwongan and multiple factors may interact to affect encroachment. Results have shown that changes in native mammal fauna are unlikely to be a main factor causing encroachment, and therefore the reintroduction of native mammal species is unlikely to affect this process. Increased fire intervals appear to be a likely factor driving *A. huegeliana* encroachment in kwongan. However, further research is required to determine whether this is the case and, if so, how best to use fire as a tool to manage *A. huegeliana* encroachment.

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