EFFECTS OF SHEEP, KANGAROOS AND RABBITS ON THE REGENERATION OF TREES AND SHRUBS IN THE CHENOPOD SHRUBLANDS, SOUTH AUSTRALIA

by

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Conference papers

F. Tiver, J. Boland, K. Rosenberg, L. McArthur, I. Watson, T. Auld, A. Denham, **R. Palisetty,** A. Stokes, & L. Farroway (2006) A stage-structured projection model incorporating the effects of grazing management and rainfall on populations of shrubs and trees in the Australian rangelands. In *Proceedings of the Australian Rangeland Society Conference*, 4-7th Sept 2006, Renmark, 380-383.

R. Palisetty, F. Tiver, J. Boland, K. Rosenberg, L. McArthur, I. Watson, T. Auld, A. Denham, A. Stokes, & L. Farroway. (2006) Using a stage-structured projection model to predict the sustainability of populations of shrubs and trees in the chenopod rangelands of eastern South Australia. In *Proceedings of the Australian Rangeland Society Conference*, 4-7th Sept 2006, Renmark, 304-308. **(Invited for submission to a Special Edition of "The Rangelands Journal").**

To my grandmother for her endless love and affection

Abstract

After European settlement, Australian rangelands especially in South Australia underwent significant changes because of the main land use of pastoralism. Many studies have revealed that the plant communities are negatively effected by herbivory mainly by sheep. The main aim of this study is to separate the different effects of sheep, rabbits and kangaroos. This was examined by survey supported by experimental and modeling research.

A 32,000 km^2 area previously surveyed by Tiver and Andrew (1997) in eastern South Australia was re-surveyed to monitor populations of perennial plant species at sites of various intensity of grazing by sheep, rabbits and kangaroos (goats populations are low in the study area), the most important vertebrate herbivores. Plant population data were collected in both sheep paddocks and historically ungrazed by sheep (road reserves) by using the Random Walk method and analyzed using Generalized Linear Modeling (GLM) to separate the effects of sheep and rabbits on plant regeneration and their regeneration in response to grazing. These data were also compared to similar data collected by Tiver and Andrew in 1992 (1997) to ascertain if the reduction in rabbit numbers through introduction of RCV had allowed increased regeneration. Regeneration of many species inside paddocks were negatively affected and species in roadside reserves neither did not significantly increase from 1992 to 2004. However, some species showed increase of populations in spite of sheep grazing, with some species being less susceptible than others. This research also indicates kangaroo grazing impact on some plant species. Reduction in rabbit numbers following the 1995 release of calicivirus has not been effective in restoring regeneration. Another experiment was conducted at Middleback Field Station near Whyalla to identify herbivore grazing pressure on the arid zone plant species *Acacia aneura* using unfenced, sheep fenced and rabbit fenced grazing exclosures. This experiment was set up with seedlings in exclosures, ten replicates of each treatment, at plots four different distances from the watering point to identify the survivorship of seedlings. Data were collected by recording canopy volumes of seedling over an 18 month period and analyzed by Residual Maximal Likelihood (REML). Seedlings both near and far from the watering point were severely effected by large herbivores, either sheep, kangaroos or both, and in a separate experiment kangaroo grazing effects on the seedling were also identified. Seedlings browsed by the rabbits were recovered better than the seedlings grazed by the large herbivores. Decreasing kangaroo activities has been noticed when the rabbit movements increased. Computer modeling was conducted to predict the future plant population structure over 500 years using a matrix population model developed by Tiver *et al.* (2006) and using data collected in the survey as a starting point. Extinction probabilities of populations of *Acacia aneura* near watering points, far from watering points and under pulse grazing scenarios were compared. Sheep grazing was found to cause eventual extinction of populations in all parts of sheep paddocks. Together, the results indicate that sheep are the major herbivore suppressing regeneration of perennial plant species. Kangaroo and rabbits have an identifiable but lesser effect. The results have implications for conservation and pastoral management. To achieve ecological sustainability of arid lands a land-use system including a network of reserves ungrazed by sheep and with control of both rabbit and kangaroo numbers will be required.

Declaration

I declare that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge it does not contain any material previously published or written by another person except where due reference is made in the text.

Raghunadh Palisetty September 2006

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Glossary

ABARE	Australian Bureau of Agricultural and Resource Economics
Age-class	The abundance of plant individuals recruited at the same time
Age structure	The relative abundance of different age-classes in a population
CASL	Community Adaptation and Sustainable Livelihoods
CSIRO	Australian Commonwealth Scientific and Industrial Research Organization
DKCRC	Desert Knowledge Cooperative Research Centre
GLM	Generalized Linear Modeling
ICV	Index of Canopy Volume
NPWSA	National Parks and Wildlife Service of South Australia
Pastoralism	The extensive grazing of livestock
PSSADEH	Pastoral Secretariat (South Australian Department of Environmental and Heritage)
Rangelands	Land used for pastoralism
RCD	Rabbit calicivirus disease (also known as RHD)
REML analysis	Residual Maximal Likelihood analysis
RHD	Rabbit haemorrhagic disease (also known as RCD)
SA	South Australia
SAMM	Spatial Analysis Mixed Models
Stage-class	Abundance of different individuals of uniform size, even they recruited at different time intervals
Stage structure	The relative abundance of different stage-classes in a population
λ (lambda)	Population growth rate

Chapter 1

Introduction

Arid lands and rangelands

Rangelands are one of the largest and most widespread terrestrial natural resource regions on the Earth's surface (Tueller 1988), occupying approximately 47% of global land surface (Williams *et al.* 1968). When the term rangeland first came in to use, it was only used to describe extensive, unforested lands having at least one of the following characteristics: very high temperature fluctuations, unpredictable rainfall, poor soil characteristics, or extended drought periods, which together limit agricultural practices (Box 1986; Tueller 1988). Now most of the natural grazing lands come under this category which includes a variety of ecosystems: alpine communities, wetlands, grasslands, savannas, shrublands, steppes, mountain plains and deserts. Arid lands are characterized by low precipitation that supports only sparse vegetation and reduced human and animal populations, and are often referred to as deserts. World deserts are grouped into four categories: subtropical (hot), coastal, cold winter and polar regions, on the basis of their climatic and environmental conditions. Arid and semiarid rangelands are the most common type occupying 33% of the world land surface (Perry 1979). Although cultivated agricultural practices are minimal, rangelands support human populations by providing living areas, grazing lands for pastoralism, mining and wood products (CASL 2006). In recent years tourism and recreational use of rangelands have increased.

Australian arid lands

According to the Bureau of Australian Statistics, 75% of the Australian continent (about 6 million km^2) is arid or semi arid. The Australian deserts are hot deserts (Evenari 1985) with plant species dominated by *Acacia*, *Casuarina*, and *Atriplex.* Australian arid and semi arid lands include native grasslands, shrublands and woodlands (ABARE 1993). Australian arid lands are unusual in having a higher cover of deep rooted trees, shrubs and perennial grasses for a given aridity than those elsewhere (Williams & Calaby 1985;

Stafford-Smith & Morton 1990). Soils are sorted, highly weathered and of low fertility. The levels of nitrogen and phosphorus are half those of the other hot deserts (Stafford-Smith & Morton 1990).

Australian rangelands

Nearly 75% of Australia (Harrington *et al.* 1984; Wilson 1990) and 80% of South Australian land is considered as semi arid or arid (Osborn 1926). The southern Australian arid lands are dominated by shrubs in the family Chenopodiaceae and are called chenopod shrublands. As a resource base they play an important role for the pastoral industry by providing fodder to domestic animals (Hacker 1987) especially when herbage is limited in biomass or low in protein content (Preece 1971).

Effects of grazing on Australian rangelands

There is a considerable evidence showing that herbivores are capable of selectively eliminating the juveniles of various trees and shrub species in the southern Australian rangelands: sheep and rabbits have been shown to affect regeneration of a range of species in chenopod shrublands of South Australia (e.g. Lange & Purdie 1976; Lange & Graham 1983; Andrew & Lange 1986a; Tiver & Andrew 1997; Hunt 2001; Heshmatti *et al.* 2002; Tiver & Keiermeyer 2006) and the survival of some species is at risk (Crisp & Lange 1976; Crisp 1978; Harrington 1979; Lange & Willcocks 1980; Chesterfield & Parsons 1985; Lange *et al.* 1992). These reduced levels of regeneration mean that populations of some palatable species are declining whilst others, unpalatable to herbivores, are being maintained or even increasing, hence gradually altering the composition and/or overall cover of vegetation. In the long term, this could result in loss of palatable species valuable to the pastoral industry for animal production and/or the dominance of large areas by undesirable "woody weed" species. The loss or reduction in cover of a number of tree and shrub species is in itself a significant loss of biodiversity and one which could lead to other consequences. The habitat and resource loss caused by removal of the important structural dominants may cause enhanced soil erosion and reduce biodiversity of other organisms in the system such as birds and small mammals which are dependent on the plants for food and shelter (Graetz & Wilson 1984).

Although a few anecdotal and scientific studies has reported that RCD is have a the potential of increase regeneration of native tree and shrubs of Australian rangelands. But a few studies compare effects of sheep and rabbit simultaneously (exception of this is (Crisp & Lange 1976)).

Role of watering points in Australian rangelands

Artificial and natural water resources have a major influence on the distribution of animals and plants in arid and semi-arid regions worldwide (Valentine 1947; Lange 1969; Fusco *et al.* 1995). Their influence on Australia's flora and fauna after European colonization is well documented (Osborn *et al.* 1932; Lange 1969; Andrew & Lange 1986a; James *et al.* 1995; Landsberg *et al.* 1997; James *et al.* 1999; Hunt 2001; Heshmatti *et al.* 2002). Most livestock visit watering points every day and their impacts are most evident on the vegetation around the watering points by grazing, browsing and trampling. This results in positive or negative impacts on different plant species (Landsberg *et al.* 1999b; Heshmatti *et al.* 2002). Plant communities around the watering points are often lost altogether leaving bare soil around the water source (Landsberg *et al.* 1997).

Plant demographic studies and management practices

Maintaining the natural plant communities in a productive state that continuously provides fodder to livestock and protects the land from erosion is the principle aim of rangeland management (Harrington *et al.* 1984). The initial stage of deterioration of rangelands is not necessarily noticeable and managers are often only alerted when drastic changes such as bare patches become visible (Snyman 2003). Effective management practices depend upon a sound knowledge of the medium to long-term demographic structure of plant populations (Smith 1988). Demographic studies explore recruitment, regeneration and mortality to explain the life cycle of a population (Begon *et al.* 2006).

Use of matrix models to develop long-term projections of plant populations

Matrix population models are widely used to analyse the dynamics of animal and plant populations (Lefkovitch 1965; Werner & Caswell 1977; Caswell & Werner 1978; Huenneke & Marks 1987; Smith & Trout 1994). These models use past and present trends to predict the future populations of a species by calculating the population growth rate and the impact of various management practices (Caswell 2001). These models can be constructed on the basis of age-classes (Leslie 1945), statge-classes (Gatsuk *et al.* 1980) or both (Van Groenendael & Slim 1988). The flexibility allowed in construction of matrix population models makes it a popular tool for investigating population dynamics.

Need of vegetation conservation and planning

Tiver and Andrew (1997) stated that a large proportion of southern Australian arid land is not preserved as parks or reserves, but is subject to extensive grazing by herbivores. It is therefore essential that the effects of domestic and feral herbivores are taken into account when planning for conservation and management of biodiversity in the arid lands. Knowledge of the effects of domestic herbivores is becoming increasingly critical. Regional natural resource management plans are being developed, whereas before, management plans were restricted to a network of ungrazed parks and reserves, which are generally unaffected by domestic herbivores.

Aims of the research

This project aims to examine the effects of rabbits and large herbivores (sheep and kangaroos) on the population dynamics of native trees and shrubs in the chenopod shrublands of South Australia. It will contribute to ecological knowledge of plant population dynamics and the effects of domestic and feral herbivores on arid zone vegetation, and help to provide appropriate grazing management strategies for arid shrublands, both in Australia and the rest of the world. An initial task was a assessment of the plant communities by various age stage classes at sites first monitored in 1992 by Tiver and Andrew (1997). They examined the effects of rabbit herbivory by comparing plant population structures of sheep-grazed and non sheep-grazed sites in 1992. I then repeated this comparison in 2004 after the release of Rabbit Calicivirus Disease (RCD) in 1995. The aim was to identify if there had been improved regeneration of shrubs and trees in the arid zone since the release of RCD in 1995. In order to directly assess effects of grazing, an exclosure trial was performed to investigate how sheep, rabbits and kangaroos affect seedling survival of the arid zone perennial tall shrub *Acacia aneura* var. *aneura*.

Strategies

To fulfil this aim the following strategies have been employed:

- re-monitor population structures of trees and shrubs previously assessed in 1992 by Tiver and Andrew (1997), by using nine life-stage-classes as determined previously at each site.
- develop frequency diagrams of life-stage-classes for each population and compare these with data from the same populations taken in 1992, before RCD was introduced and determine whether there has been altered regeneration success since rabbit control.
- compare the grazing affects of various herbivores on the transplanted seedlings of *Acacia aneura* var. *aneura* using sheep and rabbit proof exclosures and unfenced controls in a sheep paddock. Observe herbivore activity by collecting rabbit, sheep and kangaroo dung thus providing a record of grazing intensity over time which is then correlated to the seedling survivorship data.
- examine the demographic variations in the arid zone plant species *Acacia aneura* var. *aneura* by using a matrix population model developed by Tiver *et al.* (2006b) to develop long-term projections of population dynamics of *Acacia aneura* var. *aneura* under various herbivory, rainfall and management regimes.

The re-monitoring survey of plant populations was conducted in the North-East Pastoral District of South Australia and the grazing exclosure trail was conducted at Middleback Station near Whyalla (SA).

Thesis Structure

In order to put this thesis into context and ensure its relevance to improving the management of the rangelands, a review of the literature pertaining to pastoralism in Australia, including the use and effects of artificial sources of water on the rangelands, grazing effects of various herbivores, studies on exclosure treatments, and the importance of demographic studies to assess in the long-term population dynamics of plant species, is presented in Chapter 2.

Chapter 3 presents the results of re-surveying of sites in the north east pastoral properties and adjacent road side reserves and a review of the effects of different herbivores on the regeneration of 20 arid zone tree and shrub species.

Chapter 4 presents the results of different grazing exclosure treatments in sheep-paddocks to assess the effect of large herbivores and rabbits on regeneration of the arid zone tree species *Acacia aneura* var. *aneura*.

Chapter 5 separates the effect of sheep, rabbits and kangaroos on the regeneration of arid zone tree species *Acacia aneura* var. *aneura* by repeating the different exclosure treatments in sheep-paddocks and a neighbouring sheep-fenced plot.

Chapter 6 develops projections of population structure of *Acacia aneura* var. *aneura* rangelands in the North-East Pastoral District of South Australian using the matrix model; various projections are developed for a range of rainfall and grazing management regimes.

Chapter 7 integrates the findings of the individual chapters and discusses the implications for population dynamics of arid rangeland plant species and their management.

Chapter 2

Literature review

Introduction

Biota in the Australian rangelands have undergone many changes since European settlement due to changed land use practices (Harrington *et al.* 1984; James *et al.* 1999). Tiver and Andrew (1997) pointed out that the rangelands contain very few parks or reserves, which means that the pastoral zone is divided only by the boundary fences of the stations and the sub-dividing paddock fences within the stations. This means there are very few areas within the pastoral zone that are not subject to grazing by livestock. This chapter therefore describes previous literature dealing with the effect of grazing by native, feral and domestic herbivores on plant communities with particular emphasis on Australian arid lands, the effect of herbivory on plant population dynamics and the use of matrix population models to explore potential long-term effects of climate and herbivory on plant populations.

Vegetation patterns of chenopod shrubland

Chenopod shrublands of Southern Australia are typically a combination of a sparse upper storey of trees and tall shrubs of the genera Acacia., Casuarina and Eremophila (Specht 1972) and a lower storey of low shrubs and grasses. Low shrubs Atriplex, Maireana and Chenopodium of the family Chenopodiaceae (James et al. 1999; Heshmatti et al. 2002) are regularly spaced because of competition for water (Wotton 1993). Regeneration levels are low (Crisp 1978; Tiver & Andrew 1997) and wet seasons are favourable for regeneration.

Pastoralism in Australia

Nearly 53% of the land area of Australia, and 70% of the arid and semi-arid zones is used for pastoralism (James *et al.* 1999). Their management is characterized by low inputs and low returns per unit area. Sheep pastoralism is the major land use in the chenopod shrub lands of the southern rangelands and cattle pastoralism in the northern and central areas largely because of the exclusion of dingoes from the southern regions by the dingo-proof fence. Earlier research has shown that grazing by a combination of domestic and feral animals has reduced levels of regeneration of a number of species of native trees and shrubs in the Australian arid rangelands (Crisp & Lange 1976; Hodgkinson *et al.* 1989; De Steven 1991; Hulme 1996; Tiver & Andrew 1997; Tiver & Keiermeyer 2006). Many pastoralists adopted land use practices towards a sustainable pastoral industry by the subdivision of paddocks and increased number of watering points, maintaining low stocking rates to restore and retain the cover of perennial shrubs (Waite 1896; Lange *et al.* 1984).

The piosphere

Initially, pastoralism was concentrated near the permanent natural water resources (Condon 1983) but became more widespread as technology allowed the construction of earth tanks (dams) and bores to provide artificial watering points. In rangelands, natural or artificial watering points have a major controlling influence on the animal and plant distribution. This grazing pressure near the watering point is more severe and was described by Waite (1896) as the 'ring round the water'. Osborn *et al.* (1932) and Ratcliffe (1936) also recognized the radial symmetry in grazing intensity that develops around watering points and examined the effects of grazing on vegetation along transects radiating from a watering point. They reported that forage disturbance near the water points was more severe than at distant corners of paddocks. The effect was greater in the summer season than in the winter season because sheep need to drink more often in hot weather. Valentine (1947) described the same phenomenon of forage use of the black grama (*Bouteloua eriopoda*) grassland in the Chihuahuan Desert of North America declining gradually from watering point. Lange (1969) named this phenomenon of decreasing grazing intensity away from the watering point the 'piosphere' (from the Greek "pios = to drink). Barker and Lange (1970) noted that the species composition was different along the piosphere gradient as a result of sheep grazing. *Kochia sedifolia* [now *Maireana sedifolia*] and *Cratystylis conocephala* showed high density away from the watering points while *Bassia paradoxa* [now *Dissocarpus paradoxus*] and *Kochia triptera* [now *Maireana triptera*] showed high density nearer to the watering point. The development of a piosphere pattern was observed by Andrew and Lange (1986a; 1986b) in a newly-developed paddock and watering point with about 117-200 sheep on a previously ungrazed site at Middleback station. They found increased dung deposition and degradation in lichen crust in the first three months and observed a gradual reduction in grass biomass and cover and severe degradation of palatable shrub species near the watering point after eight years of stocking. Zumer-Linder (1976) and Skarpe (1983) found that herbage utilization was affected to a distance of 20 km or more from the watering point in the southern Kalahari of Botswana which has a very long herbivore grazing history. The piosphere is also intensified under increased stocking numbers (Andrew & Lange 1986b).

Many studies have used the piosphere as a basis for grazing research (e.g. Hunt 2001; Heshmatti *et al.* 2002) because it provides a grazing gradient along which response variables to grazing can be observed. Andrew (1988) divided the area nearer the watering point into three different zones. The first zone lies very near to the watering point where the grazing pressure, trampling and erosion is very high: this is often called the "sacrifice zone" (Valentine 1947; Riginos & Hoffman 2003). A second zone lies a little further out where there is an abundance of unpalatable annual plants (James *et al.* 1999; Heshmatti *et al.* 2002). A third zone lies further beyond the watering point where grazing intensity is less and palatable perennial plants are more prolific (Graetz 1978; Barker 1979; Andrew & Lange 1986a; Barker *et al.* 1989; Van Rooyen *et al.* 1990; Wilson 1990; Perkins & Thomas 1993b, a; Fusco *et al.* 1995; Thrash *et al.* 1995; Thrash 1998). The pattern of the piosphere however, is rarely symmetrical because sheep are also affected by prevailing winds and prefer to graze away from the wind direction (Andrew & Lange 1986a). Sheep also tend to preferentially graze parts of the paddock with better forage (Stafford-Smith 1984). Wind direction and shade also alter the grazing impact around the watering points. Sheep will walk long distances in search of palatable plant species by ignoring unpalatable species. Over time this is a major factor affecting the piosphere patterns. Hunt (2001) and Heshmatti *et al.* (2002) have also observed that the degraded area around watering points is expanded by continuous grazing over many years with the older paddocks having more extended areas of bare soil and less palatable shrubs than the newer paddocks.

Extreme summer temperatures are one of the characteristic features of Australian arid rangelands and these high temperatures and extended hot and dry conditions intensify the piosphere effect (Osborn *et al.* 1932; Lange 1969; Squires 1976). In the hot summers water intake by sheep is more frequent so the forage range in summer reduces to less than 3 km (Lange 1969; Squires 1976; Low *et al.* 1978). During periods of high temperatures sheep rely on unpalatable species near the watering points but this pattern is less noticeable in wet and cold conditions because sheep can then utilise water content present in the forage (Wilson 1978).

Effects of grazing by various herbivores in chenopod shrub lands

In Australian arid rangelands plant seedlings are severely affected by rabbits, sheep and other herbivores (Crisp & Lange 1976; Lange & Purdie 1976; Crisp 1978; Barker 1979; Lange & Graham 1983; Read 1995), threatening the sustainability of populations of trees and shrubs in grazing lands (Scanlan 2002). Many of the threatened species including *Acacia aneura* and *Myoporum platycarpum* are structural dominants in arid land ecosystems and loss of these species would have severe consequences for the sustainability of rangeland ecosystems. There is a substantial literature on the impact of various herbivores in the chenopod shrublands of South Australia (Tiver & Andrew 1997; Hunt 2001; Heshmatti *et al.* 2002; Tiver & Keiermeyer 2006), but many of the studies were limited to one or few paddocks and did not investigate long-term changes in plant population dynamics under continuous grazing by different herbivores.

Sheep and goats

Previous research indicates that grazing by sheep reduces the levels of regeneration of a number of species of trees and shrubs in the chenopod shrublands of southern Australia having a major impact at both spatial and temporal scales in the vegetation communities (Ealey 1967; Newman & Condon 1969; Leigh 1974; Wilson & Graetz 1979). Lange and Purdie (1976) found that sheep grazing suppressed the recruitment of *Acacia papyrocarpa* in sheep paddocks but that recruitment was sufficient for population maintenance where there had been restricted sheep grazing for 50 years. Lange and Willcocks (1980) found that sheep grazing had the capability to remove favoured forage items in all parts of the paddocks. Tiver and Andrew (1997) surveyed the north-eastern chenopod shrub lands and concluded that long-term sheep grazing reduced the regeneration of most tree and shrub species.

Capra hircus (the goat) was brought to the mainlands of Australia as a domestic animal and some of them escaped to form feral populations. They are now commonly found in the rangelands of Queensland, New South Wales, South Australia and Western Australia. In South Australia feral goats are commonly found in the Flinders and Olary Ranges (Pople *et al.* 1996). After the provision of artificial water and successful control of dingoes the feral goat populations increased and in the early 1990's their numbers were estimated at 1.5–2.0 million by aerial survey (Parkes *et al.* 1996). In the low-lying regions, including both study areas of this thesis, goat numbers are much lower and therefore they are not considered further in this study.

Kangaroos

Kangaroos are the largest extant native marsupials and are found throughout the Australian rangelands (Dawson 1998). Before European settlement kangaroos mostly occupied riparian areas and depended on natural springs (Ealey 1967). Their numbers were probably minimal during drought when herbage was scarce but increased with favourable conditions (Landsberg *et al.* 1999a). As a result of an increase in artificial watering points for modern pastoralism kangaroos have increased their range and population size (Ealey 1967; Newsome & Corbett 1977).

Kangaroos mostly graze native grasses with a dietary preference for young, low fibre and more nutritious green plants (Newsome 1965; Kirkpatrick 1965a; Ellis *et al.* 1977; Newsome 1980; Jarman & Phillips 1989; Dawson & Ellis 1994). Sheep prefer green grasses when they are available but will consume the much more fibrous chenopod shrubs (Dawson & Ellis 1994). However some work has shown that kangaroos will graze more woody vegetation when herbs and forbs are scarce (Dawson & Ellis 1994) which raises the possibility that kangaroo grazing could have an impact on tree and shrub seedlings in dry times.

Most literature has focused on the competition of kangaroos with livestock: their diets will overlap when green material is scarce (Gibson & Young 1987; Dawson & Ellis 1994) during which times kangaroos compete with sheep and cattle for forage (Gibson & Young 1987). Edwards *et al.* (1995; 1996) found that the competition occurred when herbage is <50-60g/m^2 of pasture area. This seasonal effect of kangaroos on perennial species could suppress their regeneration (Gardiner 1986a). Red kangaroos (*Macropus rufus)* are less selective than the other large kangaroos (Dawson 1989) and show a greater dietary overlap with sheep (Griffiths & Barker 1966).

Rabbits

In most of the literature rabbits Oryctolagus cuniculus (L), are cited as the herbivore causing most risk to plant populations (Jessup 1951; Hall et al. 1964; Crisp & Lange 1976; Lange & Purdie 1976; Lange & Graham 1983). European rabbits, were brought to the Australian continent in the 1840s (Drollette 1997). Their numbers rapidly reached millions, as the climate was similar to their native lands of the Southern Mediterranean, where soils were sandy and very good for warrens and also because livestock grazed and eliminated many of the shrubs and native grasses, encouraging annual grasses and forbs (Armstrong 1982; Norman 1988; Stodart & Parer 1988). Most annual plants appear only after good seasonal rainfall, so the rabbit populations increase in good seasons and consume the green grasses and are rapidly reduced to lower numbers when the forage is scarce (Reid 1993). When herbage is scarce Ratcliffe (1936) observed that rabbits can cause a major problem by stripping bark and killing seedlings of shrubs and trees. Johnson and Baird (1970) noticed that the vegetation changes in the Nullarbor Plain from 1930 and 1953 were mainly caused by kangaroos and rabbits. Here large areas of bluebush were destroyed and regeneration of Acacia spp was prevented wherever rabbits were present. At one time rabbit populations measured nearly 750 million (Wilson 1990) and had a drastic effect on the regeneration of native plant species. Even though rabbits cause a problem by ringbarking the stems and roots, Beadle (1948) did not consider them a major cause of loss of shrubs in western New South Wales. However rabbit densities of 3 per ha were a serious cause of loss of regeneration of woody plants in central Australia (Friedel 1985). It is difficult to estimate the impact of rabbits on the regeneration of plant species in arid Australia, because in almost all places pasture is degraded by livestock grazing (Foran 1986).

A number of research studies in the arid zone in South Australia and other places of Australia emphasize the competence with which rabbits suppress regeneration of trees and shrubs. Gooding (1955) reported that rabbits affected shrub regeneration over large areas in the Western Australia. Cochrane and Mc Donald (1966) noticed that rabbit suppressed the juveniles of Callitris columellaris in Hattah Lakes Conservation Park in Victoria by grazing 134 out of 350 plants. Similar findings were reported by Crisp and Lange (1976) who described the reduction of regeneration of Acacia burkittii in Koonamore Reserve by rabbits. They also observed that the effect was significantly higher when both rabbits and sheep were present. Cooke (1987) in Coorong National Park, found that rabbits destroyed the seedlings of Allocasuarina verticillata. The experimental results of Austin and Williams (1988) demonstrated that the loss of recruitment in Callitris from 1880 to 1950 [prior to Myxomatosis] was mostly caused by rabbits.

Lange and Graham (1983) used 50 m x 50 m rabbit-proof enclosures to identify the rabbit pressure on four Acacia spp. They used nursery-grown seedlings and cuttings to test the ability of rabbits to find and eat seedlings. They observed that rabbits could (but did not always) consume seedlings of A. papyrocarpa in enclosures at very high densities of 24 rabbits ha–1, showing that rabbits are capable of grazing with extreme selectivity, and will switch their dietary preferences to soft herbs and grasses whenever these are available.

Drought was the only effective control of rabbit populations until 1950 when CSIRO introduced the Myxomatosis virus to control rabbit populations (Anderson 1995). This virus was initially very effective and restricted rabbit populations to lower levels. However the rabbits that remained were myxomatosis-resistant and this enabled the rabbit population to recover (Fenner & Ratcliffe 1965; Wilson 1990). Myxomatosis has a major effect on rabbit populations and their numbers oscillate, rising in good rainfall seasons when annual herbage is present and falling during dry seasons and during disease outbreaks (Kemper 1980).

In 1995 another virus, Rabbit Calicivirus Disease (RCD), also known as Rabbit Haemorrhagic Disease (RHD), was introduced as a biological control agent (Pech & Hood 1998). RCD rapidly decreased rabbit numbers by up to 90% (Anderson 1995; Williams *et al.* 1995). The decline in rabbit numbers was particularly dramatic when combined with other control methods such as poisoning and ripping of warrens (Mutze *et al.* 1998; Saunders *et al.* 1998; Sharp *et al.* 2001). In South Australia numbers dropped from 85-419 km^{-2} to 0-12 km^{-2} (Mutze *et al.* 1998). Sharp *et al.* (2001) noticed remarkable changes in western New South Wales, rabbit numbers decreasing from 0.6-11.6 km^{-2} in winter 1996 to 0.2-1.8 km^{-2} by spring 1996. Many anecdotal claims have been made on how rabbit control has dramatically increased regeneration of native plant species such as *Alectryon oleifolius* (rosewood), *Callitris glaucophylla* (native cypress pine), *Acacia* and other shrubs since the release of Calicivirus (Clausen 2001) and some more controlled studies have shown such effects (Cooke 1998; Lord 2000) . However some previous work has shown that the Rabbit Calicivirus has provided little improvement in regeneration (Mutze *et al.* 1998; Denham & Auld 2004).

In conclusion, the evidence for the effects of rabbits is contradictory, with different conclusions reached by various authors conducting research at different sites in different years and on different plant species.

Exclosure experiments

Fencing such as exclosure (herbivores fenced out) and enclosures (herbivores fenced in) techniques are a widely recognised manipulative technique recommended for the study of plant animal interactions (Mueller Dombois & Ellenberg 1974; Harper 1977)**.**

Gardiner (1986b) applied fenced and unfenced site techniques to monitor the direct effects of kangaroos on various arid land tree species and explain the effects of destocking on the vegetation. He noted that survival rates of grazed juvenile plants

(<3 years old) were consistently lower than for adults and he proposed that removal or reduction of livestock and kangaroos can improve regeneration of rangeland plant species.

Cooke (1987) used 20 m x 25 m rabbit, kangaroo and wombat exclosures to study herbivory effects on arid land trees in Coorong National Park, SA. Tree guards were used to exclude kangaroos and wombats but allowed rabbit access. He recorded that rabbit grazing could suppress the plant seedlings in the summer seasons as the annual pastures dried off and rabbits sought alternative foods.

Valone *et al.* (2002) used exclosures to examine vegetation change in shrub dominated arid grasslands in USA and monitored the recovery of perennial grasses such as *Bouteloua eriopoda* and *Aristida* spp. They observed that the density of grass communities inside the exclosure became significantly higher than outside the exclosure.

Surveying techniques in plant vegetation

Broad scale surveying and comparison of previous data is a widely used field technique. Such data sets are most useful for assessing the effect of land use practices and increases or decreases in land cover and density of vegetation. Monitoring is necessary to detect changes over time (Stevens *et al.* 2004). Many practices have emerged to detect changes in the vegetation patterns through historical documentation such as old survey records and explorers' notes (Humphrey 1958; Lay 1972; Oxley 1987; Fensham 1997; Fensham & Fairfax 1997): aerial photographs (Cooke 1987; Archer *et al.* 1988; Archer 1989; Knight *et al.* 1994); ground photography and photo points (Nelson & Beres 1987; Archer 1994; Hoffman *et al.* 1995; Sinclair 2004); and isotopic analysis of soil carbon (Witt *et al.* 1997; Witt *et al.* 1998; Witt *et al.* 2000).

Lay (1972) conducted a broad-scale survey of the tree and shrub populations in the north western chenopod shrublands of South Australia. His survey repeated a previous survey carried out by Jessup (1951) and showed that there had been a decline in populations of a range of trees and shrubs, including *Atriplex vesicaria* (bladder saltbush). He assumed that this was attributable to livestock grazing though no attempt was made to separate the effects of different herbivores.

Tiver and Andrew (1997) used current stage-classes of plant populations as a measure of long-term population dynamics in their survey of shrubs and trees in the North-East Pastoral District of S.A. Populations of the woody species present at each site were scored as belonging to one of nine possible stage-classes closely related to the 11 phenological condition classes described for annual plants by Mueller-Dombois and Ellenberg (1974) and the 10-state classification of Gatsuk *et al.* (1980). They concluded that sheep were the major vertebrate affecting regeneration of over 50 species.

Experimental trial sites

It is difficult to detect vegetation changes in arid and semi-arid regions. Changes generally emerge in two main ways: short term (years) and long term (decades) because of rare climatic events, grazing pressure, altered disturbance regimes or a combination of these factors (Hoffman et al. 1990; Darkoh 1996). It is not possible to survey the entire arid rangeland to identify variables that affect regeneration and revegetation. Therefore, it is imperative that trial areas (samples of the rangeland) should be assessed from which conclusions can be made and recommendations developed for vegetation retention. It is necessary to have suitable replicated trials in order to arrive at statistically meaningful conclusions, bearing in mind the difficulties inherent in achieving true replication in a relatively uncontrolled and variable environment (Greig-Smith 1983).

Grazing impacts on plant population dynamics

In long lived perennial plants, a wide range of demographic processes contribute to the life-cycle including seed production, recruitment, regeneration, type of reproduction (whether by seed or vegetative propagation) and mortality (O'Connor 1993; Caswell 2001). In general the size of a population is basically determined by the equilibrium reached between the number of births, deaths, immigrants and emigrants (Begon *et al.* 2006). Variables which can cause disruption of any of these processes are very important because small perturbations can lead to severe effects on the long term survival of plant populations (Harper 1977; O'Connor 1993).

One of the most common external factors influencing plant demography is grazing. Herbivory causes a wide range of complex effects on plant population dynamics (Belsky 1986; Bigger & Marvier 1998) through direct effects such as grazing, trampling and defoliation; and indirect effects such as changing the soil physical and chemical properties and microclimate; and altering phenological events such as flowering (Charley & Cowling 1968; Crawley 1983; Andrew & Lange 1986a; Louda et al. 1990; Archer & Smeins 1991). Grazing can reduce the flowering of plants (O'Connor 1991; Milton 1994), the seed production (Milton & Dean 1990; Hodgkinson 1991), size of the seed (Marshall et al. 1986), the survival of seedlings (Silander 1983; Gardiner 1986a; Tiver & Keiermeyer 2006), growth of plants (Crawley 1983; Louda et al. 1990; Milchunas & Lauenroth 1993), and adult plant survival rates (Chambers & Norton 1993). Graetz (1980) found three times greater Atriplex vesicaria population turn-over rates in grazed populations than in the ungrazed populations. Similar results were found by Yan et al (1996) in Maireana pyramidata populations. They observed 7% and 14% variation in ungrazed and grazed sites. But on the other hand Eldridge et al. (1990) found 8% variation in ungrazed and 3% in grazed sites. These effects depend on a wide range of factors including behavior of the animal (Arnold 1987), the density and phenology of the plant population (Crawley 1983), availability of water, temperature (Squires 1981), duration and intensity of grazing (McNaughton 1992) and time of grazing (Harper 1977; Marquis 1992).

Grazing can increase or decrease the population size and debate on the effect of grazing by herbivores on plant populations has not led to consensus (Grainger 1992; Zervas 1998). Before reaching a final conclusion about the long-term impact of grazing on a plant population it is necessary to closely identify the demography of the plant and its responses to grazing (Harper & White 1974; Silander 1983).

Plant demographic studies under grazing in Australian rangelands

In Australia survey and experimental work has recorded the effect of grazing on different arid rangeland plant population dynamics (Williams 1968, 1970; Crisp & Lange 1976; Crisp 1978; Orr 1991; Orr & Evenson 1991a; 1991b; Tiver & Andrew 1997; Hunt 2001) all concluding that the extensive grazing by herbivores can alter the plant populations substantially.

Need for demographic models in the future assessment of rangelands

The most significant characteristic feature of rangelands is their unpredictability (Harrington et al. 1984). In arid zones the long-lived plant population dynamics are often controlled by episodic events (Watson et al. 1997) which are therefore difficult to observe by short term field studies (Wiegand & Jeltsch 2000). Therefore long-term monitoring is required to detect changes in the dynamics of plant populations. But because of short (3-5 year) research funding cycles, long-term ecological research projects generally are carried on only because of the commitment of individual scientists (White 1985; Westoby 1991) and very few projects have been continued over more than human life spans. An exception is the Koonamore reserve in South Australia maintained by the University of Adelaide (Sinclair 2004), where valuable data has been obtained on the longevity and population dynamics of various arid plant species.

Because of the long lifespan longevity of many plants, population models are widely recognised as tools for analysing demographic data. The use of models allows projection of population dynamics over a much longer time span and also shows greater flexibility of input parameters (Caswell 2001). Since their formulation by Lewis (1942) and Leslie (1945) matrix projection models have been widely used in population biology. They have advantages over other types of models in that they may be used to identify several useful processes such as population growth rate, longevity and extinction (Caswell 2001). Matrix models can be constructed using age-classes (Leverich & Levin 1979; Sarukhán 1980; Law 1981) by age class (Gatsuk et al. 1980) by size-classes (Law 1983; Van Groenendael & Slim 1988) by size class (Werner 1975; Werner & Caswell

1977; Tiver et al. 2006b). Matrix models have been used to project both animal and plant population dynamics (Werner & Caswell 1977; Caswell & Werner 1978; Huenneke & Marks 1987; Rogers-Bennett & Leaf 2005). Matrix models have been used on plant populations in Australia (Werner & Caswell 1977; Caswell & Werner 1978; Huenneke & Marks 1987; Hunt 2001; Regan et al. 2003; Rogers-Bennett & Leaf 2005; Palisetty et al. 2006).

Discussion

There is consensus that grazing pressure by large herbivores (sheep and kangaroos) is deleterious to the regeneration of shrub and tree species in chenopod shrublands. There is less agreement about the level of the effects of rabbit grazing, but it is widely accepted that they are a major cause of suppression of regeneration. Their current reduced numbers (due to Myxomatosis and Calicivirus) could allow regeneration in more recent times. Exclosure trials and repeat surveys are frequently used techniques to understand the grazing responses of plant species to different herbivores. Matrix models are useful for making long-term projections of plant species and enabling the evaluation of the sustainability management practices.

Chapter 3

Effects of herbivory from 1992-2004: reassessment of plant population structures in the pastoral properties and roadside reserves in north-eastern South Australia

Introduction

Because many plant species are palatable to herbivores, herbivory can be extremely significant in determining the relative abundance of different species in a habitat because grazing is a major factor controlling plant recruitment (Harper 1977). It is very important to know the factors that can cause disruption of plant populations, because a minute change can lead to severe effects on the long-term survival of plant populations (Harper 1977). In the Australian rangelands herbivory has been considered either directly or indirectly responsible for the decline of many plant species (Tiver & Andrew 1997; Tiver & Keiermeyer 2006) and has caused severe change to vegetation cover over the last two centuries (Ludwig & Tongway 1995).

In the South Australian arid lands, pastoralism is the major land use and there is substantial influence by herbivores including domestic, native and feral animals. There is considerable evidence to suggest that various arid zone plant populations are under threat because of selective elimination of their seedlings (Crisp & Lange 1976; Lange & Purdie 1976; Fatchen 1978).

Three major vertebrate herbivores are present in the study area: sheep, kangaroos and rabbits (goat numbers are relatively low on the lower elevation areas and their effects not considered in the current study). The effects of the three herbivores are discussed in Chapter 2 and are summarised as follows.

The negative impact of sheep grazing on the chenopod shrublands has been well established, particularly the radial grazing pressure which results in high grazing impacts in a gradient around the watering point (Lange 1969). Sheep are highly selective herbivores and in winter seasons can travel 4 km from the watering point in search of fodder (Squires 1976). Sheep have the capacity to reduce the regeneration of some woody plant species even at low stocking rates (Lange & Willcocks 1978).

Rabbits are also considered a major herbivore affecting regeneration of plant species in southern Australia (Johnston 1969; Crisp & Lange 1976; Auld 1990). Rabbits are well known for their ability to ring-bark trees (Catling & Newsome 1992). Crisp and Lange (1976) showed that sheep and rabbits together affect regeneration of *Acacia burkittii*, but the effects of each herbivore could not be separated by their research. It is considered that drought was the only significant agent to reduce rabbit populations until *Myxomatosis* was introduced in 1950 (Ratcliffe *et al.* 1952; Norris *et al.* 1991). Reduction in perennial grass establishment and favourable rainfall events has facilitated increase in population numbers of woody weeds after suppression of rabbit numbers by *Myxomatosis* (Tatnell & March 1991). The effect of *Myxomatosis* was very high in the initial stages causing a sudden collapse in rabbit populations but the few escaped immune rabbits have allowed a substantial recovery of populations. In 1995 the release of Rabbit Calicivirus (RCV) (Kovaliski 1998) was extremely effective in the eradication of rabbit populations in many parts of Australia (Mutze *et al.* 1998; Saunders *et al.* 1998; Edwards *et al.* 2002a). However, although there are some reports of increased plant regeneration as a result of RCV (Cooke 1998; Lord 2000), other research has not found significant increase (Denham & Auld 2004).

Tiver and Andrew (1997) surveyed pastoral areas in the North east District of South Australia in 1992 and provided a substantial record of tree and shrub population structures of this region. These records were taken before the release of Rabbit Calicivirus in 1995. I re-monitored a sample of Tiver and Andrew's (1997) populations to determine if the control of rabbit numbers by RCV is associated with increased regeneration of plant species.

Aims

i. to compare the present plant population structures (2004, which were taken after the release of RCV) with previous data (1992 prior to the release of RCV),

ii. to determine the changes in regeneration of various plant species, and hence to observe which species are increasing, decreasing or stable since the reduction of rabbit populations by RCV.

Materials and methods

Study area

The study area in the North-east District of South Australia (Fig. 3.1) is nearly 32 000 km^2 with varying topography. The Olary Spur, a series of low ranges to 600 m stretching across the study area from south-west to north-east, is the most significant topographic feature. Northcote (1968) described the soils of the ranges as shallow calcareous loams, with soils of the surrounding plains being brown calcareous clay loams with a marked clay B-horizon whereas parts of the south-east of the study area are covered in sandy aeolian deposits of late Tertiary and Quaternary origin.

The climate of the region is characterised by short mild winters with regular overnight frosts from May to September and hot summers during which maximum daily temperatures occasionally reach over 40^0C between October and April. Rainfall is low, between 175 mm per annum on the northern plains and up to 300 mm per annum on the ranges and southern plains (Tiver 1995). Series of drought years alternate with episodes of higher rainfall each often lasting for 3-4 years or longer. Plant establishment in this region is restricted to occasional good rainfall seasons because normally evaporation exceeds precipitation levels, preventing seedling establishment (Specht 1972).

The vegetation is predominantly chenopod shrublands with *Atriplex vesicaria* and *Maireana pyramidata* on the southern plains with the latter replaced by *M. astrotricha* to the north. On the foothills the chenopod shrublands have a sparse overstory of *Casuarina* or *Myoporum* on the southern plains, and *Acacia aneura* in the north (Wood 1937; Specht 1972). In the sandy areas in the south of the study area are scattered woodlands with an overstorey of *Eucalyptus oleosa* (mallee). The ranges have mixed communities of *Dodonaea*, *Eremophila* and *Senna* spp.

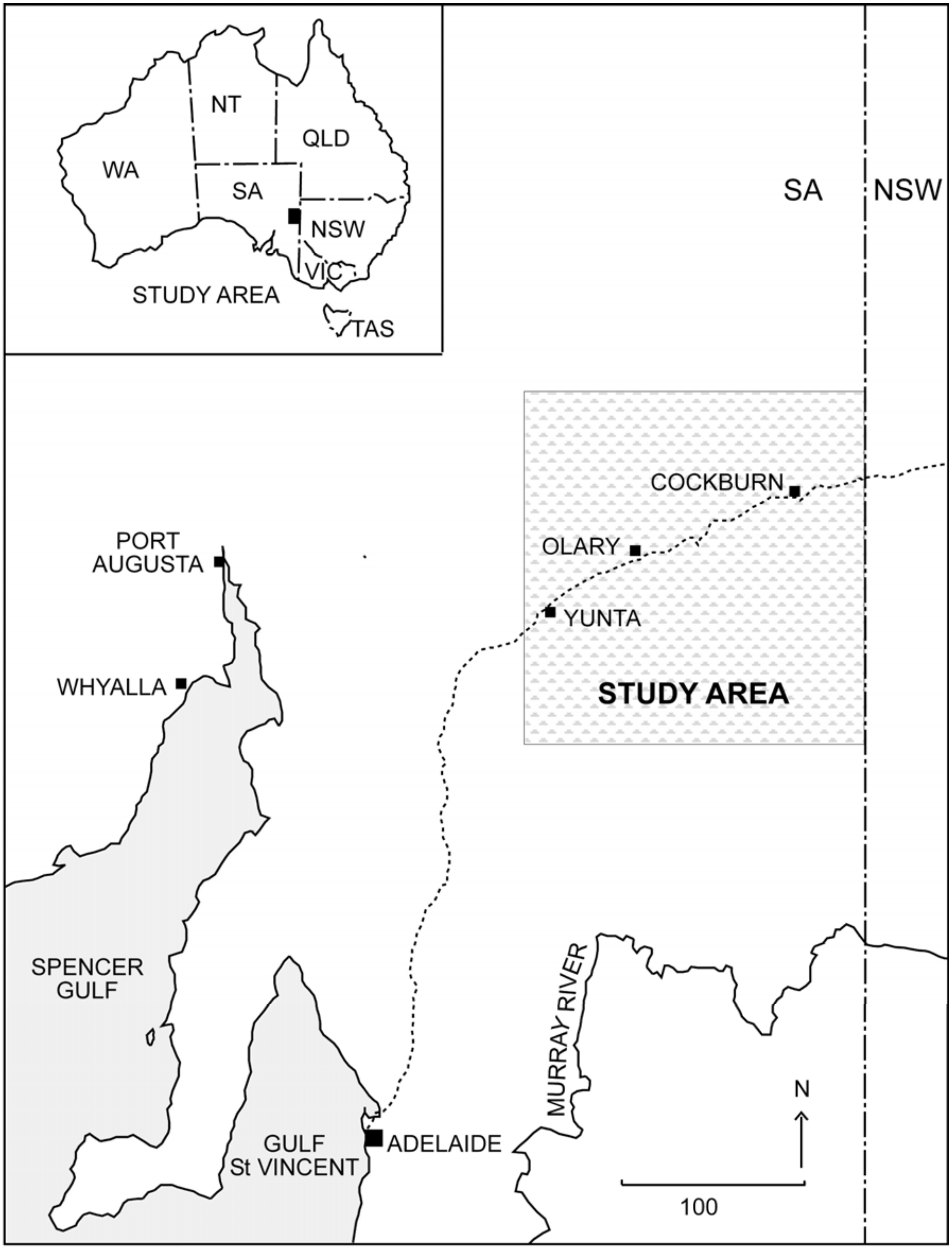


Figure 3-1 Location of the study area on the Australian continent (inset), and in South Australia (SA) against the border with New South Wales (NSW)

Sheep farming is the major land use in this area. Paddocks are bounded by sheep-proof fences and contain one or more artificial or natural watering points (Graetz 1978).

Site selection

Comparing the roadside vegetation reserves where domestic stock movements are effectively zero (apart from when the livestock are driven along the road to other paddocks) with the paddock sites where all the herbivores (domestic, native and feral) have access provides the opportunity of monitoring a " natural experiment" to detect herbivore effects on regeneration of plant species. Over 300 sites were chosen from the original 1992 data set (Tiver & Andrew 1997) and reassessed in 2004. At least 10 sites (five within paddocks and five road reserves) including representation of the major overstory species were re-monitored to provide a minimum number of sites for valid statistical analysis.

Herbivory levels

The 1992 data contained records of the grazing intensity of different herbivores using a 0 to 4 scale (Table 3.1). These records were checked again in consultation with pastoral managers about present stock numbers, any newly established watering points or closure of old watering points, and recorded again in 2004 using the same scale. A brief description of the methods for measuring each variable is as follows: recent (1992-2004) history of sheep grazing was estimated from station records, or estimated by proximity to the watering point location using survey maps. This was based on the assumption that sheep grazing pressure is highest near watering points: the "piosphere effect" (Lange 1969, 1985). Grazing intensity of the other two herbivores, rabbits and kangaroos, was estimated by observing the presence of recent spoor and activity of rabbit warrens and buck heaps at the sites, as explained in more detail in Table 3.1.

Table 3-1 Herbivore grazing levels used by Tiver and Andrew (1997) in the North-East of South Australia

Sheep Grazing
0 = Nil (ungrazed) 1 = Light or intermittent (>5km from water, or rarely stocked, old spoor only) 2 = moderate (1-5km from water, fresh spoor) 3 = Heavy (500m-1km from water, frequent fresh spoor) 4 = severe (<500m from water/heavy fresh spoor)
Rabbit Grazing
0 = Nil (dung and soil scratching absent) 1 = Light or intermittent (old dung, soil scratchings infrequent) 2 = Moderate (fresh dung and scratchings present, more frequent) 3 = Heavy (100-500m from warren) 4 = Severe (within 100m of warren)
Kangaroo Grazing
0 = Nil (dung and tracks absent) 1 = Light or intermittent (old dung, tracks infrequent) 2 = Moderate (fresh dung and tracks present) 3 = Heavy (frequent fresh dung and tracks, animals may be seen) 4 = Severe (heavy fresh dung tracks, animals usually seen)

Collection of plant population data

Individuals of each plant species at each site were recorded as one of nine possible stage classes (Fig. 3.2) (Tiver & Andrew 1997). This stage-class classification was adapted from the phenological condition classes described by Mueller-Dombois and Ellenberg (1974), in which plant species were divided into 11 life-cycle stages. Tiver and Andrew (1997) modified this to nine life-stages to suit a range of long lived perennial arid-zone plants. These stage-classes closely resemble the ten-state classification of Gatsuk *et.al.* (1980), which was designed for over 100 perennial and annual plant species. These types of stage-class distributions have previously been used to study long lived perennials in South Australia (Lange & Purdie 1976; Tiver & Andrew 1997; Hunt 2001).

Inclusion of a class of dead standing and dead fall (lying dead) individuals in this classification was one of the major differences with the other classifications. The main reason to include these two classes was that these dead and decaying individuals can give a good indication of past population history (Ogden 1985; Sinclair 2004)**.**

LIFE-STAGE		DESCRIPTION	APPEARANCE
I	SEEDLING / SUCKER	≤ 20 cm high single stem often with juvenile foliage	
II	BUSHY JUVENILE	Branching apparent often multi-stemmed rounded shape	
III	OLDER JUVENILE	One stem gaining dominance	
IV	YOUNG MATURE	Crown not fully formed reproductive growth vigourous	
V	MATURE	Full size crown fully developed fully reproductive growth vigourous	
VI	OLD MATURE	Canopy spreading dead branches appearing growth vigour decreased	
VII	SENESCENT	Many dad branches some fallen branches pronounced canopy spread	
VIII	STANDING DEAD	Completely dead still standing many branches fallen	
IX	LYING DEAD	Whole tree fallen over many branches rotting	

Figure 3-2 Nine life-stage classes recognizable in woody perennial plant species, the rules for assigning individuals to classes, and a theoretical diagram of each stage. Adapted from the phenological condition classes of Tiver and Andrew (1997), which were developed from those of Muller-Dombois and Ellenberg (1974) and Gutsuk et al. (1980)

Population survey method

Populations were assessed by a modified "random walk" method (a modified strip-transect method) (Kent & Coker 1992) which replicates the technique followed by Tiver and Andrew (1997). At each site, the recorder left a fixed point and followed a roughly circular path covering several hundred metres and returning to the starting point. Plants of all stage-classes were recorded, including seedlings of 5 cm height and over which could be observed within about 20 m either side of the transect line. A minimum of 50 individuals of each species were classified where possible, which was considered a sufficient number for statistical analysis. Where possible paddock sites were paired with sites at neighbouring roadside vegetation reserves so that inherent variability due to site characteristics could be minimized.

At some sites, where trees had been felled in the past for fence posts, standing dead individuals of *Acacia aneura* var. *aneura* and *Casuarina pauper* within stage-classes IV and V were recorded. Following Tiver and Andrew (1997), these individuals were not included in the data for the analysis, because they were not naturally senescent, so as to avoid confusion about which class to which they should be assigned.

It is relatively easy to recognize individuals regenerated by seed (distinct genets): these individuals are usually spatially well-separated from the parent (Silvertown & Doust 1993). Many Australian arid zone perennial plant species regenerate largely or completely by vegetative propagation, by root suckers (Maconochie 1982). In this case the resulting populations are genetically indistinct clones (ramets) (Silvertown & Doust 1993). Vegetatively regenerating species present in the study area include *Casuarina pauper* and *Alectryon oleifolius spp. canescens.* For the purposes of this study all plant individuals, whether ramets or genets, were counted as a separate individuals.

Analysis of data

The proportion of plants in the various stage-classes for a particular species were analyzed to investigate the changes in population structure between 1992 and 2004.

If the reduction of rabbits between 1992 and 2004 has resulted in increased regeneration, then there would be an increase in juvenile (Stage-classes I-III) plants in 2004. On sheep-grazed sites, any increase in plant numbers in stage-classes I-III would be much smaller than on ungrazed sites so it would be expected that the increase would be greater on roadside sites. Consequently, for the analysis, Stage I-III are combined into a category designated Juveniles. I considered that the 12 years between 1992 and 2004 would be too short a time to detect any change in numbers of the older individuals (V-IX), so these were combined into a Mature stage. The stage-class IV was retained as a separate category, because it was possible that plants previously recruited in 1992 as Stage III could have matured to Stage IV by 2004, if unaffected by grazing. Hence, the analysis utilized the factors Grazed with levels yes (sheep-grazed, inside paddock) and no (non sheep-grazed, outside paddock), Years (with levels 1992 and 2004) and Stages (with levels Juvenile, Stage IV, Mature).

Results

GLMM analysis

Tables of counts, frequencies of life-stages are included in Appendix 1 and are summarized in Table 3.2 and Figures 3.3a-c and 3.4a-c. GLMM (Generalized Linear Mixed Models, (Schall 1991) were used to analyse the data using Genstat (Payne *et al.* 2000). The total number of plants for a particular species observed for a Site-Year combination, i.e. at a site in one of the years, was variable (the random walk method does not ensure that the same plants or the same number of plants are recorded) and so the raw counts cannot be regarded as comparable. Hence the total numbers of plants for a Site-Year combination were treated as fixed and all conclusions based on the proportion of plants in a particular stage. To give effect to this, each of the combined stages (Juveniles, Stage IV and Mature) were analysed separately assuming that the counts for a life-stage at each site in a year were binomially distributed with the total number of observations being the total number of plants for the Site-Year combination. Consequently a GLMM with distribution binomial and logit link was used. The logit transformation is also referred to as the “logs odd” as it is the log of the probability of being in a Stage or not being in a Stage:

$$\operatorname{logit}(p) = \log\left(\frac{p}{1-p}\right)$$

A maximal variance model, that includes terms involving sites and allows for a dispersion parameter to be estimated, was fitted to the proportions for a species and any bounded terms were removed. If the dispersion term was close to one, it was set to one. The maximal variance model for each analysis was Pairs + Pairs x Sites + Pairs x Years + Pairs x Sites x Year and the maximal fixed model was Grazed + Years + Grazed x Years, with terms fitted in this order. In some cases there were so few pairs that these were omitted from the analysis and the maximal variance model became Sites + Sites x Year. The Wald statistics were examined for each analysis to decide which fixed effects were significant, starting with the term Grazed x Years. The other terms (Years, Grazed) were not examined if this term was significant.

Sheep, Kangaroo and Rabbit populations

Between 1992 and 2004 grazing indices for rabbits in all the study sites decreased, all falling in the 0 and 1 range on the grazing scale in 2004 (Table 3.3). By contrast sheep and kangaroo grazing indices increased at all paddock sites: in some places kangaroo numbers increased to level 3 where they were in level 1 in the year 1992, probably as a result of lowering rabbit numbers and hence the removal of grazing competition with rabbits (Mutze & Hawker 2006). Kangaroo activity was almost the same in the grazed (paddock) and ungrazed (roadside) sites. In most of the paddock sites sheep activity was at level 3 and 4, even at the sites further from the watering point. These high levels of sheep movement at the further sites do not support the rules of Tiver and Andrew (1997) index because they considered sheep grazing pressures as levels 2 and 1 when they are >1.5 and >5 km respectively from the watering point.

Table 3-2 Summary table of GLMM results showing where there were significant differences in proportions of life stages in tree and shrubs in the North-East district of South Australia between 1992 and 2004

GxY= Grazed x Years. *** = p<0.001, **p<0.01, *=p<0.05; life-stages I-IX described in Fig.3.2 (Tiver & Andrew 1997). Plant taxonomy as per (Barker et al. 2005)

	Juvenile I-III *GxY*	Stage IV *GxY*	Mature V-IX *GxY*
Acacia aneura var. *aneura*	-	-	-
Acacia carneorum	***	-	***
Acacia oswaldii	**	-	**
Acacia tetragonophylla	-	***	***
Acacia victoriae ssp. victoriae	***	**	***
Alectryon oleifolius ssp. canescens	-	-	-
Atriplex vesicaria ssp. calcicola	-	-	-
Casuarina pauper ssp. pauper	-	-	-
Dodonaea viscosa ssp. angustissima	-	-	-
Eremophila duttonii	-	-	-
Eremophila sturtii	**	-	**
Eremophila scoparia	-	-	**
Exocarpos aphyllus	-	-	-
Maireana pyramidata	-	-	-
Maireana sedifolia	-	-	-
Myoporum platycarpum ssp. platycarpum	-	**	-
Rhagodia parabolica	***	-	-
Rhagodia spinescens	-	**	**
Senna artemisioides ssp. × coriacea	-	-	-
Senna artemisioides ssp. petiolaris	-	**	***

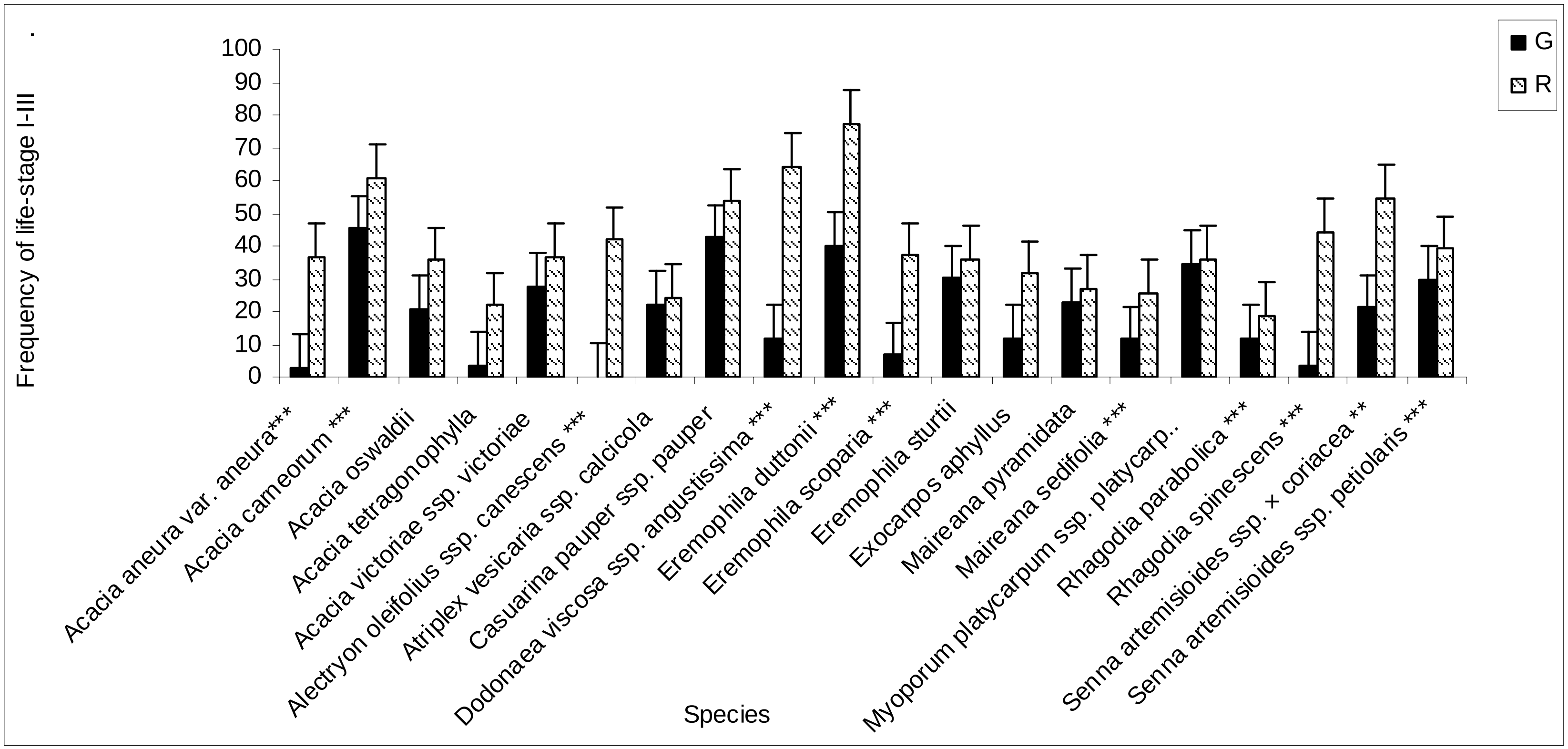


Figure 3-3 (a) GLMM results showing increases and decreases in proportions of Juvenile stages (I-III) in tree and shrubs in North-East of South Australia between paddock and roadside reserves

G = Grazed sites, R = Roadside Reserves; *** = p<0.001, ** = p<0.01, * = p<0.05; life stages I-III described in Fig. 3.2 (Tiver & Andrew 1997). Error bars are ± 1 standard error

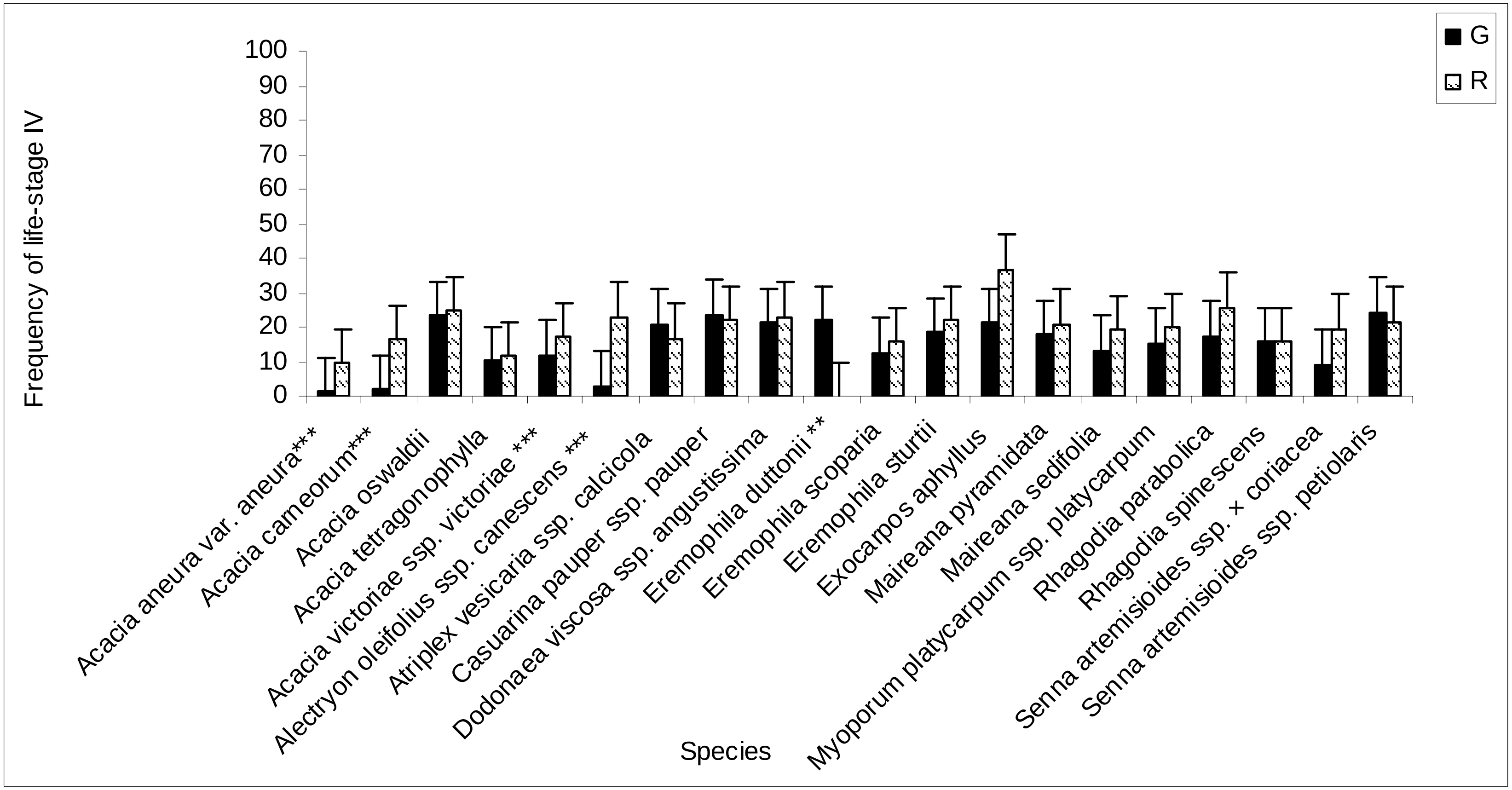


Figure 3-3 (b) GLMM results showing increases and decreases in proportion of stage (IV) in tree and shrubs in North-East of South Australia between paddock and roadside reserves

G = Grazed sites, R = Roadside Reserves; *** = p<0.001, ** = p<0.01, * = p<0.05; life stage IV described in Fig. 3.2 (Tiver & Andrew 1997). Error bars are ± 1 standard error

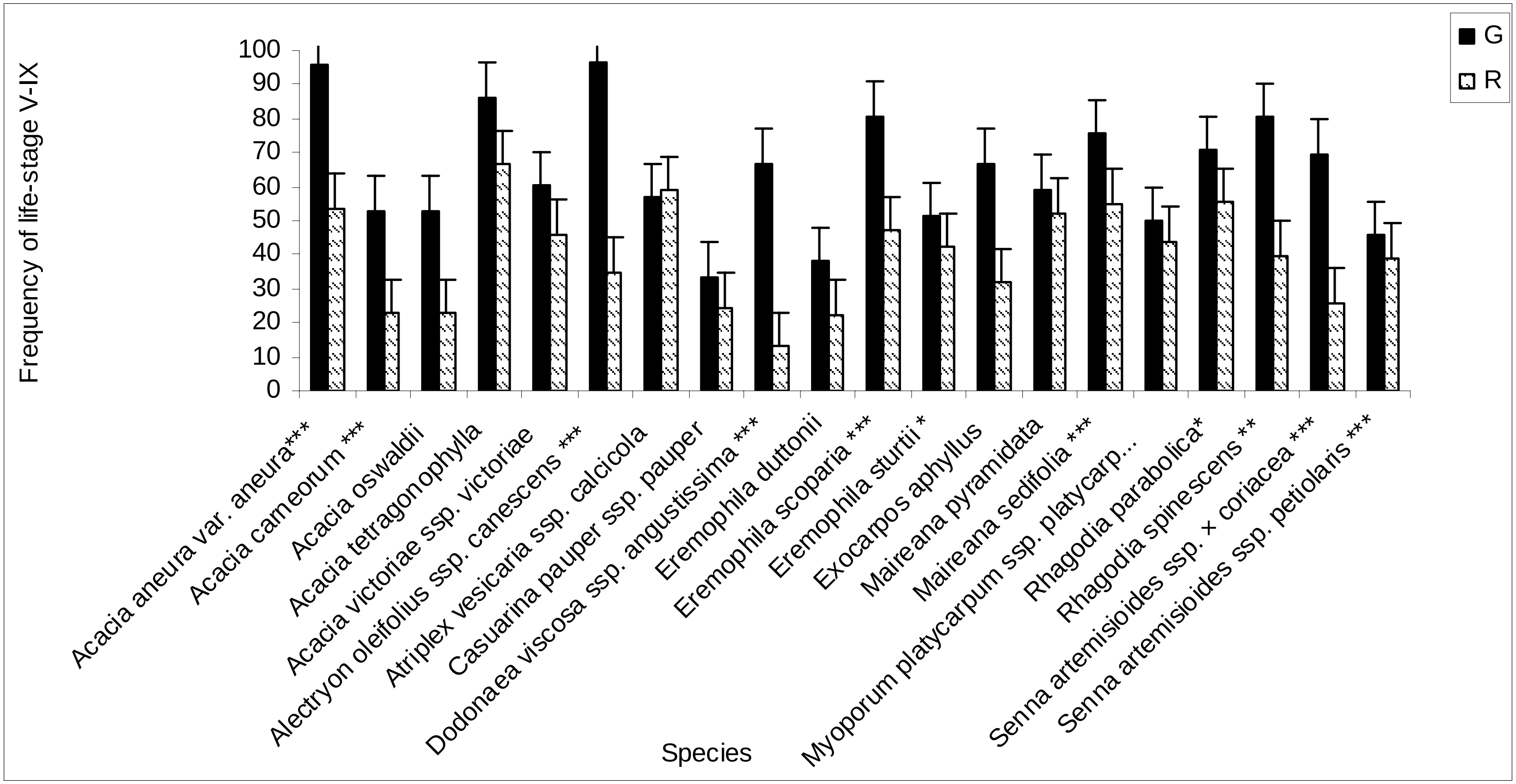


Figure 3-3 (c) GLMM results showing increases and decreases in proportion of Mature stages (V-IX) in tree and shrubs in North-East of South Australia between paddock and roadside reserves
G = Grazed sites, R = Roadside Reserves; *** = p<0.001, ** = p<0.01, * = p<0.05; life stages V-IX described in Fig. 3.2 (Tiver & Andrew 1997). Error bars are ± 1 standard error

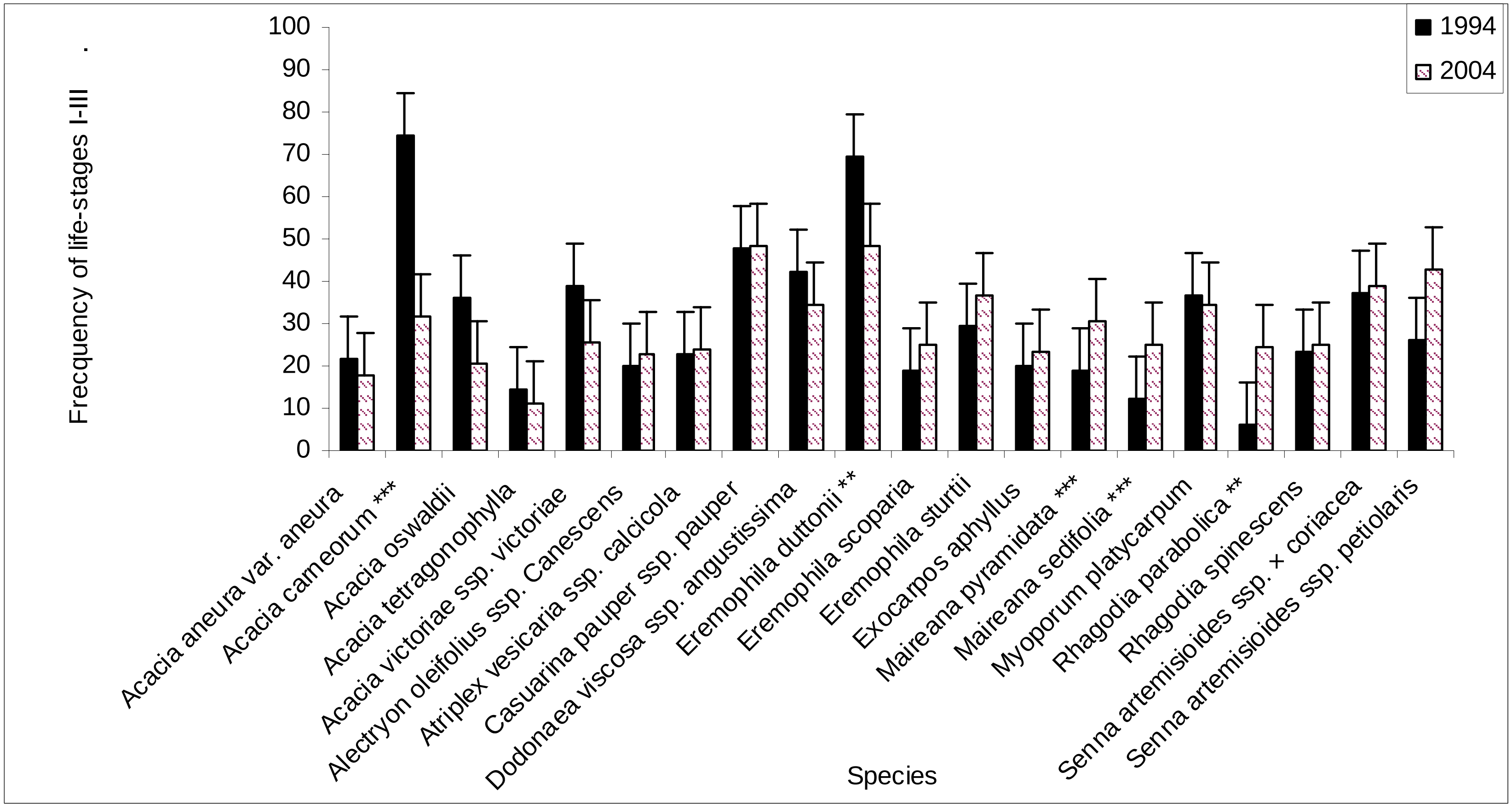


Figure 3-4 (a) GLMM results showing increases and decreases in proportions of Juvenile stages (I-III) in tree and shrubs in North-East of South Australia between 1992 and 2004

*** = p<0.001, ** = p<0.01, * = p<0.05; life stages I-III described in Fig. 3.2 (Tiver & Andrew 1997). Error bars are ± 1 standard error

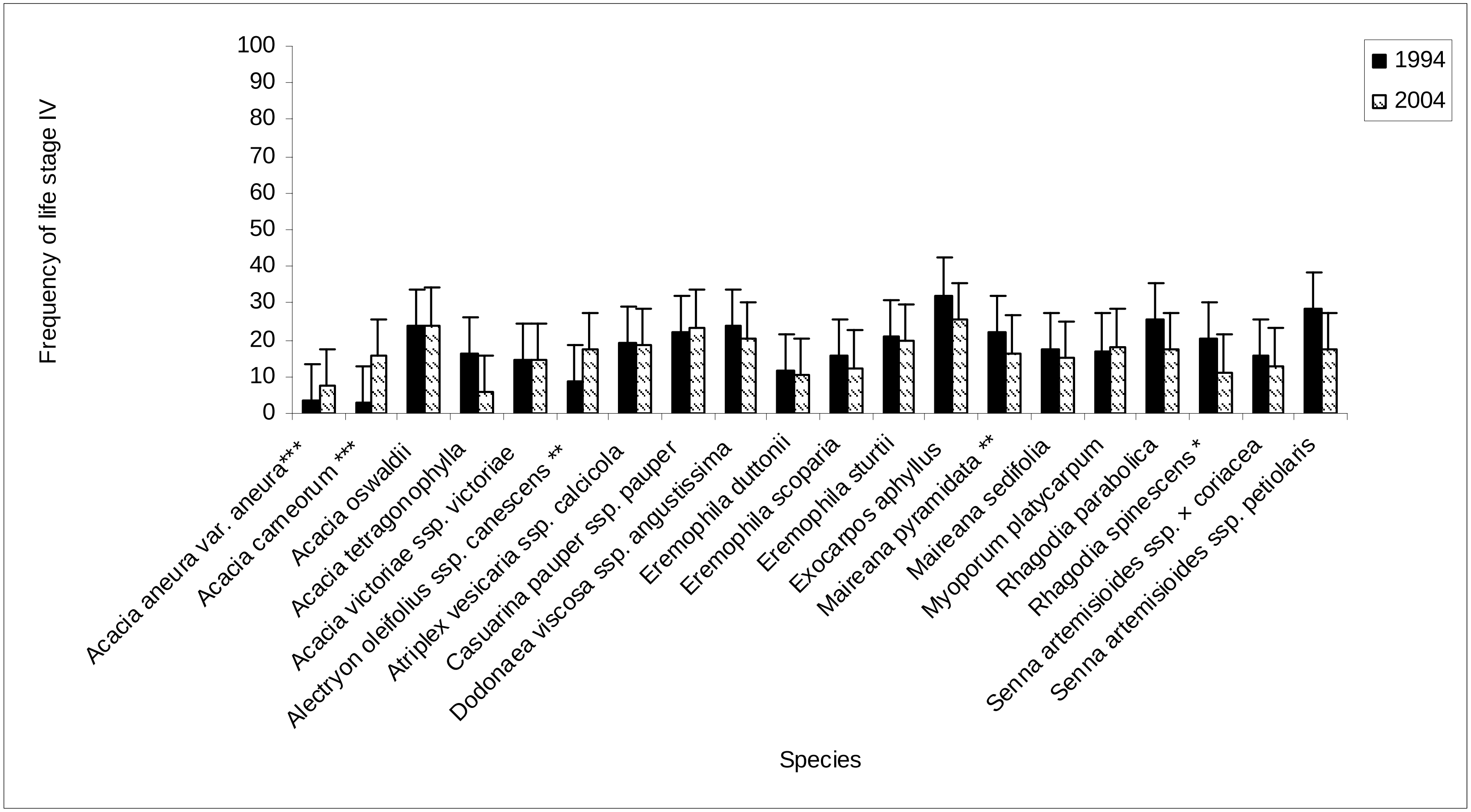


Figure 3-4 (b) GLMM results showing increases and decreases in proportion of stage (IV) in tree and shrubs in North-East of South Australia between 1992 and 2004

*** = p<0.001, ** = p<0.01, * = p<0.05; life stage IV described in Fig. 3.2 (Tiver & Andrew 1997). Error bars are ± 1 standard error

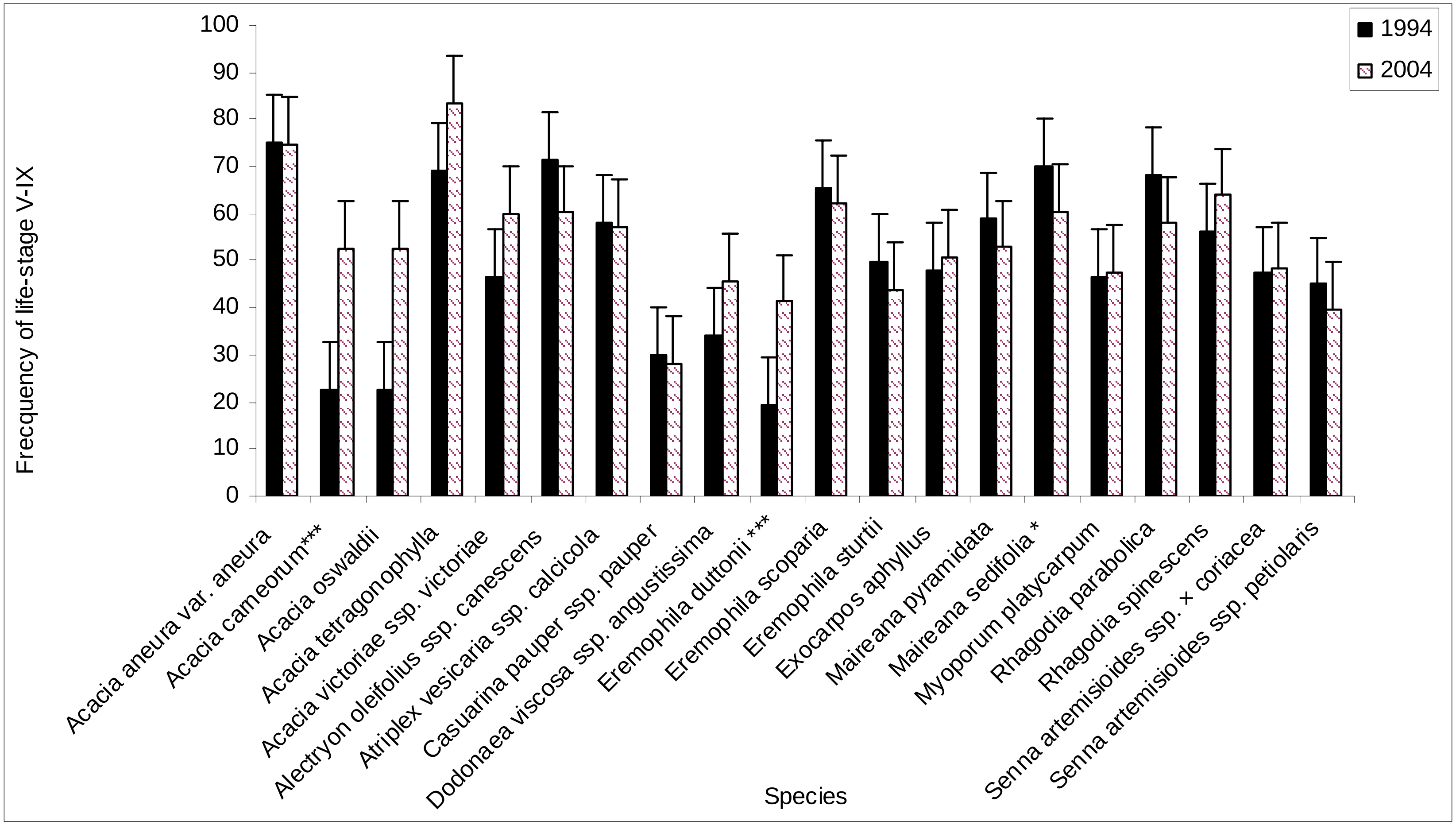


Figure 3-4 (c) GLMM results showing increases and decreases in proportion of Mature stages (V-IX) in tree and shrubs in North-East of South Australia between 1992 and 2004

*** = p<0.001, ** = p<0.01, * = p<0.05; life stages V-IX described in Fig. 3.2 (Tiver & Andrew 1997). Error bars are ± 1 standard error

Table 3-3 Mean index score (Table 3.1) of different herbivore activity at sites in North-East South Australia

Site	Sheep	Rabbits	Kangaroos
1992 Ungrazed	0	2.2	0.9
2004 Ungrazed	0	0.52	2.1
1992 Grazed	2.1	2.6	1.1
2004 Grazed	3.1	0.72	1.3

Effects of herbivores on regeneration

Mature stages

When the proportion of juvenile (I-III) and stage IV increases, the mature stage (X-IX) must decrease. This is because of the use of proportional data, so there is a problem of degrees of freedom when interpreting the data. Therefore mature stage results although presented are not interpreted further.

i. Changes in frequency of life-stage classes by both grazing x year

Five species (*Acacia carneorum*, *Acacia oswaldii, Acacia victoriae ssp. victoriae, Eremophila sturtii* and *Rhagodia parabolica*) out of 20 showed significant interaction between year and grazing in Juvenile stage (Table 3.2). In Stage IV, five species showed significant results (*Acacia tetragonophylla*, *Acacia victoriae ssp. victoriae, Myoporum platycarpum*, *Rhagodia spinescens* and *Senna artemisioides spp. petiolaris*).

ii. Changes in frequency of life-stage classes by grazing

Most of the plant populations showed a significant difference between the grazed and ungrazed sites. Juveniles of twelve species out of 20 species showed a significant increase in roadside reserves: (*Acacia aneura* var. *aneura, A. carneorum, Alectryon oleifolius spp. canescens , Dodonaea viscosa ssp. angustissima, Eremophila duttonii, E. scoparia, Maireana sedifolia*, *Myoporum platycarpum*, *Rhagodia parabolica, R. spinescens, Senna artemisioides spp*. x *coriacea*, *S. artemisioides spp. petiolaris*) showed significant increases (Fig. 3.3a). In stage IV (Fig. 3.3b), sixteen out of 20 species increased in the roadside reserves, four significantly (*Acacia aneura* var. *aneura, A. carneorum, Alectryon oleifolius spp. canescens, Myoporum platycarpum ssp. platycarpum*) increased and only one, *Eremophila duttonii,* decreased in the ungrazed areas. This could be the results of higher survivorship of Stage III plants from 2002.

iii Changes in frequency of life-stage classes by year

When comparing differences over time in the juvenile stage, out of 20 species, thirteen showed increase in their proportion of stages I-III between the years, five species significantly (*Acacia carneorum*, *Eremophila duttonii, Maireana pyramidata, M. sedifolia, Rhagodia parabolica*) (Fig. 3.4a). Over time, in stage IV (Fig. 3.4b), seven species increased proportionally (*Acacia aneura* var. *aneura, A. carneorum A. oswaldii, A. victoriae ssp. victoriae, Alectryon oleifolius spp. canescens, Casuarina pauper spp. pauper, Myoporum platycarpum spp. platycarpum*) four plants significantly (*Acacia aneura* var. *aneura, A. carneorum*, *Alectryon oleifolius ssp. canescens, Rhagodia spinescens*). In contrast *Maireana pyramidata* significantly decreased its stage IV proportion over time.

Discussion

Herbivore assessment and effect of Rabbit Calicivirus (RCV)

Rabbit abundance both in the paddocks and the road reserves was less in 2004 than 1993 as a result of the release of RCV in 1995. These results are consistent with other findings (Saunders *et al.* 1998; Sharp *et al.* 2001; Sandell 2002; Saunders *et al.* 2002). Sheep and kangaroos were found in all parts of the paddocks. In the road reserves kangaroo movements are high compared to 1992 probably because of lowered rabbit numbers. This supports Mutze and Hawker (2006) who found decreased rabbit numbers and increased movements of kangaroos and sheep in areas which were severely effected by rabbits before the release of RCV.

Herbivore interactions and Plant populations

Increase in the juveniles as a proportion of the populations is explained by the regeneration of plant species after 1995, after release of RCV. Tiver and Andrew's (1997) survey demonstrated that the absence of regeneration of plant species is correlated with sheep grazing. There has been no significant recovery in those populations inside the paddocks since the release of RCV.

In the road reserves a number of species showed significant regeneration in 1992 but there was no increase over time, so no recovery following the release of calicivirus. The failure of recovery may also be because of lack of rainfall related regeneration 'events' between 1992-2004. It is considered that the water is a controlling factor in regeneration of plant species (Johnston 1969; Silcock 1977; Grice & Westoby 1987; Auld 1990; Harrington 1991; Auld 1995a, b; Milton 1995; Owens *et al.* 1995; Read 1995; Lloret 1998; Barnes 2001; Yates & Broadhurst 2002; Denham & Auld 2004).

Lack of regeneration could also be due to palatability to kangaroo grazing (Chapter 5). In the road reserves it is noticeable that there were higher kangaroo movements in the absence of rabbits. Kangaroos have previously are been thought to rely on green grass for most of their diet (Newsome 1965) but more recent work shows that they cause damage to other plant species (Neave & Tanton 1989; Kimberly & David 2004). Kimberly and David (2004) found that excluding kangaroos allowed a large increase in survival rates of *Themeda australis* seedlings. Results of Chapter 4, consistent with the present results, showed *Acacia aneura* var. *aneura* seedlings were unable to recover from kangaroo grazing.

Inside the paddocks no regeneration has occurred. Sheep are the most significant large vertebrate suppressing plant regeneration because they are restrained by fences and numbers can be maintained at high levels under dry conditions as long as water is available, and long after rabbits have ceased to have any impact (Reid 1993). Sheep therefore have the potential to cause more damage over time than rabbits.

Results found in this study are consistent with previous results of Harrington (1979) who found sheep grazing reduces the regeneration of a number of species including *Acacia aneura* var. *aneura* and *Dodonaea viscosa* but has no effect on *Senna* spp. and *Eremophila sturtii* in western New South Wales. In this study *Senna artemisioides spp. petiolaris* populations increased inside the paddock as well as on roadsides. Lack of regeneration of *Alectryon oleifolius ssp. canescens* is consistent with the results found by Hall (1964) and Barker (1970), who observed little regeneration over most pastoral lands of South Australia. The stable populations of *Casuarina pauper ssp. pauper* were consistent with results found by Chesterfield and Parsons (1985) who found that the sheep grazing is not threatening the populations of this species in south-western New South Wales. The stable population of *Atriplex vesicaria* showed that the sheep grazing did not suppress these populations, as observed by Graetz (1980), Eldridge *et al.* (1990) and Yan *et.al* (1996). Lack of regeneration of *Myoporum platycarpum* is consistent with Tiver and Keiermeyer (2006), who observed the total elimination of its seedlings in the unfenced treatments in the South Australian chenopod shrublands.

Four out of 20 species showed significant interaction between year and grazing of Stage IV, but there was no significant interaction between year and grazing in the juvenile stages. Any increase in Stage IV must be due to Stage III plants present in 1992 which had successfully progressed to Stage IV by 2004.

Woody weeds

Almost all of the plants (eighteen) in this study showed lack of regeneration caused by grazing, but in some species (*Eremophila duttonii, Eremophila scoparia, Eremophila sturtii, Exocarpos aphyllus, Maireana pyramidata, Maireana sedifolia, Rhagodia parabolica, Senna artemisioides spp. petiolaris*) regeneration occurred in both grazed and ungrazed sites. This supports Silvertown & Doust (1993) who described that although the landscape's theoretical carrying capacity is resource-based, herbivory may mean that not all possible locations are filled within grazed landscape. Some species are less palatable than others and can therefore increase their cover dominance in relation to more susceptible ones. Tiver & Andrew (1997) concluded that the weediness in woody plants is not an isolated phenomenon of a plant species, but may be change over a landscape due to the varying susceptibility, of species to herbivores. This explains why plants such as *Acacia aneura* var. *aneura* have been cited as woody weeds in western New South Wales. Greater increase in the juvenile stages of *Senna artemisioides spp. Petiolaris* than *Senna artemisioides spp.* x *coriacea* supports the view of West (1997) who noticed *Senna artemisioides spp.* x *coriacea* is more palatable than *S. artemisioides spp. petiolaris.* In the present study *Eremophila sturtii* has showed significantly increasing numbers in both grazed and ungrazed sites which was consistent with Harrington (1979) who described this species as unpalatable to sheep.

Conclusion

Elimination of rabbit numbers alone is not enough to restore plant species in the rangelands. Even though rabbit numbers are currently lower in the study area due to the release of Calicivirus in 1995, kangaroo and sheep grazing (and possibly drought) has continued to suppress regeneration. It will be important to maintain low numbers of kangaroos and spell paddocks from sheep grazing to restore regeneration.

Chapter 4

Herbivore effects on the survival of *Acacia aneura* var. *aneura* seedlings: Exclosure trials

Introduction

In Australian rangelands, sheep farming is one of the major land uses. Land is mainly divided into paddocks with one or more watering point (Graetz 1978). In general it is considered that in the past century overgrazing by sheep along with other native and feral herbivores has led to degradation of Australia's rangelands around the watering points (James *et al.* 1999). The daily congregation of sheep around the watering point produces a noticeable "piosphere effect" a radial grazing zone decreasing with distance from the watering point (Lange 1969; Andrew 1988). The distribution of animals away from watering points depends on seasonal conditions, physiological condition and forage availability (Newsome 1965; Wilson 1974; Squires 1976). This uneven movement of animals round the watering point leaves different grazing gradients which are useful to assess rangeland condition (Foran 1980; Andrew & Lange 1986a; Andrew & Lange 1986b; Stroleny & Mentis 1989). Sheep movement in paddocks is not random (Landsberg & Stol 1996) and unpredictable and is related to water availability and wind direction even when herbage is readily available (Andrew & Lange 1986b; Stafford-Smith & Morton 1990). Many studies adopted this piosphere concept directly in their studies (Andrew & Lange 1986b; Landsberg *et al.* 1999b; Hunt 2001; Heshmatti *et al.* 2002; Palisetty *et al.* 2006). Many native species which are under threat from the livestock grazing (Tiver & Andrew 1997) persist only on areas remote from water (Landsberg *et al.* 1999b; Hunt 2001).

Kangaroos are the largest extant herbivore and are found throughout the Australian rangelands (Dawson 1998). Sheep and kangaroos have comparable body size (Stranhan 1983; Cottle 1991) and many previous studies have shown that kangaroos will more competent for shrubs when herbs and forbs are scarce (Dawson *et al.* 1975; Barker 1987; Dawson 1989; Edwards *et al.* 1995). In drought periods kangaroos are most commonly found around watering points (Newsome 1965; Dawson *et al.* 1975; Norbury & Norbury 1993; Gibson 1995).

It has been shown that rabbits along with large herbivores have suppressed the recruitment of some perennial plant species in semi-arid and arid Australia (Johnston 1969; Lange & Graham 1983; Silander 1983; Auld 1990, 1993, 1995a, b), but separation of the effects of sheep and rabbits is less clear. After release of calicivirus rabbit numbers dropped to low levels (Pech & Hood 1998) and which provided a chance for recovery of plant species (Sandell 2002).

Many previous studies of grazing by sheep were conducted during high densities of rabbit populations (before calicivirus). These earlier studies concluded that under current sheep-grazing regimes with high level of rabbit populations, the levels of regeneration of arid and semi-arid trees would continue to be low or zero; some of the plant species for which this effect has been shown are *Acacia burkittii* (Crisp & Lange 1976), *Acacia aneura*, *Maireana sedifolia*, *Atriplex vesicaria* (Crisp 1978) and *Cassia nemophila* [*Senna artemisioides*] (Silander 1983).

To identify the grazing pressure of different animals under grazing regimes, exclosures are widely employed (Lange & Graham 1983; Cooke 1987; Tiver & Keiermeyer 2006). These techniques allow assessment of the relative importance of each herbivore in the suppression of regeneration.

Aim

To determine the survival of *Acacia aneura* var. *aneura* seedlings under rabbit-reduced regimes within a piosphere by recording survivorship of *Acacia aneura* var. *aneura* seedlings planted at various distances from a watering point.

Methods

The study area

This part of the research was conducted on the Eyre Peninsula at Middleback Research station (32^{o} $57'$S, 137^{o} $24'$E) (Fig. 4.1) which is located approximately 21 km west of the city of the Whyalla, South Australia. The climate of this area is predominantly arid, with long hot summers, short cool winters and with low and unpredictable rain fall. Because of its inland position average monthly temperatures oscillate from maximum 28.9^{0}C and minimum of 18.7^{0}C in summer and maximum 16.8^{0}C to minimum 7.3^{0}C in winters. The average rainfall at Middleback Homestead from the years 1925-2004 is 214 mm but is highly variable ranging from 98 mm (1943) to 511 mm (1973) (Nicolson *pers. Comm.*). Soils are predominantly brown calcareous earths with a clay loam texture (Northcote 1968) and originally derived from alluvial and aeolian sedimentary parent material (Jessup & Wright 1971). Topsoils range from sand to clay-loam in texture and are commonly reddish-brown in colour, slightly alkaline and with low nutrient availability (Crocker 1946). Four vegetation associations are commonly found in the Middleback region (Reid 1984): chenopod low open shrubland, in which *Atriplex vesicaria* and *Maireana sedifolia* are the dominant plant species; *Maireana pyramidata*, *Atriplex stipitata* and *Rhagodia ulicina* commonly found in the washes and basins; *Acacia papyrocarpa* low open-woodland; and *Casuarina pauper* low woodland.

Research design

An experimental study at Middleback was set up to assess current herbivory of seedlings by rabbits and large herbivores (sheep and kangaroos) (Fig. 4.2). Only one paddock was used because our statistical advice recommended that if funding is limited, it is better to have increased replicates at one paddock, rather than insufficient replicates at more than one paddock. An initial inspection was conducted in January 2002 for paddock and research plot selection. In June 2002 the experiment was laid out with four distinct plots at increasing distances from the watering point: 0.5, 1.5, 3.0 and 5.0 km (Fig. 4.2). The approximate area of each plot was 100 m x 100 m.

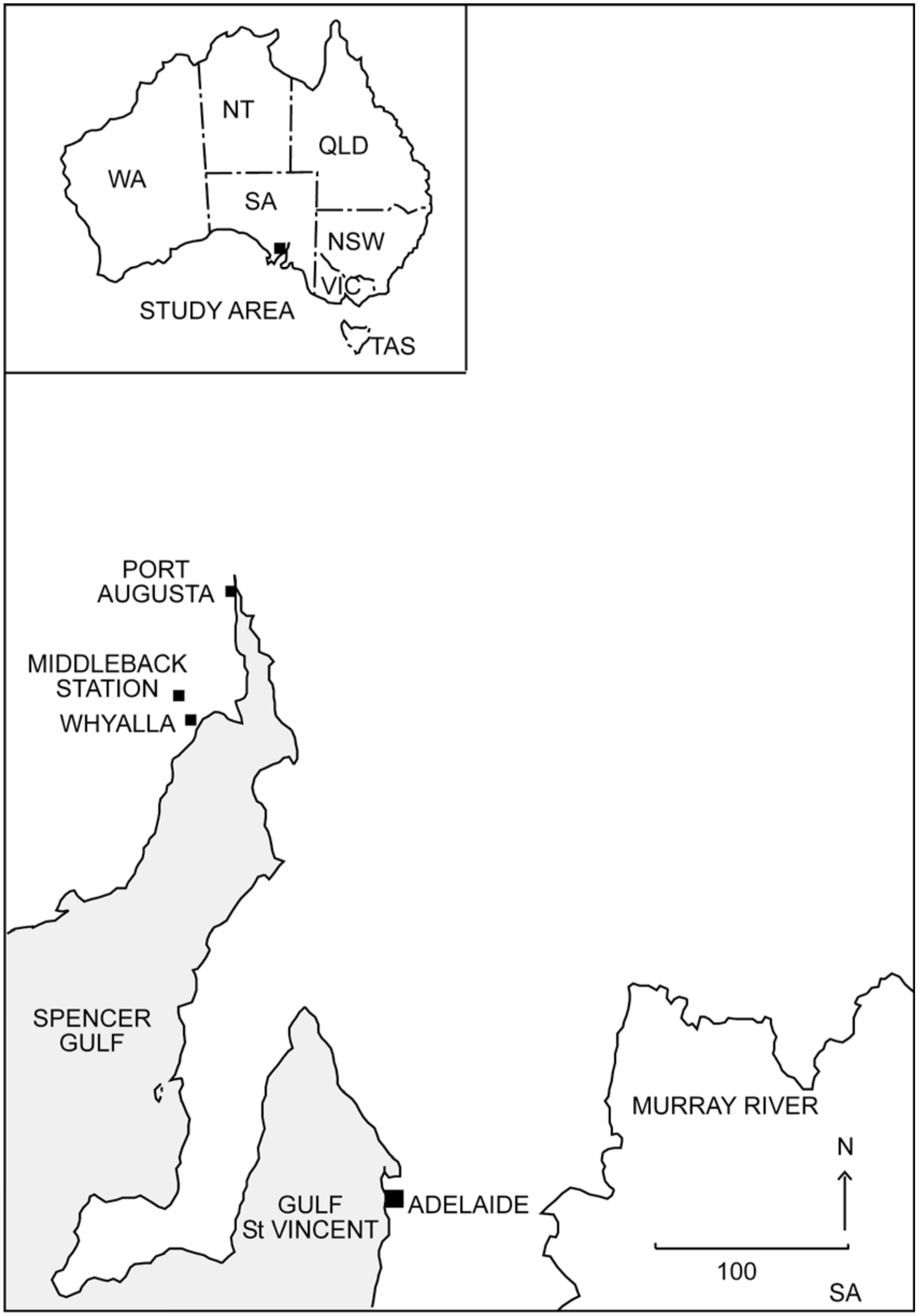


Figure 4-1 Location of the study area on the Australian continent (inset), and in South Australia (SA)

At each plot, 10 replicates of the following treatments were installed: unfenced (U), sheep-fenced (S) and rabbit-fenced (R) giving a total of 30 exclosures in each plot (Figs. 4.2 & 4.3). The treatment (U) had no exclosure (exposed to all herbivores) but was marked with two metal stakes and tagged. The second treatment (R) was fenced with rabbit proof netting (where no vertebrate herbivores can graze). The diameter of the (R) exclosure was 70 cm and the height 1.1 m. It was supported with three metal stakes and tightly tied with wire and tagged. The netting was buried 5 cm deep into the ground to prevent the rabbits burrowing to reach the plant. The third treatment (S) was fenced with sheep-proof "cyclone netting" with 10 cm by 8 cm holes (where rabbits can graze but sheep and kangaroos can not). The diameter of the (S) exclosures was 2 m. This larger diameter was to prevent sheep and kangaroos from reaching the seedling if they put their heads inside the exclosure. The exclosure was supported with 4 metal stakes because of the large circumference. Tags on all treatments recorded plot and treatment number and the date and year of establishment to give easy identification throughout the project.

Seedling establishment

Because of time limitations and slow growth of *A. aneura* var. *aneura*, seedlings were purchased from Forest S.A during the early winter of 2003. In order to adapt them to the lower humidity of the arid regions of South Australia the seedlings were "hardened off" in open conditions for one month at Middleback station. Seedlings were planted in the field in June 2003. The seedlings were approximately one to two years of age at the time of planting and were between 10 to 17.5 cm tall.

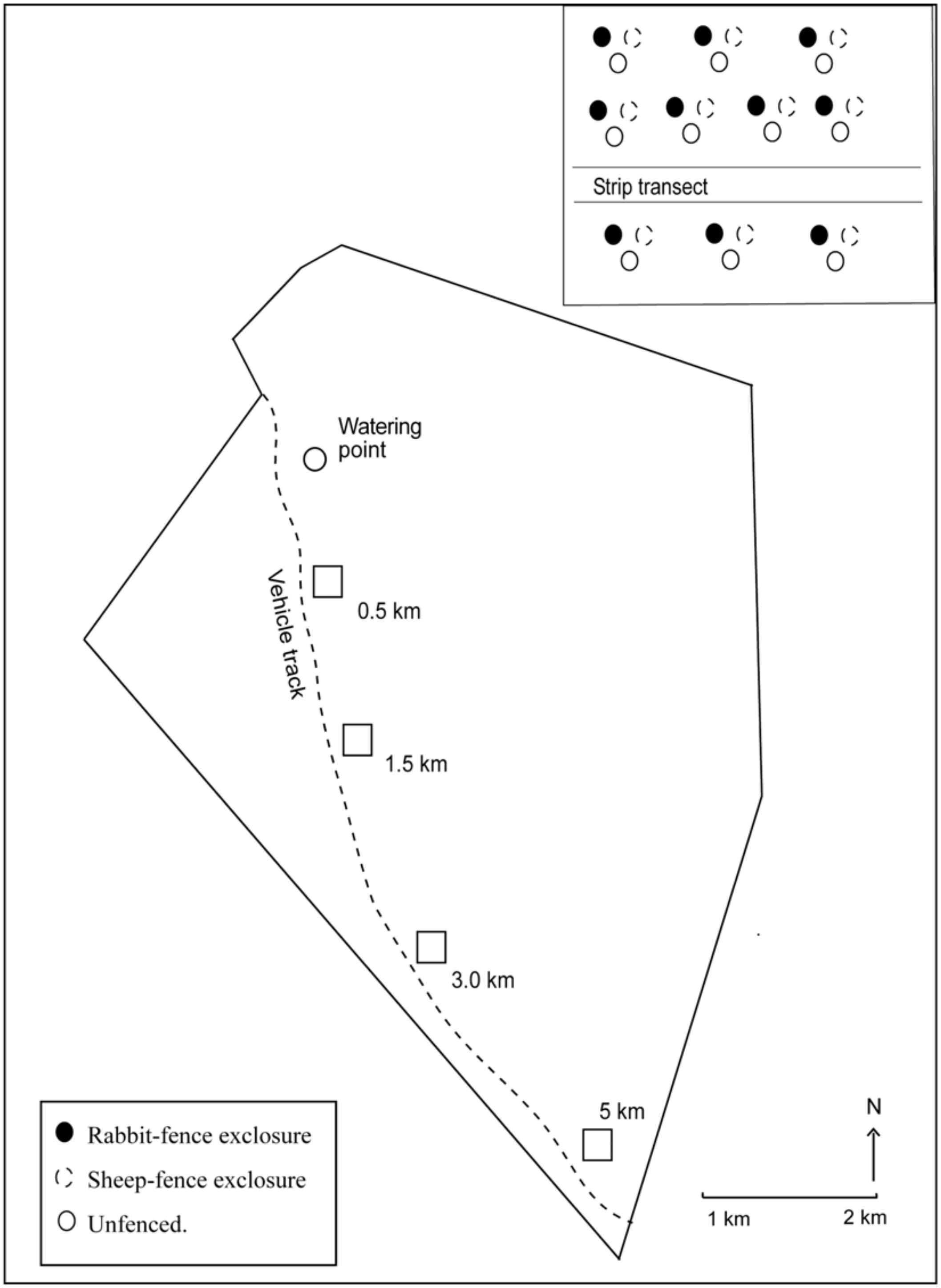


Figure 4-2 Location of the plots at various distances from the watering point in Railway Paddock, Middleback Station, Whyalla
Inset is a diagrammatic representation of the treatments and replicates

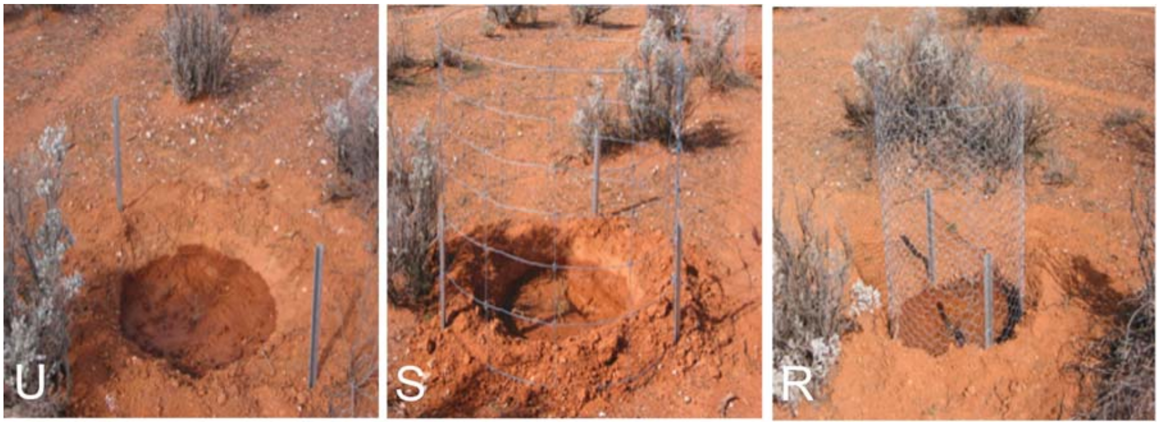


Figure 4-3 Seedlings exposed to different exclosure treatments
U=Unfenced, S=Sheep-fence exclosure, R=Rabbit-fence exclosure

In each exclosure treatment a planting hole was dug of 50 cm diameter and 5 cm deep and one *A. aneura* var. *aneura* seedling was planted. Plants were immediately watered (20 L). Watering of the seedlings was essential for their establishment in the new location because of high death rates from desiccation in transplanted seedlings (Jusaitis 2005) and even in naturally germinated seedlings (Auld 1990; Harrington 1991; Read 1995). A total of 120 seedlings were planted (30 at each of the 4 plots). Supplementary watering of the newly established seedlings at a rate of 20 L per plant was carried out at two-weekly intervals for the first 90 days (from June to August 2003), and thereafter once per month (from September 2003 to November 2004. Seedlings were monitored over 482 days (18 months) at monthly intervals for height (H), width (maximum width W1 and W2 its orthogonal equivalent) and condition: alive and ungrazed (AU); alive and grazed (AG); dead though grazing (DG) and dead though desiccation (D). After each monitoring visit an Index of Canopy Volume (ICV) was calculated: for each seedling according to the formula:

$$ICV= [\ (W_1+W_2)/4]^2 \times \pi \times \text{Height-----------------} \qquad \text{Equation 1}$$

Herbivore faecal weights

Faecal samples were collected from 200 m x 2 m long strip-transects located across each plot. The transect was marked out by measuring tape and two small stakes were placed at the beginning and the ending of the transect, to ensure that the same transect could be re-monitored. After exclosure treatments were established in June 2003 at all plots, all the faecal matter within the strip-transects was cleared and made ready to take the first faecal count in July 2003. From July 2003 to October 2004 all the faecal matter from the strip-transects was collected during the monthly monitoring visits. All the faecal matter that had been deposited since the previous visit was categorised into rabbit, sheep or kangaroo by its physical appearance (Landsberg *et al.* 1994). Faecal samples were oven-dried overnight at 60-65^{0}C in the laboratory and the dry dung weight per unit area, assumed to be proportional to herbivore time per unit area, was taken to represent relative grazing pressure (Lange 1969), was recorded.

Data analysis

The objective of the analyses was to establish differences between treatments in the trend shown by an index of canopy volume (ICV) over the experimental period. Separate analyses were conducted at each of the four plots (different distances from the watering point). Firstly, profile plots of the data were obtained to give a graphic description of the data. The data were then analyzed using mixed models to investigate differences between the treatments in the ICV trend. A preliminary stage in this analysis was the selection of an appropriate model for the variation in the data. As the data is longitudinal, in that measurements of the same units are taken at monthly intervals during a period of 482 days, there may be unequal correlation between the measurements on different days and the variance may not be the same for all measurement days. Further, there may be other sources of unequal variation. Having established a suitable model for the variances, cubic smoothing splines were used to capture the smooth trend in ICV over time and it was investigated whether these trends varied between treatments and if there was significant random deviation from the trends. All the analyses were performed using the SAMM function (Spatial Analysis Mixed Models) add-in library (Butler *et al.* 2004) for S-Plus 6.2 for Windows (Insightful-Corporation 2003).

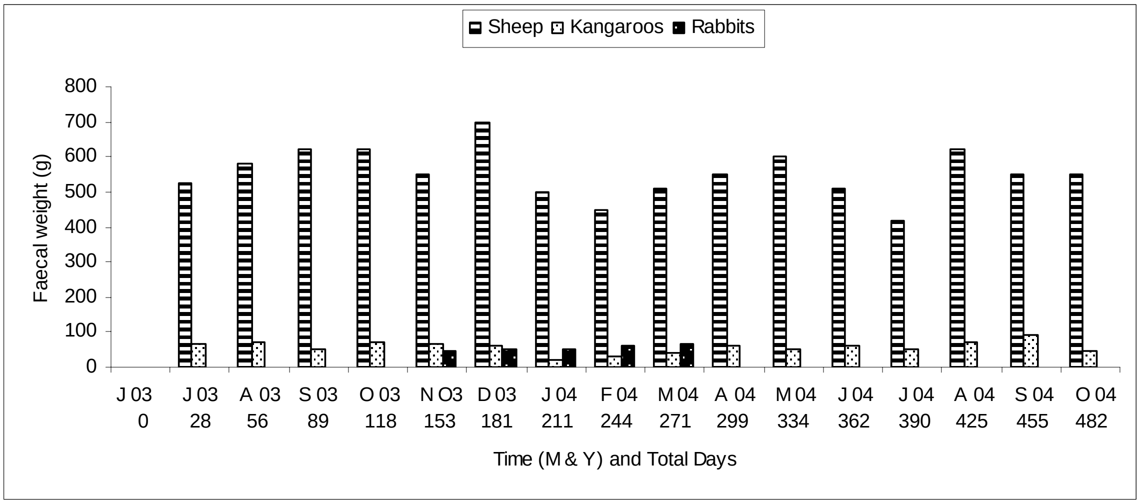
Results

Herbivore counts by faecal weight

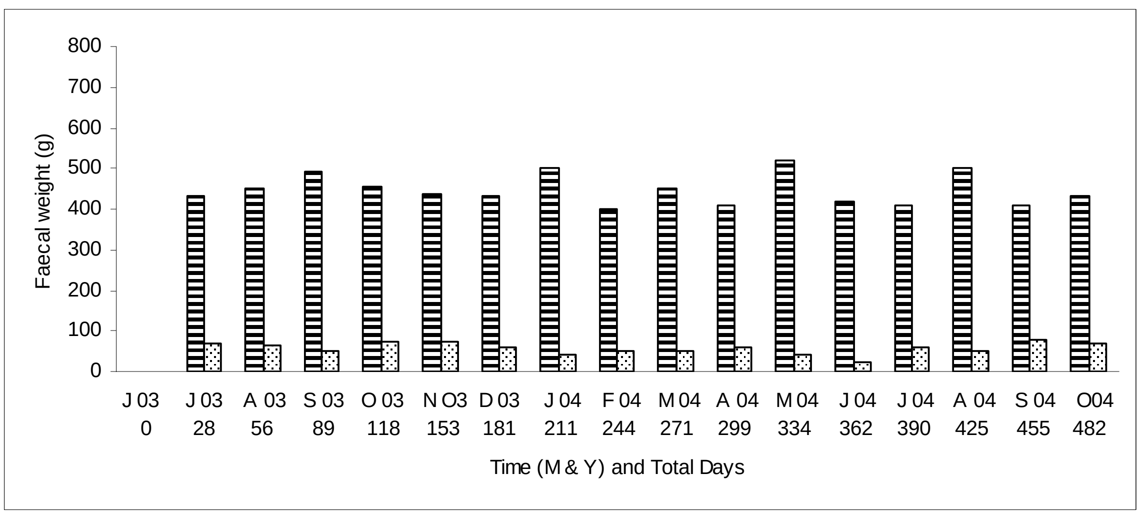
Examination of the faecal weight data shows that sheep exert the highest and most considerable grazing pressure over all plots and throughout the experiment period

(Fig. 4.4). Sheep were present at all the plots throughout the study period, higher at the plot near at the watering point than the further plots, but the difference between the plots was negligible: sheep movement (dung weights) was not significantly related to distance from watering point ($p>0.05$) (Fig. 4.5). Kangaroos were also evenly present at all the plots. Kangaroo faecal weights did not show any relationship with distance from the watering point ($p>0.05$) (Fig. 4.5). Rabbit numbers showed highly patchy fluctuations in both time and space throughout the study period. No rabbit faecal matter was present during the first 118 days (four months) at any of the four plots. After 118 days (fifth month) a weighable amount of rabbit faecal matter was found only at the first plot 0.5 km plot, closest to the watering point. Rabbits were then present only from 153 to 271 days (for five months from October 2003 to February 2004) at the 0.5 km plot, but no rabbit activity was found at any of the other plots (Fig. 4.4).

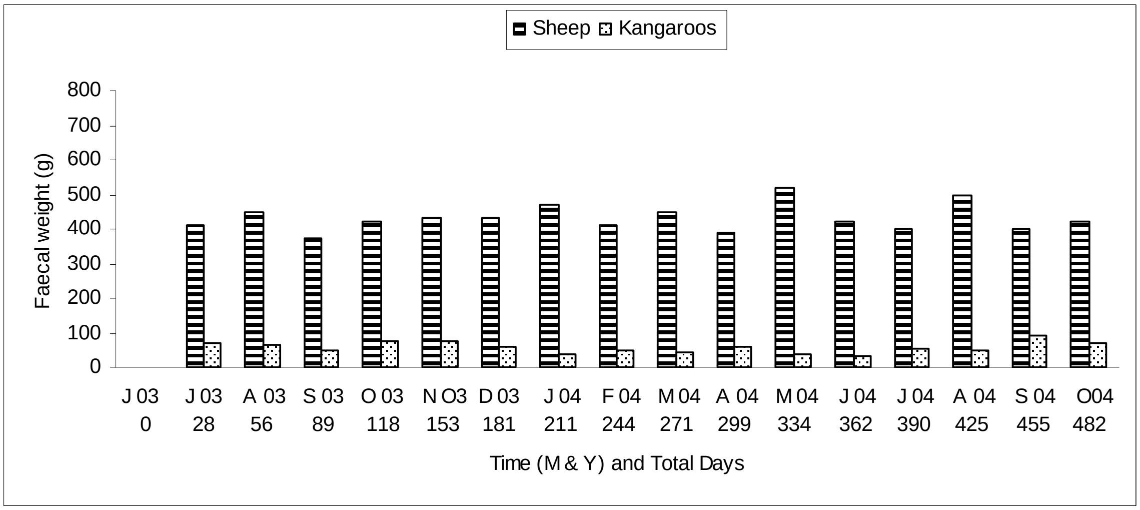
(a) 0.5 km


Sheep Kangaroos Rabbits
Faecal weight (g)
800
700
600
500
400
300
200
100
0
J 03 0
J 03 28
A 03 56
S 03 89
O 03 118
N O3 153
D 03 181
J 04 211
F 04 244
M 04 271
A 04 299
M 04 334
J 04 362
J 04 390
A 04 425
S 04 455
O 04 482
Time (M & Y) and Total Days

(b) 1.5 km


Faecal weight (g)
800
700
600
500
400
300
200
100
0
J 03 0
J 03 28
A 03 56
S 03 89
O 03 118
N O3 153
D 03 181
J 04 211
F 04 244
M 04 271
A 04 299
M 04 334
J 04 362
J 04 390
A 04 425
S 04 455
O04 482
Time (M & Y) and Total Days

(c) 3.0 km



(d) 5.0 km

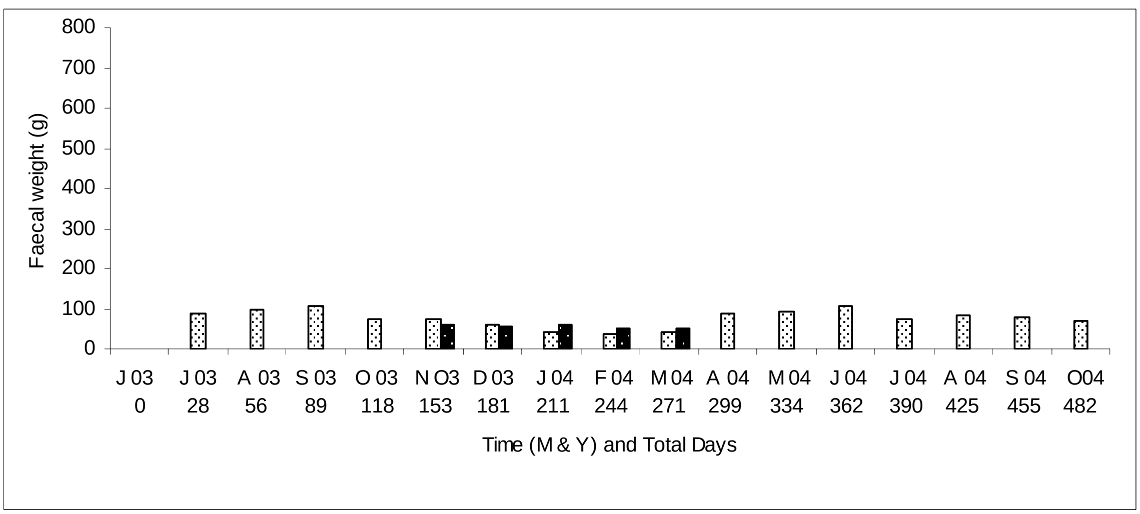


Figure 4-4 Herbivore faecal weights in 200 m strip transects over time. (a) 0.5 km (site 0.5 km distance from watering point), (b) 1.5 km (site 1.5 km from watering point), (c) 3.0 km (site 3.0 km from watering point), (d) 5.0 km (site 5.0 km from watering point). a, b, c, d refer to different distances from the watering point

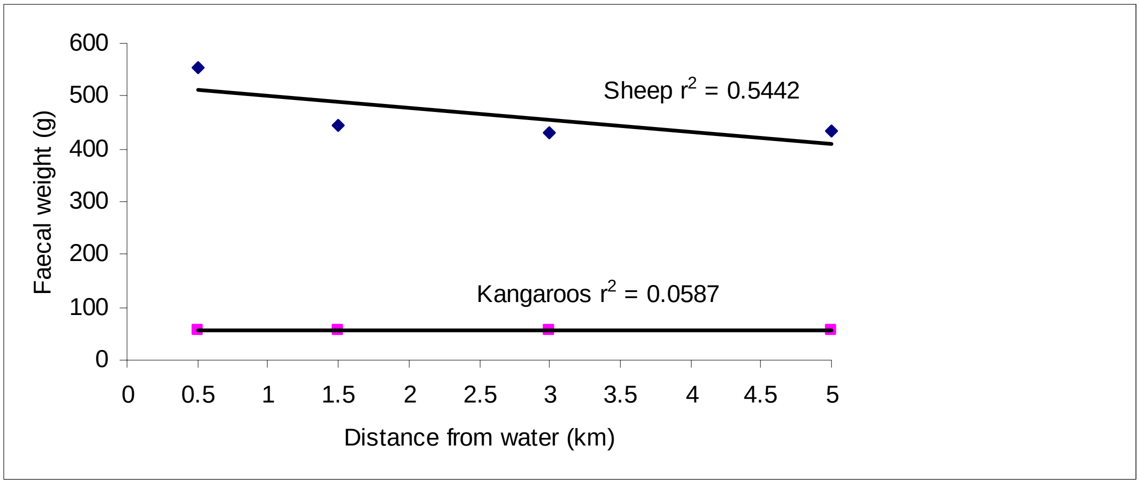


Figure 4-5 Grazing intensity at each of the four sites against different distances from the watering point
Rabbits were present at only one site and are not plotted

Desiccation loss

There were low losses of seedlings to desiccation at all plots (only in sheep-fenced and rabbit-fenced treatments). At the end of the study, an average 15% (Fig. 4.6) of seedlings had died by desiccation at all plots. In the unfenced (U) treatments in all plots no desiccation loses were observed, possibly because plants were lost to herbivory before desiccation could occur.

Grazing effects of the herbivores

At all four distances from water all the unfenced seedlings (U) were grazed by herbivores in the first 90 days (June 2003 to August 2003) (Fig. 4.6a-d), but the results did not show any distinct piosphere effect with losses appearing similar at all plots. Seedlings in the sheep fenced treatment (S) were grazed after 118 days (November and December 2003) at the 0.5 km plot; at the rest of the plots no rabbit grazing occurred. Apart from desiccation losses seedlings in the rabbit fence treatment all remained intact. This was related to the lower rabbit activity at the 1.5 km, 3 km and 5 km plots (Fig. 4.6 b,c & d).

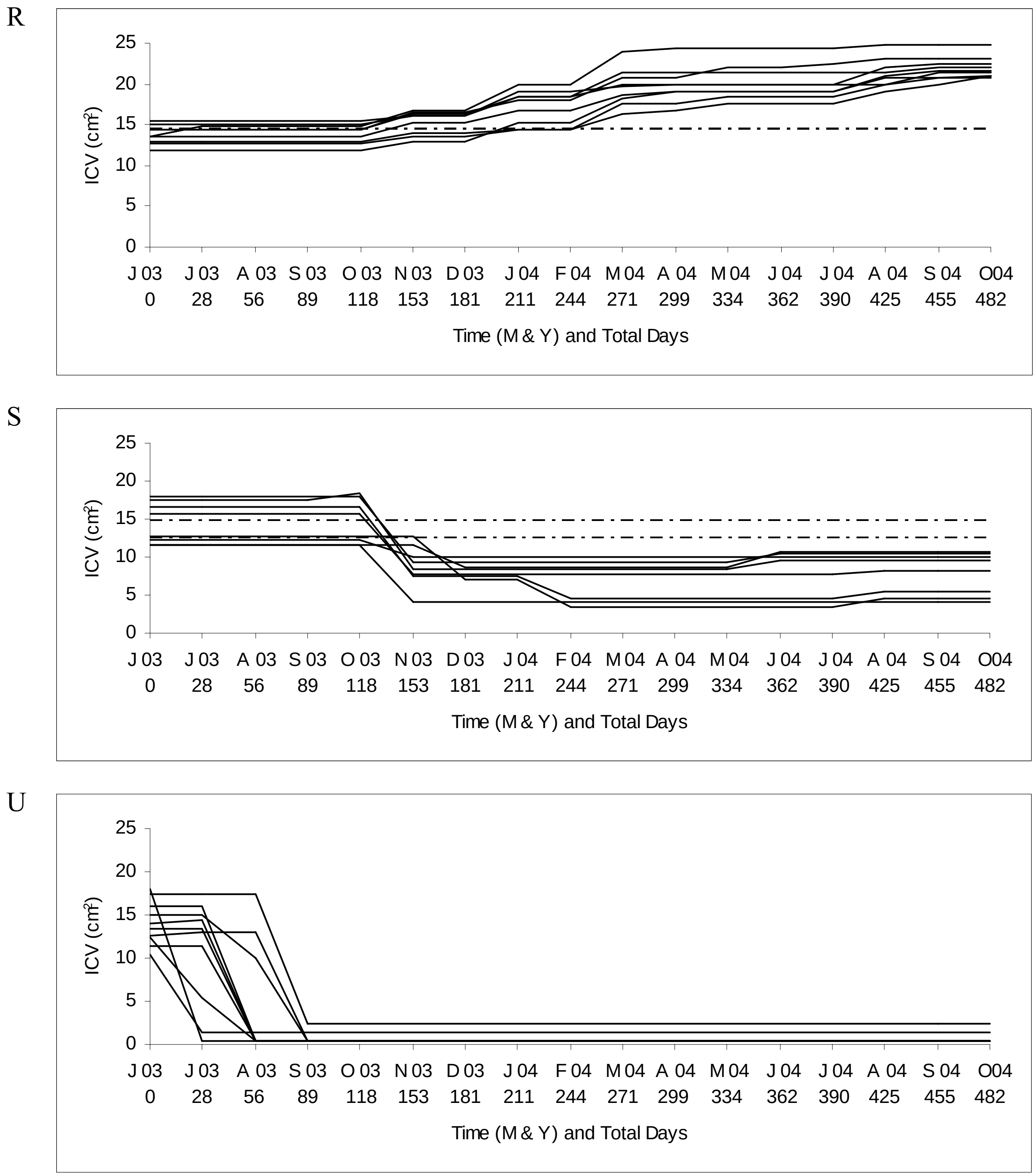


Figure 4-6 (a) Index of Canopy Volumes (ICV) of seedlings in different exclosure treatments at the 1.5 km plot
(R) Rabbit-fenced treatment, (S) Sheep-fenced treatment, (U) Unfenced. Dotted lines indicate desiccated plants

R

S

U

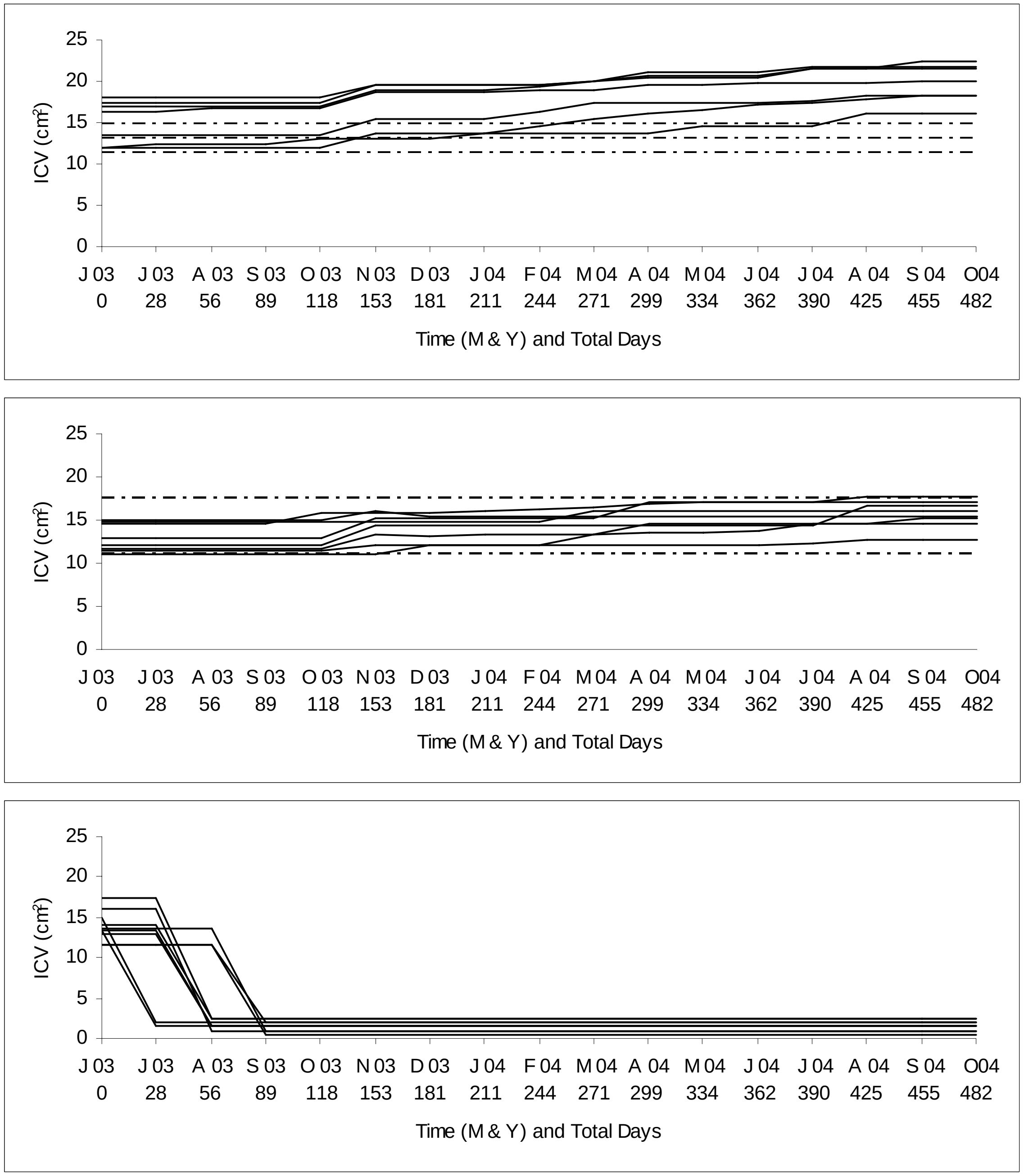


Figure 4-6 (b) Index of Canopy Volumes (ICV) of seedlings in different exclosure treatments at the 1.5 km plot

(R) Rabbit-fenced treatment, (S) Sheep-fenced treatment, (U) Unfenced. Dotted lines indicate desiccated plants

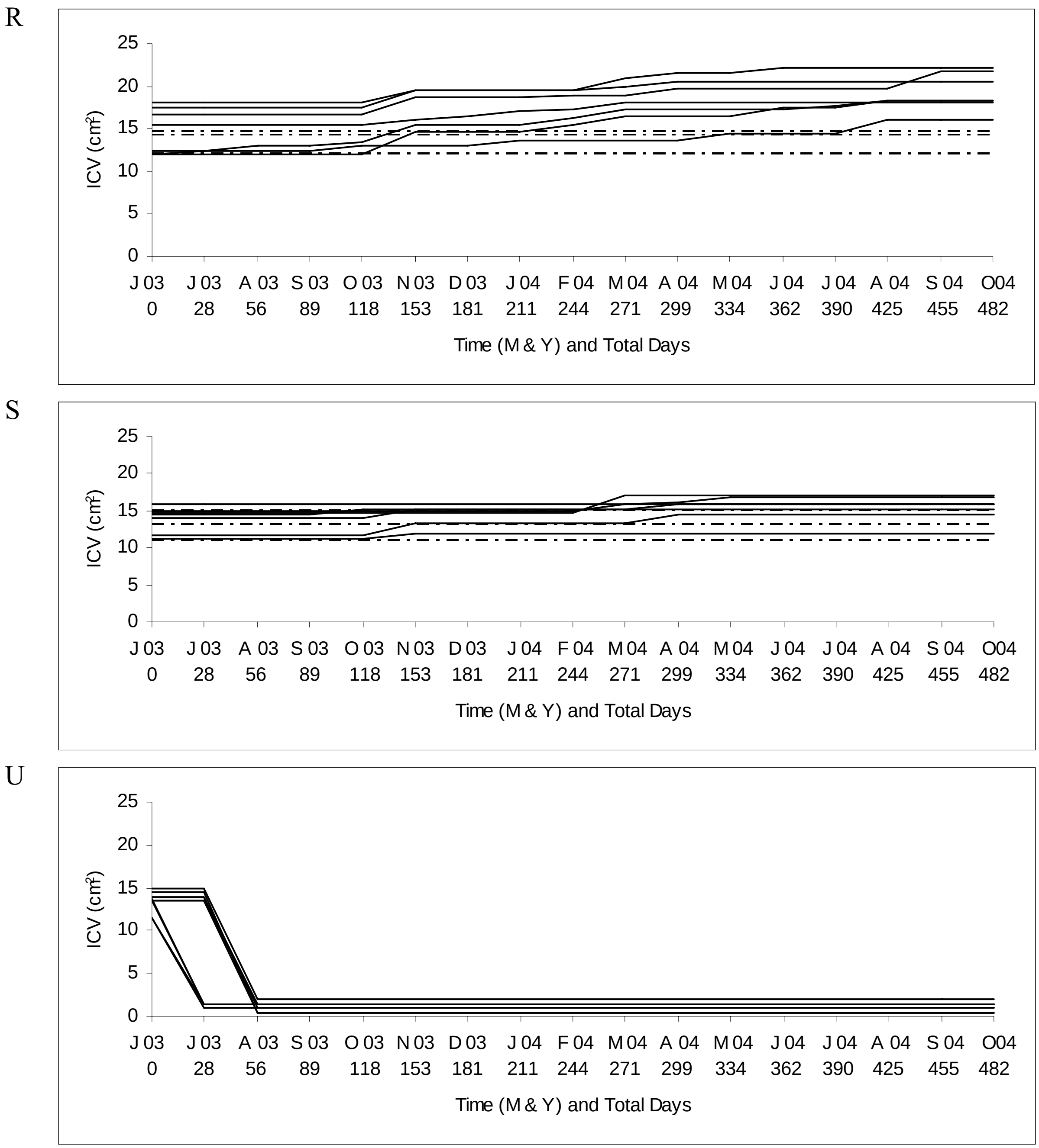


Figure 4-6 (c) Index of Canopy Volumes (ICV) of seedlings in different exclosure treatments at the 3.0 km plot

(R) Rabbit-fenced treatment, (S) Sheep-fenced treatment, (U) Unfenced. Dotted lines indicate desiccated plants

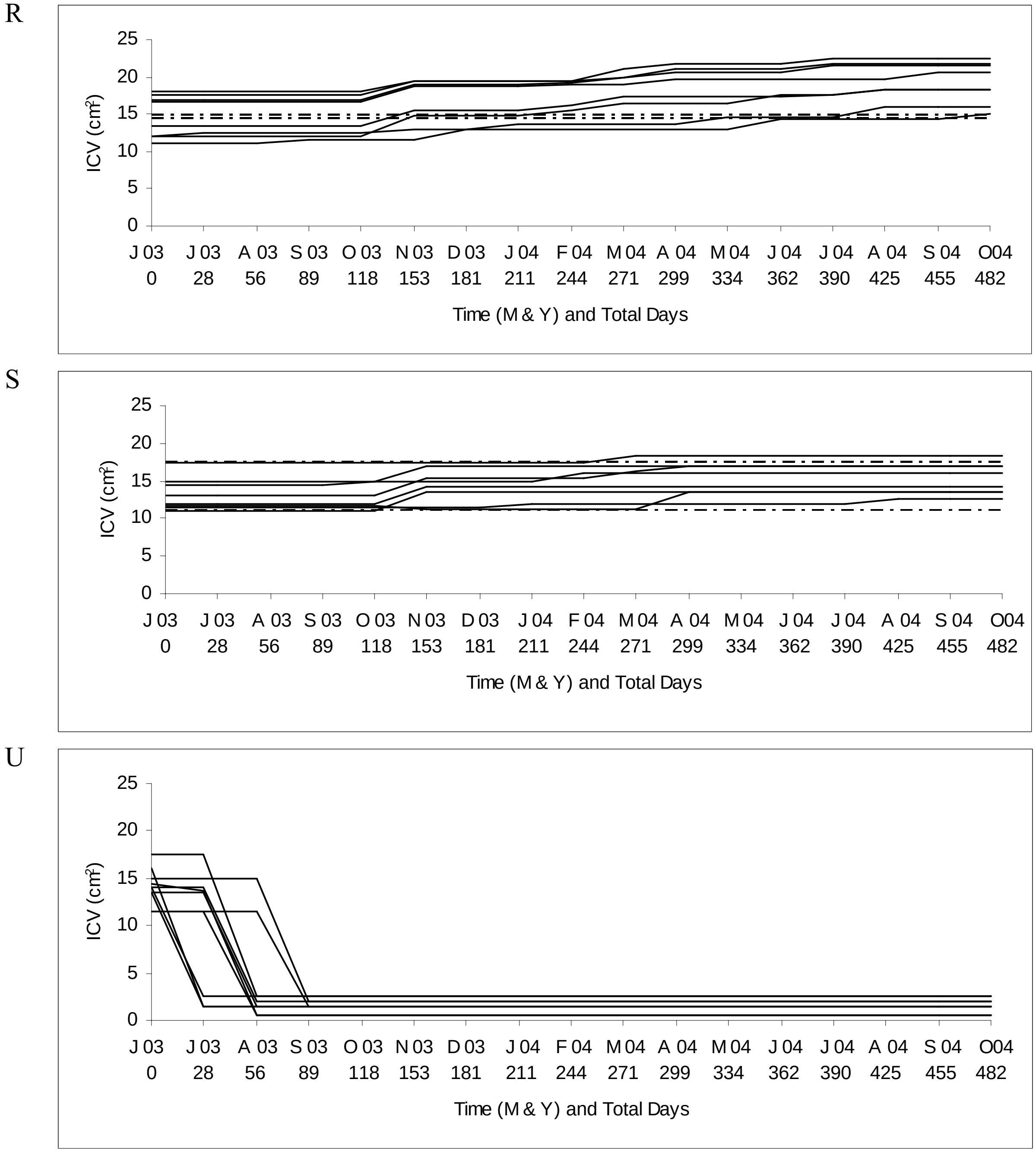


Figure 4-6 (d) Index of Canopy Volumes (ICV) of seedlings in different exclosure treatments at the 5.0 km plot

(R) Rabbit-fenced treatment, (S) Sheep-fenced treatment, (U) Unfenced. Dotted lines indicate desiccated plants

The statistical Residual Maximal Likelihood (REML) analysis (Fig. 4.7, Appendix 2), between treatments using days as a covariable confirmed the observations that the large herbivores (sheep and kangaroos) were the most significant herbivores at all the plots. Both levels of grazing protection significantly increased the survival of *A. aneura* var. *aneura* seedlings at all four plots (P<0.001) when compared with unfenced seedlings. There is no significant difference in seedling survival between sheep-fenced and rabbit-fenced treatments, indicating that rabbits were not responsible for the seedling mortality due to grazing. This was corroborated by accumulation of dung weights in the total period of the project. Desiccation and grazing pressure by the herbivores are acting together to suppress seedling survival. In the unfenced treatments grazing pressure reduced survival by 100% in under 90 days (Fig. 4.6a-d). Where sheep and/or kangaroos had access, seedlings were grazed to ground level leaving only a small part of the stem and no phyllodes for recovery after grazing. No plant was observed to recover after sheep or kangaroo grazing. The plants grazed by the sheep or kangaroos showed immediate loss of canopy volumes to ground level and no sign of recovery was observed. By faecal weights (Fig. 4.6a-d), sheep movements were greater than the kangaroos. Where large herbivores had access no desiccation loss was observed because all the plants were grazed before they could be affected by desiccation. Rabbit-grazed plants showed a different effect. Rabbits-grazed plants sustained continuous loss of canopy volumes over a period between 153-271 days (from November 2003-February 2004) during which time, some showed recovery of ICV after grazing (Fig. 4.6a.S): however, the rabbit presence was consistent with a considerable loss of canopy volume of all plants in the 0.5 km plot. But the end of the project plants recovered from grazing. Unlike sheep and kangaroos, rabbits did not graze the plants to ground level. This suggests that rabbits take less leaf material in a single grazing event.

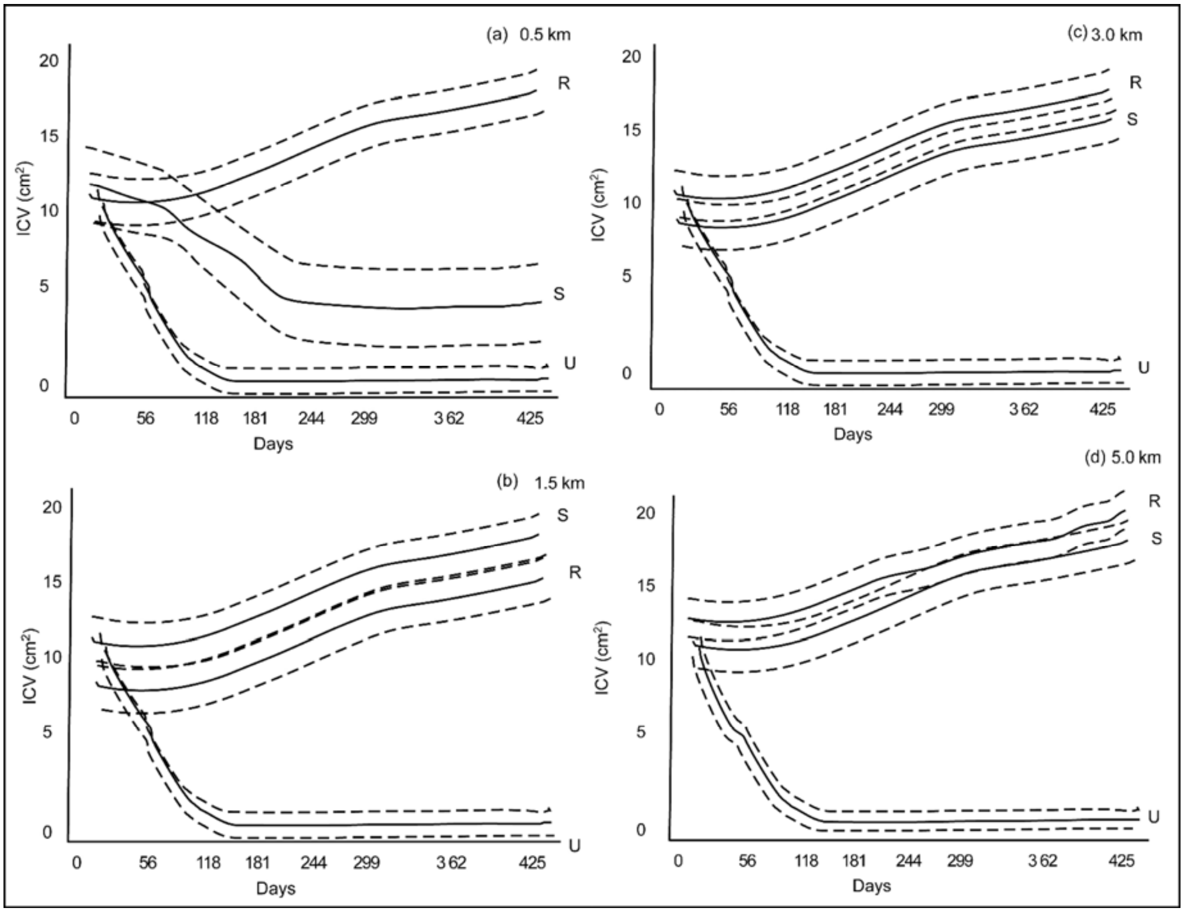


Figure 4-7 REML analysis showing the ICV (index of canopy volume) of *A. aneura* seedlings at 4 distances from the watering point under different fencing treatments R=Rabbit-fenced treatment, S=Sheep-fenced treatment, U=Unfenced. Dotted lines indicating the 95% confidence intervals

Discussion

Effects of large herbivores

The large herbivores, either sheep or kangaroos, are the major threat to survival of *Acacia aneura* var. *aneura* seedlings, grazing 100% in all unfenced treatments at ground level leaving no canopy volume. Correlation with dung weights showed that the sheep are more likely the major herbivore. These results are consistent with previous research showing that sheep grazing is the primary cause of the suppression of arid land plant communities (Pearson *et al.* 1990; Tiver & Andrew 1997; Clarke 2002; Tiver & Keiermeyer 2006). Tiver and Keiermeyer (2006) attributed the total elimination of un-caged *Myoporum platycarpum* seedling in arid rangelands of South Australia to large herbivores rather than rabbits. Grazing losses at all distances from the watering point showed that large herbivores had the ability to seek out and consume favoured species over an entire paddock, confirming Lange & Willcocks (1980), who showed the elimination of favoured food items within three weeks in all parts of a 4040 ha sheep paddock.

However, it must be remembered that correlation is not causality and there is still the possibility that kangaroos are contributing to seedling losses (Auld 1995a; Cohn & Bradstock 2000)

Effect of rabbits

RCV has caused a major decline in rabbit numbers since 1995 in Australia, declines of 60% to 70% have been observed in coastal South Australia (Bird *et al.* 1998), 68% to 91% at two sites in central-western New South Wales (Saunders *et al.* 1998) and 95% to 97% in arid South Australia (Bowen & Read 1998; Mutze *et al.* 1998). Throughout this project the rabbits were active from late spring to the early autumn. This is consistent with previous literature that dry seasons are not favourable for RCV (Henzell *et al.* 2002; Mutze *et al.* 2002). Rabbits were both spatially and temporally patchy and they appeared to be abundant only at the plot at 0.5 km from the watering point. Plots closest to the watering point are located in the "sacrifice zone" (Valentine 1947; Lange 1969; Andrew 1988) with a history of heavy grazing and reduced bush density and provide the most favourable conditions for rabbits which prefer to graze in open areas (Williams *et al.* 1995). Most of the plants grazed by rabbits recovered well with only 10% of seedlings dying after rabbit grazing. These results are consistent with previous studies which observed the recovery of seedlings after rabbit grazing (Lange & Graham 1983). These results also support the assertion that maintaining low numbers of rabbits (Mutze *et al.* 1998; Denham & Auld 2004) by a combination of calicivirus and other control methods could allow the regeneration of arid and semi arid plant species as long as large herbivores are absent.

Desiccation losses

Supplementary water provided during this experiment artificially reduced the desiccation losses. The 15% desiccation losses were similar to those observed in an irrigated experiment by Tiver and Keiermeyer (2006) but not as high as previously observed in naturally germinated seedlings in arid, semiarid regions of Australia and other parts of the world (Silcock 1977; Auld 1990; Harrington 1991; Auld 1995a; Milton 1995; Read 1995; Barnes 2001; Yates & Broadhurst 2002; Denham & Auld 2004). Auld (1990) found 90% desiccation losses in *Acacia carneorum* suckers and *A. oswaldii* seedlings while Read (1995) found 100% desiccation losses in white pine *Callitris glaucophylla* seedlings at Roxby Downs. My results confirm the importance of episodic rainfall events which are crucial to achieve regeneration of *Acacia aneura* var. *aneura.*

Conclusion

Under current levels of rabbit populations, suppressed by calicivirus since 1995 (Williams et al. 1995), grazing by rabbits did not represent a threat to this population of seedlings. However, grazing by large herbivores either sheep or kangaroos, substantially reduced the survivorship of Acacia aneura var. aneura seedlings. Restoration of tall shrub plant populations is vital to the conservation of degraded chenopod shrublands (Woodell 1990). Fencing to exclude larger herbivores is one of the most successful and widely used tools in the regeneration of major tree populations (Tiver & Keiermeyer 2006).

Chapter 5

How does Kangaroo grazing directly affect seedling survival of *Acacia aneura* var. *aneura*

Introduction

Kangaroos are the largest extant native marsupials and are found throughout the Australian rangelands (Dawson 1998). Before European settlement kangaroos mostly occupied riparian areas and were dependent on natural springs (Ealey 1967). Their numbers were probably minimal during drought when herbage was scarce but increased with favourable conditions (Landsberg et al. 1999a). As a result of an increase in artificial watering points for modern pastoralism kangaroos have increased their range and population size (Ealey 1967; Newsome & Corbett 1977).

Kangaroos mostly graze native grasses with a dietary preference for young, low fibre and more nutritious green plants (Newsome 1965; Kirkpatrick 1965a; Ellis *et al.* 1977; Newsome 1980; Jarman & Phillips 1989; Dawson & Ellis 1994). Sheep prefer green grasses when they are available but will consume the much more fibrous chenopod shrubs (Dawson & Ellis 1994). However some work has shown that kangaroos will graze more woody vegetation when green material is scarce (Dawson & Ellis 1994) which raises the possibility that kangaroo grazing could have an impact on tree and shrub seedlings in dry times.

Most literature has focused on the competition of kangaroos with livestock: their diets will overlap when green material is scarce (Gibson & Young 1987; Dawson & Ellis 1994) during which times kangaroos compete with sheep and cattle for forage (Gibson & Young 1987). Edwards *et al.* (1995; 1996) found that the competition occurred when herbage is <50-60g/m^2 of pasture area. This seasonal effect of kangaroos on perennial species could suppress their regeneration (Gardiner 1986a). Red kangaroos (*Macropus rufus)* are less selective than the other large kangaroos (Dawson 1989) and show a greater dietary overlap with sheep (Griffiths & Barker 1966).

My own work (Chapter 3) showed that large herbivores (kangaroos and sheep) reduced Acacia aneura var. aneura survival by 100% but could not clearly separate their effects.

Aim

This part of the study is an exclosure grazing trial on the effects of kangaroo grazing on seedlings of an arid zone tree Acacia aneura var. aneura by comparing two plots: one is ungrazed by sheep where kangaroos had access; and a second where both sheep and kangaroos had access.

Methods

Research area

This part of the research was conducted at the Middleback Research Centre near Whyalla. A complete description of the study area is given in Chapter 4.

Research design

Two 100 m x 100 m plots (Fig. 5.1), one in an open paddock (OP) and one with sheep proof fencing (SF) were chosen at 0.5 km distance from the watering point. These two plots were 200 m apart. A vehicle track divided the two plots. A sheep fence of 50 cm height with 10 cm x 8 cm mesh was erected around the SF plot, a design that allowed kangaroos to jump over and rabbits to get through the holes but excluded sheep. At each plot, 10 replicates of the following treatments were installed: unfenced (U), sheep fenced (S) and rabbit fenced (R) giving a total of 30 exclosures. Treatment (U) had no exclosure (exposed to all herbivores at the OP plot and kangaroos and rabbits in the SF plot). Treatment U were marked with two metal stakes and tagged.

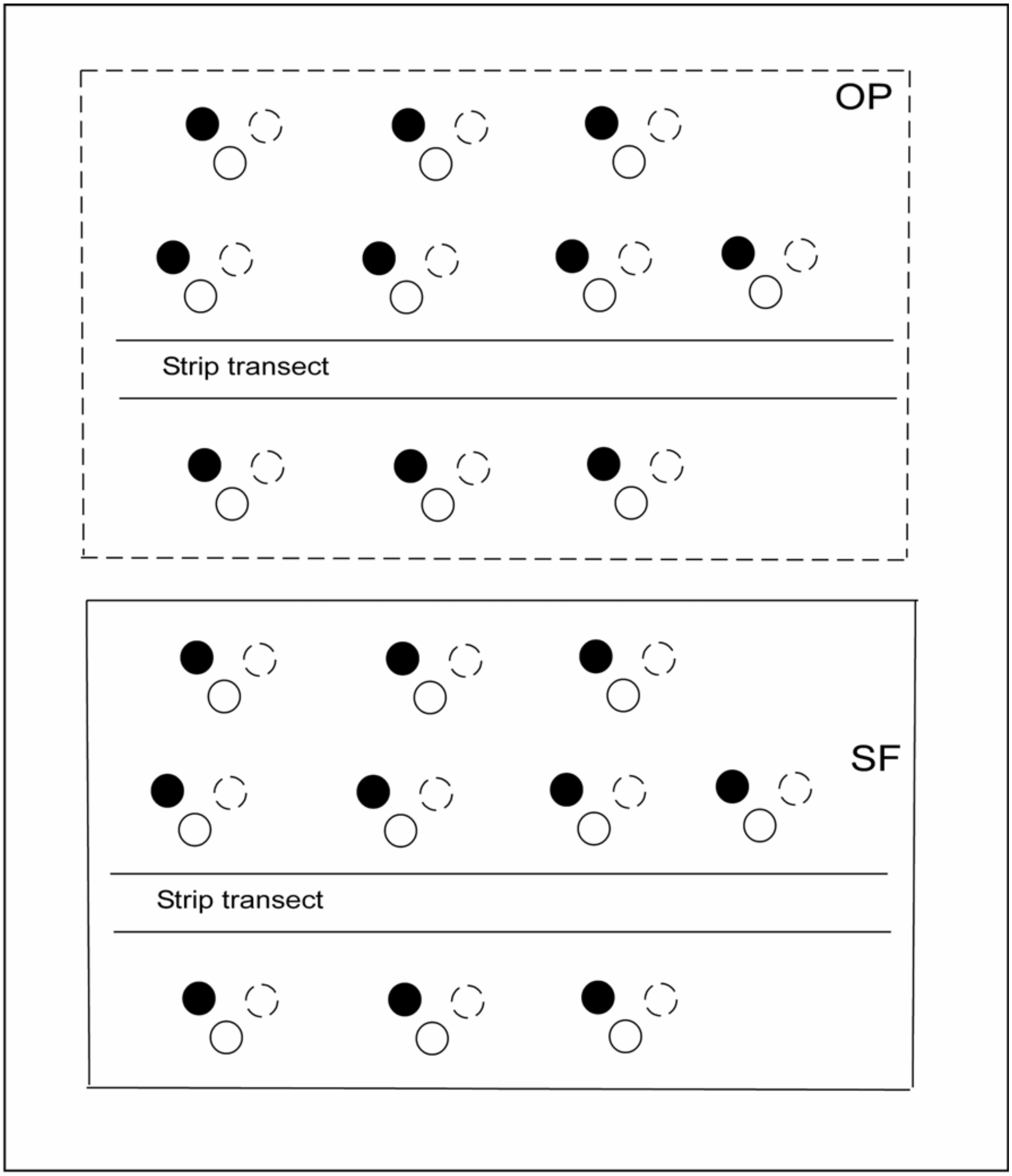


Figure 5-1 Diagrammatic representation of two plots with three exclosure treatments
● Rabbit-fence exclosure, ◌ Sheep-fence exclosure, ○ Unfenced, OP = open paddock, SF = Sheep fenced plot

The second treatment (R) was fenced with rabbit proof netting, allowing no vertebrate herbivores to graze. The diameter of the exclosure was 70 cm, and its height 1.1 m. It was strongly supported with three metal stakes, tightly tied with wire and tagged. The fence was buried 5 cm deep into the ground to prevent rabbits burrowing to reach the plant.

The third treatment (S) was fenced with sheep proof "cyclone netting" with 10 cm by 8 cm holes where rabbits could graze but large herbivores (sheep and kangaroos) could not. The diameter of the exclosure was 2 m: this larger diameter was to prevent sheep and kangaroos from reaching the seedling if they put their heads through the holes. The exclosure was supported with four metal stakes because of the larger circumference and tagged. Each tag recorded the plot and treatment number and the date and year of establishment, giving easy identification throughout the experiment.

At each plot faecal output of all vertebrate herbivores was collected and weighed at monthly intervals to monitor animal activity in the plots during the experimental period (from June 2003 to October 2004, over 482 days) by sampling along a 2 m x 100 m strip transect. All dung pellets were cleared from transects one month prior to sampling (May 2002), and thereafter collected monthly and weighed.

Because of financial limitations this experiment was not to able to be replicated, so results can be inferred for this plot only: however the plot is characteristic of the most common landscape vegetation and land-use type of the Southern Australian chenopod shrublands. So there is no reason to believe that the plot is non-representative.

Seedling establishment

Because of time limitations and slow growth of A. aneura var. aneura, seedlings were purchased from Forest S.A during the early winter of 2003. A complete description of the seedling establishment was given in Chapter 4.

Data analysis

The objective of the analyses was to establish differences between plots and treatments in the trend shown by the index of canopy volume (ICV) over 18 months. All the analyses were performed using the SAMM (Spatial Analysis Mixed Models) function using the add-in library (Butler et al. 2004) for S-Plus 6.2 for Windows (Insightful-Corporation 2003) to analyze the proportions of surviving in each treatment.

Results

Herbivore counts by faecal weight

Examination of the faecal weight data (Fig. 5.2) shows that, as expected, that of the sheep dung in the open plot (OP) is very much higher than that of the kangaroos and rabbits (SF plot) and confirms that sheep did not gain access to the plot during the experiment. Sheep were present at the OP plot throughout the study period. Kangaroos were present at both plots, but in much lower numbers when compared to the sheep at the open plot. Kangaroo numbers were also slightly lower overall at the OP plot, indicating that they preferentially grazed the SF plot. The monthly accumulation of kangaroo faecal matter was higher in the sheep fenced (SF) plot than the open paddock (OP) plot ($t = 4.449$, $df = 15$, $p < 0.001$). Rabbits showed episodic distribution over time throughout the study period. No rabbit faecal matter was present during the first four months at either of the two plots. In the fifth month a weighable amount of rabbit faecal matter was found at both the plots and rabbits were then present for the following five months from October 2002 to February 2003. After that time no rabbit faecal matter was collected or signs of rabbit activity observed at either plot. Kangaroo faecal matter was also relatively higher when the rabbits were absent and decreased with the increasing of rabbit movements (Fig. 5.2).

OP

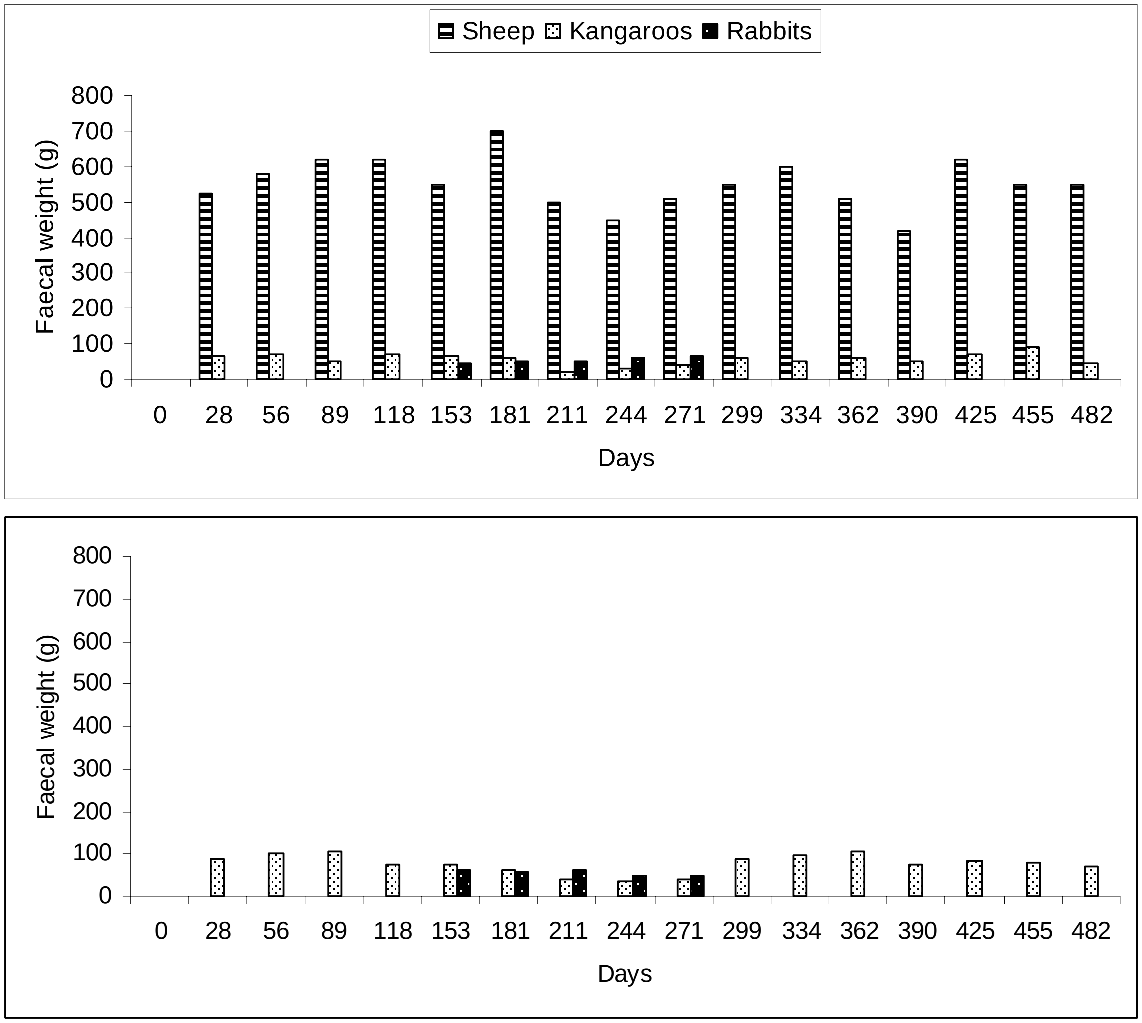
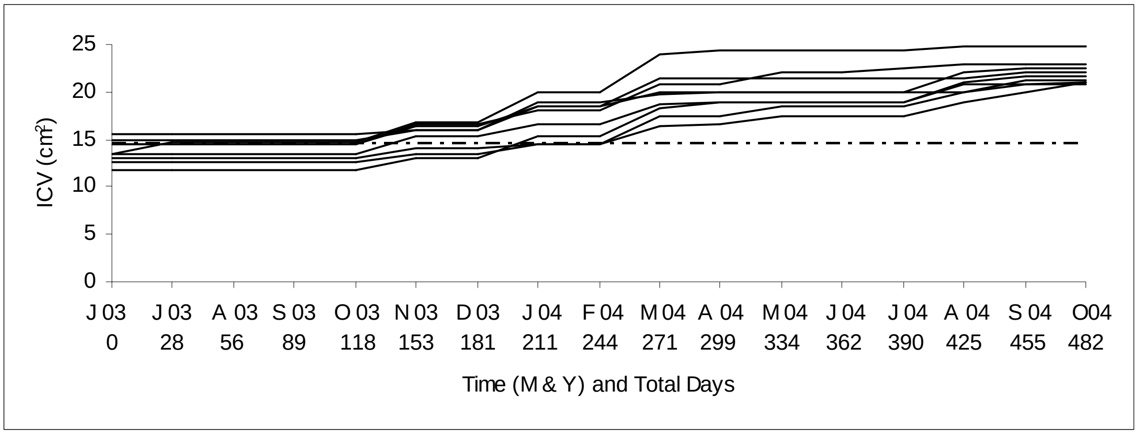


Figure 5-2 Herbivore faecal weights in the 200 m strip-transect over the experimental period at the OP (open paddock plot) and SF (sheep-fenced plot)

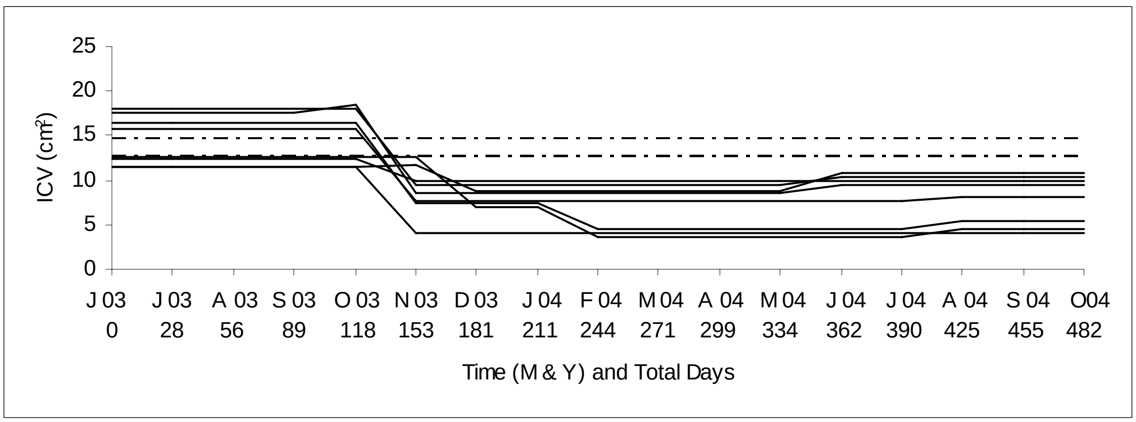
Desiccation loss

Desiccation losses were present at both the sites (only in sheep-fenced and rabbit-fenced treatments). At the end of the study, an average of nearly 10% (Fig. 5.3a&b) of seedlings had died from desiccation. In the unfenced (U) treatments in all plots no desiccation loses were observed, possibly because plants were lost to herbivory before desiccation could occur.

R



S



U

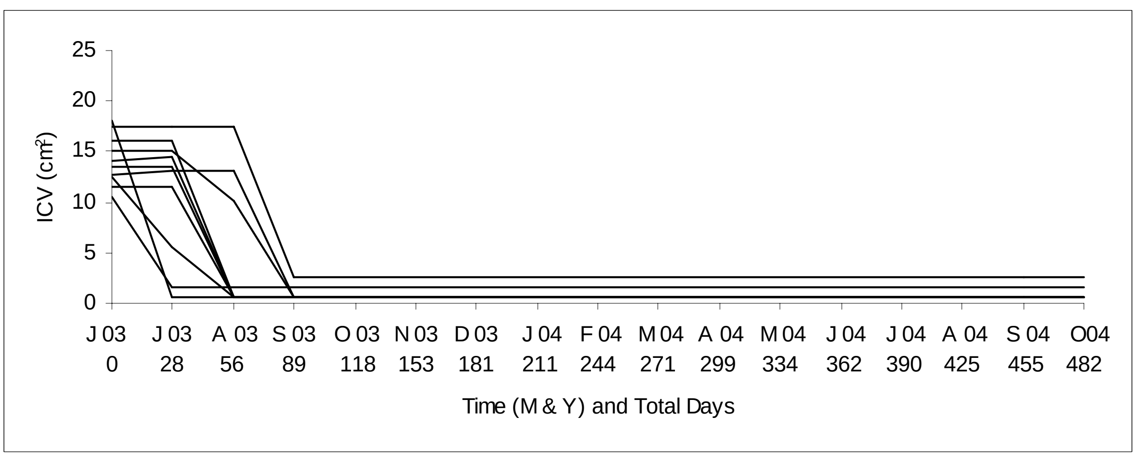
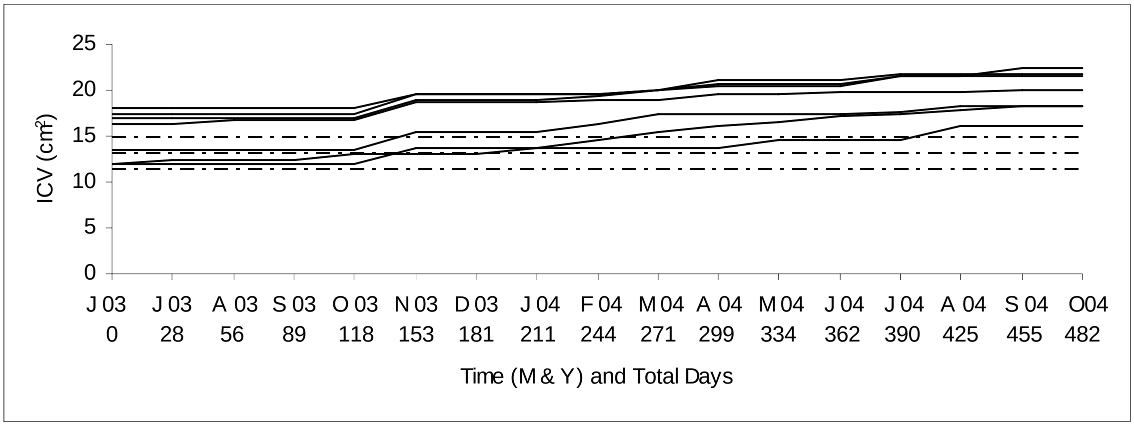


Figure 5-3 (a) Survivorship of seedlings in the different exclosure treatments in the open paddock (OP plot)

R=Rabbit-fenced treatment, S=Sheep-fenced treatment, U=Unfenced. Dotted lines indicate desiccated plants

R



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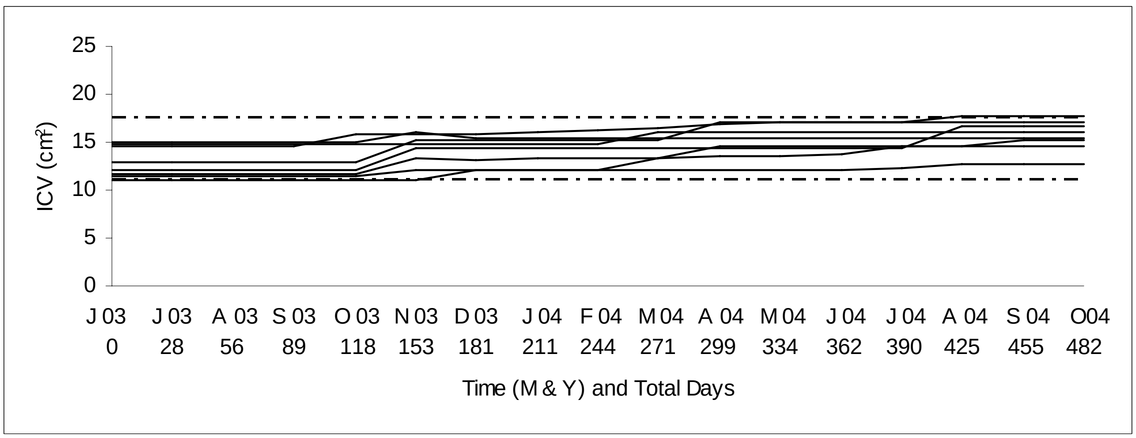

U

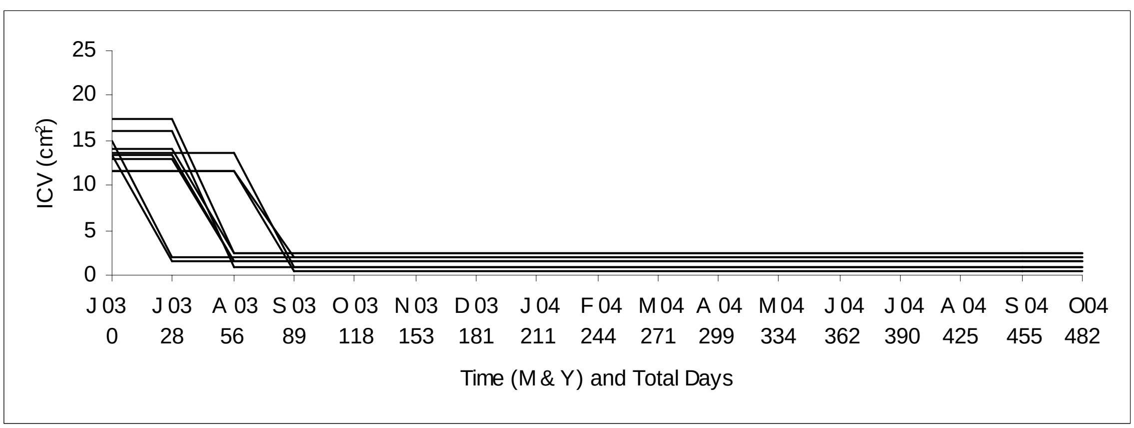

Figure 5-3 (b) Survivorship of seedlings in the different exclosure treatments in the sheep-fenced plot (SF plot)

R=Rabbit-fenced treatment, S=Sheep-fenced treatment, U=Unfenced. Dotted lines indicate desiccated plants

Grazing effects of the herbivores

Most grazing effects on *A. aneura* var. *aneura* seedlings occurred in the first 90 days (Fig. 5.3a&b). In the unfenced (U) treatments there was significantly lowered survival of *Acacia aneura* var. *aneura* seedlings, in both the OP and SF plots. By the end of the experiment, there was no seedling survival (100% reduction in the ICV of the seedlings) in the unfenced treatment (U): all seedlings (U) at both the OP and SF plots were grazed by herbivores in the first 90 days (June 2003 to August 2003). At both plots all the seedlings within the sheep-fence treatment (S) were grazed by rabbits between days 153-271 days (from November 2003-February 2004) but most of them remained alive, with reduced canopy, consisting of weak shoots from adventitious buds. In the rabbit-fenced treatment (R), apart from desiccation, all the seedlings survived and were ungrazed.

The Residual Maximal Likelihood (REML) analysis (Fig. 5.4) shows how the index of canopy volume (ICV) responds over time at the open paddock (OP) and sheep fenced plots (SF) under three different herbivore exclosure treatments. 95% confidence intervals for each treatment show that responses differ significantly from each other over time. After 118 days rabbits start to have an effect shown by the significant difference between the sheep-fenced treatments and unfenced treatments at both plots.

The smaller but still significant difference between the sheep-fenced treatments and unfenced treatments at the sheep-fenced plot (SF) indicates that kangaroos were also having a significant effect on the seedlings.

Effects of kangaroos

This experiment has clearly shown that kangaroos also graze seedlings of perennial plants along with sheep. The unfenced (U) seedlings at the SF (sheep-fenced) plot were grazed in the first 90 days during which time no rabbit faecal matter was collected. Kangaroo grazing was slightly different to the sheep grazing. They did not consume the whole seedling, only grazing the soft portion of new growth. These seedlings were not browsed more than once.

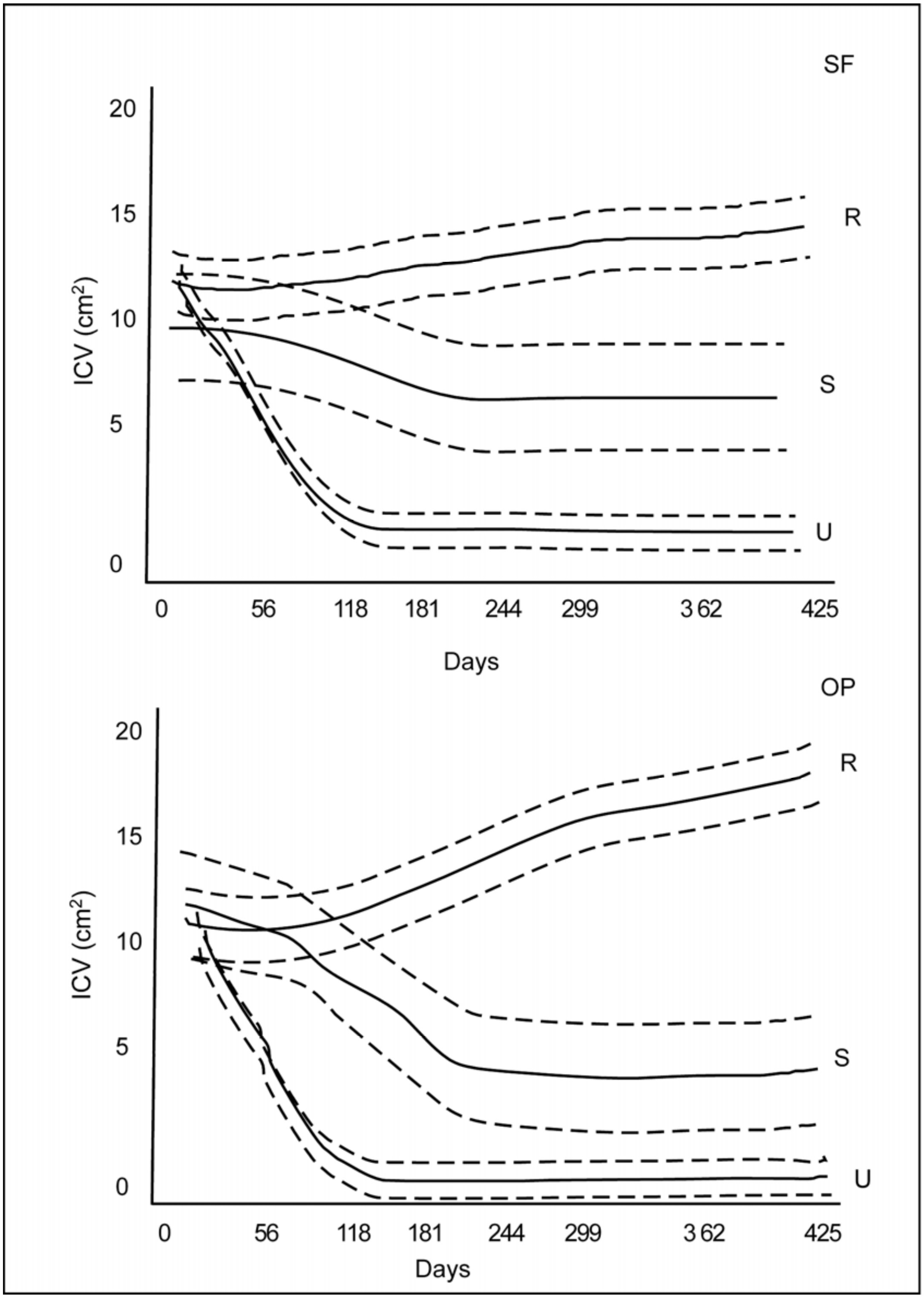

Figure 5-4 REML analysis showing the ICV (index of canopy volume) of *Acacia aneura* seedlings at the SF (Sheep-fenced) and OP (open paddock) between different herbivore exclosure treatments

R=Rabbit-fenced treatment, S=Sheep-fenced treatment, U=Unfenced. Dotted lines indicating 95% confidence intervals

Discussion

Effect of kangaroo grazing

Kangaroo grazing caused a significant effect on the survival of *A. aneura* var. *aneura* seedlings. This is consistent with some previous studies that showed that kangaroo grazing has some effect on the survival of *Acacia* spp. (Auld 1995a; Cohn & Bradstock 2000), mulga zone (western Australian) plant species (Gardiner 1986a), *Eucalyptus* spp.(Cochrane & McDonald 1966; Clarke 2002) and species in the Australian Capital Territory (Neave & Tanton 1989). Kangaroo grazing suppresses plant growth. At the beginning of the experiment grass cover in the sheep fenced area was low (*pers. obs*) and rabbit movements negligible. During this time kangaroos grazed the seedlings and when the rabbit populations increased the kangaroo population decreased. Regularly irrigating the seedlings caused the growth of herbage around the plant holes while rabbits were absent. Kangaroos obviously entered the sheep-fenced plot to graze the improved green herbage and focused on the grass species rather than the seedlings.

Competition of kangaroos with sheep and rabbits

Kangaroo abundance was greater in the sheep fenced paddock than the open paddock and numbers also gradually decreased with the increase of rabbit movements. These results support the finding Mutze and Hawker (2006) who observed increased kangaroo numbers during the absence of rabbit numbers. One of the reasons for this is kangaroos are more selective than sheep in their choice of grazing areas (Terpastra & Wilson 1989) and prefer areas ungrazed by sheep (Andrew & Lange 1986a) whereas sheep are generally found to graze at random (Landsberg & Stol 1996) in the paddocks. These results confirm that kangaroos are competing with both sheep and rabbits, and will actively seek out areas where there is less competition. Grazing by kangaroos in the sheep fenced plot strengthens the evidence for competition between kangaroos and livestock in dry seasons (Newsome 1971; Newsome & Corbett 1977; Low *et al.* 1981).

Conclusion

Kangaroo grazing affected the regeneration survival of *Acacia aneura* var. *aneura* seedlings, so kangaroos are not 100% grass eaters. Even with total removal of sheep by exclosures and lowered populations of rabbits due to RCV, grazing by kangaroos showed a significant effect on the *Acacia aneura* var. *aneura* plant species. This indicates that the total removal of stock as a management practice to assist regeneration of trees and shrubs will only be effective if the kangaroo numbers are maintained at low levels.

Chapter 6

Using a stage-structured projection model to predict the sustainability of populations of *Acacia aneura* var. *aneura* in the chenopod rangelands of eastern South Australia.

Introduction

Herbivory is a major disturbance that can alter the plant population dynamics leading to changes in the plant community structure (Knight 2004). Domestic and feral herbivore populations exist throughout the rangelands and cause numerous direct impacts on plant communities (Chapters 3, 4 & 5). Several tree and shrub species in the South Australian rangelands are strongly effected by grazing and trampling (Lange 1985; Tiver & Andrew 1997). Many past studies (Chapter 2) and my own work in Chapters 3, 4 and 5 has shown that sheep have the ability to eliminate certain tree and shrubs species in entire paddocks even at locations far from watering points.

Techniques such as pulse grazing, the total removal of livestock from some paddocks for certain periods of time, have been used for rangeland rehabilitation but their effectiveness has been minimal (Read 1999). However, there are very few data available on plant species to prove the causes of extinction. To obtain these data, long-term monitoring is required and this is not possible under current funding arrangements, which are usually short-term. Long-term ecological research projects that do exist generally carry on only because of the commitment of individual scientists (Westoby 1991). Hence there is an urgent need for population studies which can predict future structure of populations under various management strategies.

Several character sticks of plants can be altered by herbivores including growth, survivorship and fecundity (Huntly 1991; Stowe *et al.* 2000). The overall impact of a disturbance on a population is a summary of any effects on these charectersitcs (Noble & Slatyer 1980). In recent years transition matrix models have been used for modelling the impact of different management strategies on the long-term vegetation dynamics of arid and semi-arid ecosystems in Australia and other parts of the world (Lefkovitch 1965;

Usher 1976; Bierzychudek 1982; Aplet *et al.* 1994; Hunt 2001; Regan *et al.* 2003; Rooney & Gross 2003).

Matrix-based models are used to describe interactions of animal and plant population dynamics. By using matrix models quantitative vital rate information can be integrated to explore the potential consequences of various management and conservation options (Ebert 1999; Morris *et al.* 1999). These models synthesise the population dynamics of various life- stages (Silvertown *et al.* 1993; Schemske *et al.* 1994) and are used to derive several useful statistics such as population growth rates, probability of extinction, the proportion of simulations producing extinction of a population over time, and elasticities (proportional changes in finite rates of increase resulting from proportional changes in individual demographic parameters) (Menges 2006). In these models population growth rate, lambda (λ) =1 indicates that the population size remains constant through time. A λ value > 1.0 indicates an increasing population and a λ value < 1.0 indicates a populations decreasing over time.

Aims and objectives

In this chapter I use a matrix model developed by Tiver *et al.* (2006a) to evaluate the future risk of extinction of the arid zone plant species *Acacia aneura* var. *aneura* (mulga) F.Muell. ex Benth. under various herbivory and management regimes. This approach integrates the influence of different herbivores on population dynamics to predict its extinction risks in the future. I focused primarily on stochastic measures of population viability by comparing totally ungrazed populations with non sheep-grazed populations (simulated road sides) and different sheep-grazing management regimes to test the hypothesis that sheep grazing may force plant species into extinction.

Methods

Study species

Mulga is a small tree or large shrub ranging in height from 2 to 8 m, often multi-stemmed with a spreading crown. Mulga is a very common and significant plant species of arid zone vegetation, occupying a wide geographical range in Australia (Nix & Austin 1973). Flowering appears after rains and wet winters are required for seed production (Preece 1971). Light textured soils are required for good regeneration (Beadle 1948).

Study area

The study area in the North-east District of South Australia is nearly 32 000 km^2 with varying topographic and grazing conditions. A full description of the study area was given in Chapter 3.

Population survey method

Populations were measured by a modified "random walk" method (a modified strip-transect) (Kent & Coker 1992). A full description of this method was given in Chapter 3.

Population data collection

Full description of population data collecting methods were discussed in Chapter 3. For this research dead standing and dead fall (lying dead) individuals were excluded from the original data set because they cannot be assigned vital rates.

Matrix model

The matrix model developed by (Tiver *et al.* 2006a, b; McArthur *et al.* 2006; Palisetty *et al.* 2006) was used to determine projected demographic structures of populations of *Acacia aneura* var. *aneura* using as input the data collected by the population survey. I used different grazing combinations to project the possible demography of plant populations over 500 years assuming a repeated pattern of rainfall. The rainfall data used were 116 years of rainfall records from Koonamore Station (SA), the file copied and repeated to provide data for the required 500 years.

It is well known that watering points in sheep paddocks, by concentrating grazing, have resulted in drastic effects on plant populations (Barker & Lange 1969; Lange 1969; Barker 1979). Taking this into account, grazing combinations modelled heavy sheep grazing and low rabbit and kangaroo grazing near the watering points, and moderate sheep grazing and low grazing levels of kangaroos and rabbits far from the watering points (Table 3.1). In addition to this, pulse grazing (10 years of sheep grazing alternating with 10 years of no sheep grazing) was modeled to predict the usefulness of spelling in restoration of plant species within paddocks. These three scenarios were compared with a scenario of roadside vegetation reserves or conservation reserves where the domestic stock impact is nil but there is still access by rabbits and kangaroos. All four scenarios were compared against a fifth scenario showing intrinsic growth rate of populations (Lambda $\lambda > 1$) Begon *et.al*. (2006) by setting the model to $\lambda = 1.046$ and including no grazing variables.

Results

Transition rates

A total of 218 individuals of *Acacia aneura* var. *aneura* were recorded at 13 sites in the north-east of South Australia. Under the five different scenarios with their varying input parameters varying transitions were created by which individuals progress from one stage to another (Table 6.1). Plants with no grazing (A) and plants in the road reserves (B) have higher transition probability for younger stages, with higher survival and higher probability of moving to the next stage (matrix diagonals). But in the populations in the sheep paddock nearer to the watering points (C) there is no progression of young individuals to stage IV (young mature) (100% mortality) so the contribution of young stages is nil. There was little difference along the piosphere with sites far from watering points and sites under pulse grazing also showing low survival in juvenile stages (13% and12%).

Population growth rates

Populations grew in the totally ungrazed grazing scenario (Fig. 6.1a) a projected population having a set intrinsic growth rate of λ =1.046. A similar (as close as could set in the model) intrinsic growth rate (λ =1.043) to achieve a stable population against a background of grazing by rabbits and kangaroos was set for the road reserve populations (Fig. 6.1b). Stability was confirmed by a non-significant regression slope (p =0.41). This stability was maintained in spite of fluctuations in population number caused by rainfall variation. In the two set-stocked sheep-grazing scenarios (Figs. 6.1c and d), $\lambda < 0.988$, indicating extinction of *A. aneura* var. *aneura* populations over 500 years. The downward slope was confirmed by regression analysis, giving a significant negative slope ($p < 0.001$).

In the pulse grazing scenario (Fig. 6.1e), $\lambda < 0.988$, indicating extinction of *A. aneura* var. *aneura* populations over 500 years. The downward slope was confirmed by regression analysis, giving a significant slope ($p<0.001$).

Table 6-1 Transition matrices for each scenario (A) Populations with no grazing, (B) Road reserves, (C) Sites nearer to the watering point (D) Far from the watering point (E) Pulse grazing. t = 500 years

Life-stages are described in Fig.3.2 (Tiver & Andrew 1997)

		Stage at time *t*						
	Life Stage	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
A	I	0.5	0	0	0.0725	0.0967	0.0483	0.0193
	II	0.5	0.75	0	0	0	0	0
	III	0	0.25	0.857	0	0	0	0
	IV	0	0	0.143	0.96	0	0	0
	V	0	0	0	0.04	0.9881	0	0
	VI	0	0	0	0	0.0119	0.9667	0
	VII	0	0	0	0	0	0.0333	0.9
B	I	0.48	0	0	0.0725	0.0967	0.0483	0.0193
	II	0.48	0.75	0	0	0	0	0
	III	0	0.25	0.857	0	0	0	0
	IV	0	0	0.143	0.96	0	0	0
	V	0	0	0	0.04	0.9881	0	0
	VI	0	0	0	0	0.0119	0.9667	0
	VII	0	0	0	0	0	0.0333	0.9
C	I	0	0	0	0.0725	0.0967	0.0483	0.0193
	II	0	0	0	0	0	0	0
	III	0	0	0	0	0	0	0
	IV	0	0	0	0.96	0	0	0
	V	0	0	0	0.04	0.9881	0	0
	VI	0	0	0	0	0.0119	0.9667	0
	VII	0	0	0	0	0	0.0333	0.9
D	I	0.13	0	0	0.0725	0.0967	0.0483	0.0193
	II	0.13	0.188	0	0	0	0	0
	III	0	0.063	0.214	0	0	0	0
	IV	0	0	0.036	0.96	0	0	0
	V	0	0	0	0.04	0.9881	0	0
	VI	0	0	0	0	0.0119	0.9667	0
	VII	0	0	0	0	0	0.0333	0.9
E	I	0.12	0	0	0.0725	0.0967	0.0483	0.0193
	II	0.12	0.188	0	0	0	0	0
	III	0	0.063	0.214	0	0	0	0
	IV	0	0	0.036	0.96	0	0	0
	V	0	0	0	0.04	0.9881	0	0
	VI	0	0	0	0	0.0119	0.9667	0
	VII	0	0	0	0	0	0.0333	0.9

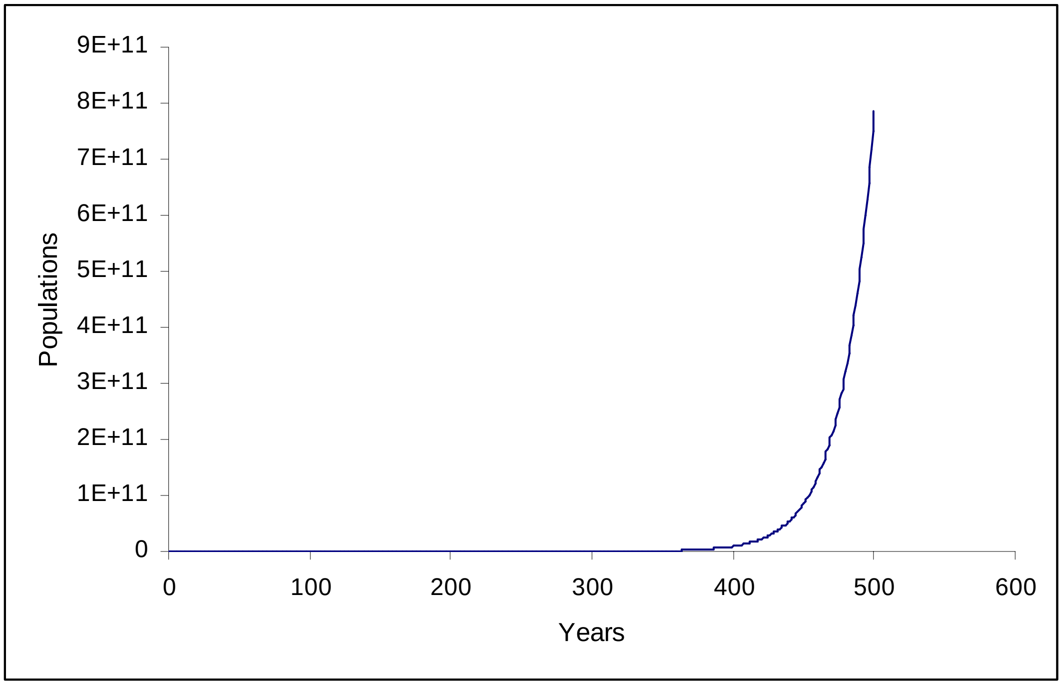

Figure 6-1 (a) Model output showing a totally (Sheep=0,Rabbit=0,Kangaroos=0) ungrazed population of *A. aneura* with an intrinsic growth rate (λ =1.046). A regression of population increase over time p<0.001

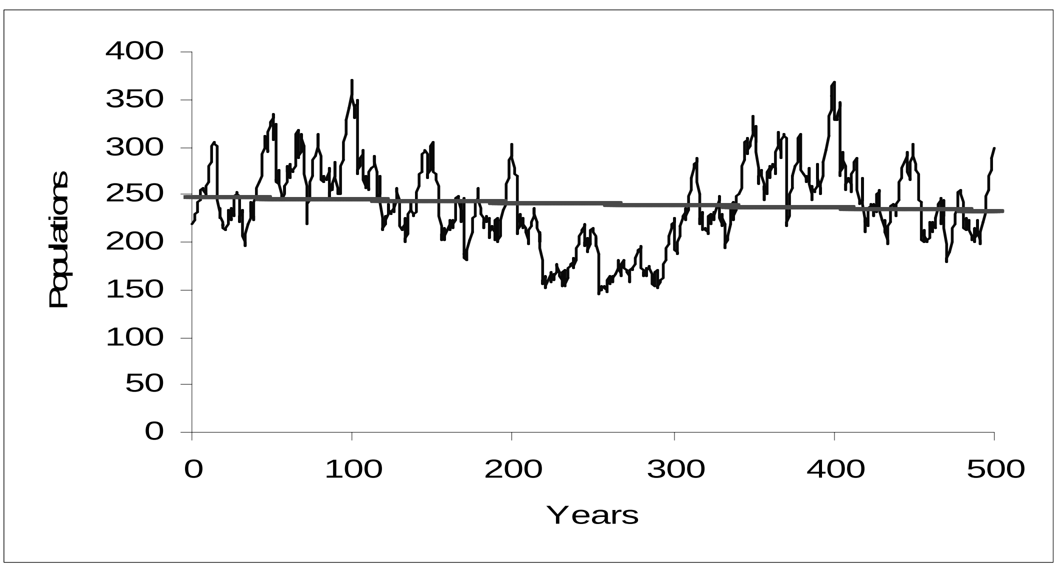

Figure 6-1 (b) Model output showing a relatively stable population of *A. aneura* in road side reserves (Sheep=0, Rabbits=1 Kangaroos=1), (λ =1.043). A regeneration of population numbers over time has an insignificant slope, p=0.41

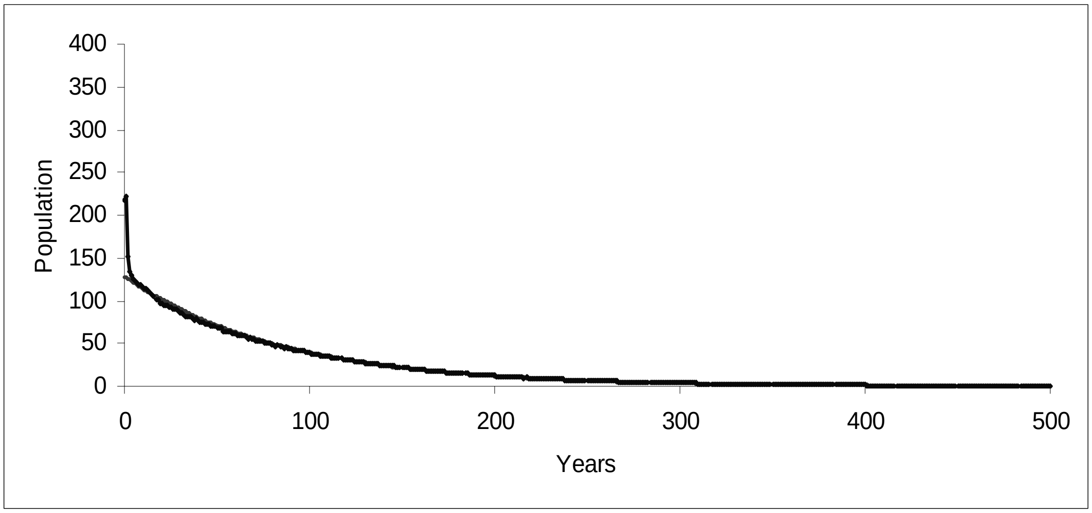

Figure 6-1 (c) Model output showing extinction of a population of *A. aneura* at sites nearest the watering point (Sheep=4, Rabbits=1 Kangaroos=1), (λ = 0.988). A regression of population extinction over time $p<0.001$.
The dotted line shows half-extinction of populations in 66 years

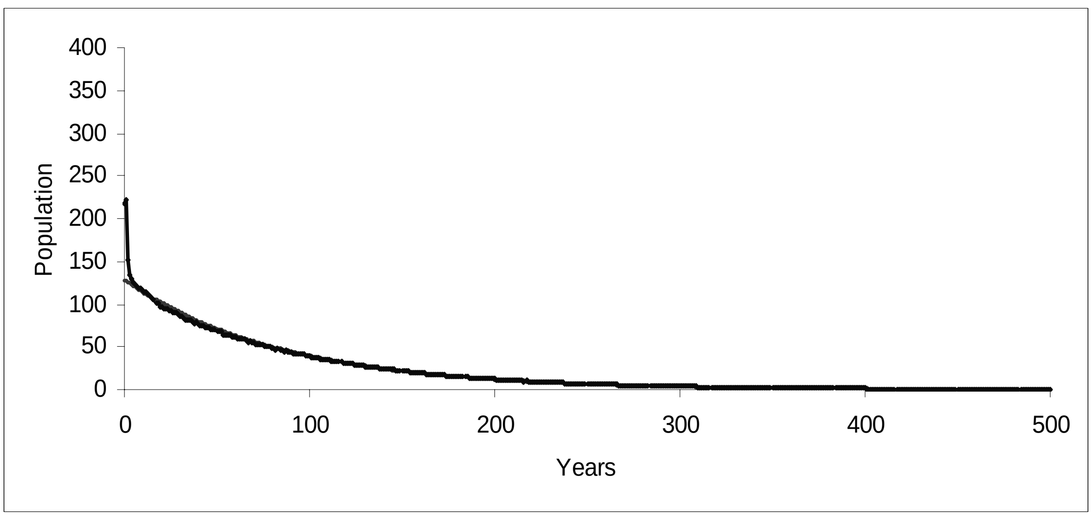

Figure 6-1 (d) Model output showing extinction of a population of *A. aneura* at sites furthest from the watering point (Sheep=2, Rabbits=1 Kangaroos=1), (λ=0.988). A regression of population extinction over time $p<0.001$.
The dotted line shows half-extinction of populations in 86 years

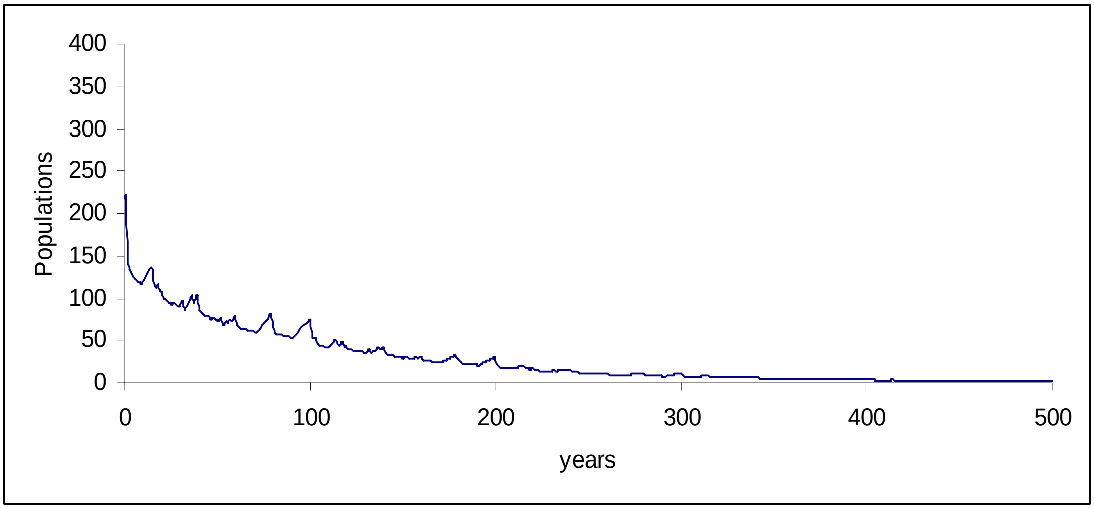

Figure 6-1 (e) Model output showing extinction of a population of A. aneura under a pulse-grazing regime (10 years of sheep grazing alternating with 10 years of no sheep grazing), (λ =0.988). A regression of population extinction over time p<0.001. The dotted line shows half-extinction of populations in 70 years

The regression analysis to the set-stocking and pulse-grazing scenarios were carried out by the following equations:

$z = \log y$ ---------- Equation 1

$z = ax+b$ ---------- Equation 2

$y = e^z = e\hat{}(ax+b)=e\hat{}b(e\hat{}(ax))$ ----------Equation 3

Because of this, the regression analysis was fitted behind the population curve, so that it apparently does not appear in Figs. 6.1c, d and e.

The identical λ of 0.988 for the set-stocking and pulse-grazing scenarios (Figs. 6.1c,d and e) is an artefact: each population declined at a different rate (indicated by the different times to half-extinction), but all three scenarios were close to extinction from 300 (Figs. 6.1c and d) and 400 years onwards (Fig. 6.1e). Hence the populations all have the same projected λ at t=500 years, giving a similar final λ of 0.988.

Extinction probability

In the total absence of herbivory, plant populations avoid extinction over 500 years (Fig. 6.1a). In the "roadside scenarios" (absence of sheep grazing with low rabbit and kangaroo grazing) plant populations maintain equilibrium populations over 500 years (Fig. 6.1b). In the sheep-grazed paddock scenario nearest to watering points (Fig. 6.1c) there is a drastic fall in the plant numbers and they reach half-extinction in 66 years. Extinction was slower in the sites far from the watering points (Fig. 6.1d), but was still inevitable, with half-extinction reached in 86 years. Pulse-grazing did not prevent extinction, with the population reaching half-extinction at 70 years (Fig. 6.1e).

Discussion

Projected population growth rates from the matrix model indicated that the sheep-grazed *A. aneura* var. *aneura* populations in all parts of paddock declined to extinction over 500 years, with the most rapid decline in the first 100 years. Plant populations in the roadside reserves, in the absence of domestic animals, were stable over 500 years. As with any model, one has to assume that the input parameters, based on literature and experimental data, are correct.

The input parameters for model are based on the most up to date literature and also data collected as part of this thesis. As such the input parameters are as correct as possible given current knowledge. However, it is obvious that there is insufficient data to derive accurate parameters for most Australian arid zone plant species. Hence, the predictivity of the model will doubtless be improved when more accurate date is obtained. Therefore, the projected outcomes described here should be interpreted as indicating the usefulness of the model, rather than being accurate predictions. Nonetheless, the range of possible outcome projected the model are discussed here in order to reflect the adoptive management for best practice.

Projections show that sheep grazing is the most critical factor affecting population dynamics of *A. aneura* var. *aneura* populations, with populations able to survive drought and grazing by both rabbits and kangaroos at low numbers. This finding is consistent with many previous studies suggesting that sheep are the main controlling factor of plant populations in the chenopod shrublands. There is a spatial variation of sheep-grazing affects on plant populations: those nearer to the watering point decline at a greater rate than those far from the watering point where the grazing pressure is less, resulting in the more rapid elimination of palatable perennial plant populations around the watering points. This is consistent with the piosphere concept (Lange 1969), that grazing is concentrated nearer to the watering point resulting in elimination of palatable species around the watering points and an increase of unpalatable species. However, this study has shown that sheep in the paddocks under set stocking could suppress *Acacia aneura* var. *aneura* plant populations even at locations far from the watering point. However, our results indicate that palatable species can also be eliminated at points further from the watering points confirming (Lange & Willcocks 1978).

The extinction of plant populations was chiefly as a result of sheep-grazing because of the marked differences between the paddocks and the road reserves, and the comparison of locations in paddocks at different distances of the water, showing varying time intervals to extinction of plant populations. These results are consistent with modelling results of Hunt (2001), who found greater extinction of *Atriplex vesicaria* populations nearer to the watering point than far from it.

The recently recommended pastoral management technique of pulse grazing (removing domestic stock from the paddock for periods of time) has been proposed to allow the recruitment of plant species (Harrington *et al.* 1990; Earl & Jones 1996) but my modelling results show that pulse-grazing at intervals of ten years is not sufficient to restore regeneration. *Acacia aneura* var. *aneura* also has very slow growth (my own work in Chapter 4 showed the tallest ungrazed *Acacia aneura* var. *aneura* seedling had attained 8 cm height in two years) so they would take a 110 years of time (Tiver *et al.* 2006b) to reach a height above sheep grazing level.

Conclusion

In this study sheep are shown to have the potential to cause extinction of *A. aneura* var. *aneura* plant populations in all parts of paddocks. Only a very small proportion of the Australian arid lands, especially chenopod shrublands, is contained in parks or reserves, so the majority of the area is subject to extensive grazing by herbivores. It is therefore essential that the effect of domestic herbivores is taken into account when planning for conservation and management of biodiversity in the arid lands. Pulse grazing is not effective for restoration.

Chapter 7 General Discussion

Introduction

The results of this study are discussed and include a number of findings which have relevance to:

- regeneration of plant species after release of calicivirus (RCD)
- survivorship of *Acacia aneura* var. *aneura* seedlings under grazing pressure of different herbivores.
- Projected fate of *Acacia aneura* var. *aneura* populations using a matrix model.
- Effective conservation and management practices to restore the chenopod shrublands.

Review of Study

Vegetation survey

The results found in Chapter 3 demonstrated that broadscale surveys assist in understanding the regeneration of plant species over the long-term under different herbivore grazing regimes. Lack of significant regeneration of many species in the north-east pastoral districts of South Australia under reduced rabbit numbers following the release of calicivirus (RCV) in 1995 showed that rabbit control would not be sufficient for restoration of many plant species. Failure of regeneration even at non sheep grazing sites may result from factors such as irregular rainfall events and increased kangaroo numbers. Sheep are the most effective herbivore inside the paddocks. These results strongly support the findings by Tiver and Andrew (1997) whose survey of over 50 plant species in 1992 showed that sheep were the major herbivore suppressing regeneration of plant species.

Exclosure trials

Exclosure trials are useful to more precisely evaluate grazing pressure by different herbivores on seedling survivorship. *Acacia aneura* var. *aneura* is a very palatable species to sheep. Many previous studies have focused on the piosphere effect in the paddocks and the need for low grazing-impact for sites regeneration of palatable species (Chapter 2). Some studies agree with this observation (Friedel 1988; Thrash *et al.* 1993), while others contradict it fully (Stroleny & Mentis 1989; Van Rooyen *et al.* 1994; Nangula & Oba 2004) or partially (Foran 1980; Andrew & Lange 1986c; Heshmatti *et al.* 2002). No piosphere effect was observed in the survivorship of *Acacia aneura* var. *aneura* seedlings (Chapter 4). Total elimination of seedlings at the plot 5 km from the watering point indicate that there was no safe-site for a palatable species in a sheep grazed paddocks. Rabbit grazing was patchy in both time and location, with low numbers. Losses of seedlings to rabbits reflected this, being much less, and restricted to a short period of five months at one plot only indicating the effect of RCV.

Competition between kangaroo and sheep diets

Some effect of kangaroo grazing on *Acacia aneura* var. *aneura* seedlings was recorded (Chapter 5). Kangaroos preferred to graze the areas ungrazed by sheep and rabbits supporting Andrew and Lange (1986c) and prefer roadside reserves to paddocks (Chapter 3).

Does control of rabbits improve regeneration?

Many earlier studies considered that rabbits were the main cause in decreasing plant populations (Crisp 1978; Lange & Graham 1983). After release of RCV, rabbit populations were lower in 2004 than 1992 in the North-East Districts (Chapter 3). But these low numbers did not result in any significant improvement in most plant species (Chapter 3) which could have been due to increased kangaroo numbers, or lack of rainfall events for regeneration since 1992. However, there was elimination of seedlings in the unfenced treatments (Chapter 4 & 5) indicating that large herbivores are capable of suppressing regeneration in the absence of rabbit populations. Hence, rabbit control alone will not restore regeneration and conservation of tree species will require modified management of domestic livestock.

Projected *Acacia aneura* var. *aneura* populations

The matrix population model projected that *Acacia aneura* var. *aneura* plant populations will become extinct at all sites within sheep-grazed paddocks, whether near or far from the watering point (Chapter 6). Neither was a pulse grazing scenario (10 years of sheep grazing alternating with 10 years of no sheep grazing) sufficient to restore regeneration. These results suggest that at least some stock-free reserves with control of kangaroo and rabbit numbers will be necessary for adequate conservation of many woody plant species.

Management practices

The current management system recommended for chenopod rangeland of small paddocks one or more watering points and fixed stock management (Lange *et al.* 1984; Eldridge *et al.* 1990) may not be an effective management practice for retaining many palatable perennial plant species. Destocking for up to ten years may not even be effective (Chapter 6). Crisp (1978) found that *Maireana pyramidata* recruitment was episodic and occurring about every 50 years following high rainfall periods but Yan *et al.* (1996) in their eight-year study found recruitment of this species at several occasions. Hence rangeland managers will need to observe recruitment periodicity of key species and prolong the destocking periods until plants regenerate and reach a above the large herbivores reachable height. Some regeneration of plant populations in the road reserves indicates the need of at least some totally de-stocked vegetation reserves. Even in conservation parks it will be necessary to keep kangaroo and rabbits controlled.

Conclusions

Sheep grazing is the major cause of suppression of plant regeneration in the chenopod shrublands. Kangaroos also had some effect in reducing seedling survivorship.
Rabbit numbers were reduced following release of RCV but their reduced numbers have so far been unable to improve the regeneration of plant species.
To restore the rangelands there is a need of a system of stock-free vegetation reserves which must be maintained at low kangaroo and rabbit numbers.

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Appendix I

Proportions of life-stages in tree and shrub populations and GLMM analysis showing the probability of significance of increase and decrease in proportions between 1992 and 2004 .

Un Gr 92=proportion of stage-class in roadside reserves in 1992; Un Gr 04= proportion of stage-class in roadside reserves in 2004;Gr 92= proportion of stage-class inside paddocks in 1992; Gr 04= proportion of stage-class inside paddocks in 2004.

GxY=Grazed x Years; Y=Years; G=Grazed.

	Juvenile I-III						Stage IV						Mature V-IX					
		proportions		wald d.	d.f	*p*		proportions		wald d.	d.f	*p*		proportions		wald d.f	d.f	*p*
Acacia aneura	Un Gr 92	0.395	GxY	0.56	1	0.45	Un Gr 92	0.0534	GxY	0.61	1	0.436	Un Gr 92	0.55	GxY	1.41	1	0.235
var. *aneura*	Un Gr 04	0.3387	Y	2.88	1	0.09	Un Gr 04	0.1374	Y	5.09	1	0.024	Un Gr 04	0.52	Y	0.22	1	0.642
	Gr 92	0.0378	G	27.54	1	<0.001	Gr 92	0.0108	G	11.09	1	<0.001	Gr 92	0.95	G	44.25	1	<0.001
	Gr 04	0.0202					Gr 04	0.0101					Gr 04	0.97				
Acacia carneorum	Un Gr 92	0.7183	GxY	18.95	1	<0.001	Un Gr 92	0.0563	GxY			0.27	Un Gr 92	0.23	GxY	28.96	1	<0.001
	Un Gr 04	0.5	Y	13.4	1	<0.001	Un Gr 04	0.2717	Y	21.48	1	<0.001	Un Gr 04	0.23	Y	41.22	1	<0.001
	Gr 92	0.7699	G	77.72	1	<0.001	Gr 92	0	G	29.3	1	<0.001	Gr 92	0.23	G	46.43	1	<0.001
	Gr 04	0.1346					Gr 04	0.0385					Gr 04	0.83				
Acacia oswaldii	Un Gr 92	0.3	GxY			0	Un Gr 92	0.2	GxY			0.387	Un Gr 92	0.5	GxY	8.66	1	0.003
	Un Gr 04	0.4118	Y	2.93	1	0.09	Un Gr 04	0.2941	Y	0.03	1	0.852	Un Gr 04	0.29	Y	3.07	1	0.08
	Gr 92	0.4167	G	1.89	1	1.67	Gr 92	0.2778	G	0.02	1	0.877	Gr 92	0.31	G	2.04	1	0.153
	Gr 04	0					Gr 04	0.1875					Gr 04	0.81				
Acacia tetragonophylla	Un Gr 92	0.2222	GxY	0	1	1	Un Gr 92	0.1296	GxY	35.23	1	<0.001	Un Gr 92	0.65	GxY	0.51	1	<0.001
	Un Gr 04	0.2167	Y	0.04	1	0.85	Un Gr 04	0.1	Y	1.53	1	0.216	Un Gr 04	0.68	Y	8.92	1	0.475
	Gr 92	0.0714	G	1.21	1	0.27	Gr 92	0.1905	G	0.65	1	0.421	Gr 92	0.74	G	0.78	1	0.376
	Gr 04	0					Gr 04	0.0127					Gr 04	0.99				
Acacia victoriae	Un Gr 92	0.3106	GxY	29.41	1	<0.001	Un Gr 92	0.1591	GxY	0.21	1	0.05	Un Gr 92	0.53	GxY	42.07	1	<0.001
ssp. victoriae	Un Gr 04	0.4272	Y	0.62	1	0.43	Un Gr 04	0.1821	Y	0.02	1	0.898	Un Gr 04	0.39	Y	2.18	1	0.139
	Gr 92	0.4727	G	2.51	1	0.11	Gr 92	0.1273	G	0.8	1	0.371	Gr 92	0.4	G	10.68	1	<0.001
	Gr 04	0.0809					Gr 04	0.1103					Gr 04	0.81				

	Juvenile I-III						Stage IV						Mature V-IX					
		proportions		wald d.f	d.f	*p*		proportions		wald d.f	d.f	*p*		proportions		wald d	d.f	*p*
Alectryon oleifolius	Un Gr 92	0.3895	GxY	0	1	0.97	Un Gr 92	0.1512	GxY	0.5	1	0.48	Un Gr 9	0.4593	GxY	0.55	1	0.46
ssp. canescens	Un Gr 04	0.4516	Y	0.1	1	0.75	Un Gr 04	0.3065	Y	14.77	1	<0.001	Un Gr 0	0.2419	Y	0.01	1	0.94
	Gr 92	0.0068	G	24.41	1	<0.001	Gr 92	0.0203	G	25.35	1	<0.001	Gr 92	0.9729	G	165	1	<0.001
	Gr 04	0					Gr 04	0.0387					Gr 04	0.9613				
Atriplex vesicaria	Un Gr 92	0.2251	GxY	0.35	1	0.55	Un Gr 92	0.1839	GxY	0	1	0.99	Un Gr 9	0.591	GxY	0.17	1	0.677
ssp. calcicola	Un Gr 04	0.2625	Y	0.24	1	0.62	Un Gr 04	0.1513	Y	0.94	1	0.33	Un Gr 0	0.5862	Y	0.05	1	0.233
	Gr 92	0.2303	G	0.06	1	0.81	Gr 92	0.1974	G	1.13	1	0.29	Gr 92	0.5724	G	1.44	1	0.823
	Gr 04	0.2162					Gr 04	0.223					Gr 04	0.5608				
Casuarina pauper	Un Gr 92	0.5333	GxY	0.02	1	0.89	Un Gr 92	0.2067	GxY	0.01	1	0.93	Un Gr 9	0.26	GxY	0.05	1	0.822
ssp. pauper	Un Gr 04	0.54	Y	0.75	1	0.39	Un Gr 04	0.23	Y	0.16	1	0.69	Un Gr 0	0.23	Y	1.74	1	0.188
	Gr 92	0.4252	G	1.24	1	0.27	Gr 92	0.2347	G	0.01	1	0.91	Gr 92	0.3401	G	1.1	1	0.293
	Gr 04	0.4267					Gr 04	0.2408					Gr 04	0.3325				
Dodonaea viscosa	Un Gr 92	0.6806	GxY	0.6	1	0.44	Un Gr 92	0.2083	GxY	0.6	1	0.06	Un Gr 9	0.1111	GxY	1.26	1	0.262
ssp. angustissima	Un Gr 04	0.6029	Y	3.19	1	0.07	Un Gr 04	0.25	Y	1.05	1	0.31	Un Gr 0	0.1471	Y	6.32	1	0.012
	Gr 92	0.16	G	19.97	1	<0.001	Gr 92	0.27	G	0.93	1	0.34	Gr 92	0.57	G	19.4	1	<0.001
	Gr 04	0.0811					Gr 04	0.1532					Gr 04	0.7658				
Eremophila duttonii	Un Gr 92	0.75	GxY	2.11	1	0.15	Un Gr 92	0	GxY		1	0.99	Un Gr 9	0.25	GxY	2.37	1	0.124
	Un Gr 04	0.8	Y	10.6	1	0.02	Un Gr 04	0	Y	0.22	1	0.99	Un Gr 0	0.2	Y	3.3	1	0.004
	Gr 92	0.6364	G	5.42	1	0	Gr 92	0.2273	G	5.71	1	0.02	Gr 92	0.1364	G	8.23	1	0.069
	Gr 04	0.1667					Gr 04	0.2083					Gr 04	0.625				

	Juvenile I-III						Stage IV						Mature V-IX					
		proportions		wald d.f	d.f	*p*		proportions		wald d	d.f	*p*		proportions		wald d	d.f	*p*
Eremophila scoparia	Un Gr 92	0.3741	GxY	0.03	1	0.865	Un Gr 92	0.1837	GxY	0.18	1	0.668	Un Gr 92	0.4422	GxY	4.9	1	0.028
	Un Gr 04	0.3695	Y	0	1	0.96	Un Gr 04	0.133	Y	1.51	1	0.22	Un Gr 04	0.4975	Y	0.2	1	0.625
	Gr 92	0	G	12.04	1	<0.001	Gr 92	0.1327	G	0.73	1	0.394	Gr 92	0.8673	G	16	1	<0.001
	Gr 04	0.1359					Gr 04	0.1165					Gr 04	0.7476				
Eremophila sturtii	Un Gr 92	0.2918	GxY	6.88	1	0.009	Un Gr 92	0.2262	GxY	0.56	1	0.453	Un Gr 92	0.482	GxY	8.3	1	0.004
	Un Gr 04	0.4289	Y	2.91	1	0.088	Un Gr 04	0.2101	Y	0.22	1	0.64	Un Gr 04	0.3611	Y	1.3	1	0.258
	Gr 92	0.2955	G	2.78	1	0.095	Gr 92	0.1894	G	0.35	1	0.555	Gr 92	0.5152	G	5.3	1	0.022
	Gr 04	0.3053					Gr 04	0.1814					Gr 04	0.5133				
Exocarpos aphyllus	Un Gr 92	0.4	GxY	5.28	1	0.083	Un Gr 92	0.4	GxY	0	1	0.953	Un Gr 92	0.2	GxY	1.7	1	0.259
	Un Gr 04	0.2333	Y	2.29	1	0.205	Un Gr 04	0.3333	Y	0.13	1	0.732	Un Gr 04	0.4333	Y	0.6	1	0.482
	Gr 92	0	G	1.01	1	0.371	Gr 92	0.2432	G	1.64	1	0.27	Gr 92	0.7568	G	3.2	1	0.147
	Gr 04	0.2364					Gr 04	0.1818					Gr 04	0.5818				
Maireana pyramidata	Un Gr 92	0.2073	GxY	0.81	1	0.369	Un Gr 92	0.2241	GxY	2.39	1	0.122	Un Gr 92	0.5686	GxY	0.8	1	0.381
	Un Gr 04	0.331	Y	20.84	1	<0.001	Un Gr 04	0.191	Y	7.97	1	0.005	Un Gr 04	0.478	Y	2.2	1	0.14
	Gr 92	0.1745	G	2.54	1	0.111	Gr 92	0.2182	G	1.17	1	0.279	Gr 92	0.6073	G	2.7	1	0.103
	Gr 04	0.2835					Gr 04	0.1381					Gr 04	0.5784				
Maireana sedifolia	Un Gr 92	0.1631	GxY	1.14	1	0.287	Un Gr 92	0.1992	GxY	1.78	1	0.182	Un Gr 92	0.6377	GxY	1.3	1	0.246
	Un Gr 04	0.3499	Y	15.05	1	<0.001	Un Gr 04	0.1861	Y	0.96	1	0.327	Un Gr 04	0.464	Y	4.7	1	0.03
	Gr 92	0.0822	G	32.24	1	<0.001	Gr 92	0.1507	G	3.34	1	0.068	Gr 92	0.7671	G	16	1	<0.001
	Gr 04	0.1459					Gr 04	0.1124					Gr 04	0.7416				

	Juvenile I-III						Stage IV						Mature V-IX					
	proportions			wald d.f	d.f	*p*	proportions			wald d.	d.f	*p*	proportions			wald d.f	d.f	*p*
Myoporum platycarpum	Un Gr 92	0.3276	GxY	1.88	1	0.171	Un Gr 92	0.1655	GxY	8.54	1	0.003	Un Gr 92	0.5069	GxY	3.61	1	0.058
ssp. platycarpum	Un Gr 04	0.395	Y	1.28	1	0.258	Un Gr 04	0.2325	Y	0.1	1	0.752	Un Gr 04	0.3725	Y	1.61	1	0.204
	Gr 92	0.4012	G	6.94	1	0.008	Gr 92	0.1754	G	3.91	1	0.048	Gr 92	0.4234	G	6.49	1	0.011
	Gr 04	0.2908					Gr 04	0.1332					Gr 04	0.5761				
Rhagodia parabolica	Un Gr 92	0	GxY	76.54	1	<0.001	Un Gr 92	0.2933	GxY	0.09	1	0.779	Un Gr 92	0.7067	GxY	6.91	1	0.058
	Un Gr 04	0.3767	Y	138.38	1	0.007	Un Gr 04	0.2192	Y	1.53	1	0.283	Un Gr 04	0.4041	Y	6.9	1	0.058
	Gr 92	0.122	G	26.29	1	<0.001	Gr 92	0.2195	G	1.9	1	0.241	Gr 92	0.6585	G	7.94	1	0.048
	Gr 04	0.1148					Gr 04	0.1311					Gr 04	0.7541				
Rhagodia spinescens	Un Gr 92	0.4218	GxY	0.27	1	0.601	Un Gr 92	0.1565	GxY	9.73	1	0.002	Un Gr 92	0.4218	GxY	0	1	0.039
	Un Gr 04	0.4641	Y	0.64	1	0.423	Un Gr 04	0.1603	Y	3.99	1	0.046	Un Gr 04	0.3755	Y	0.04	1	0.642
	Gr 92	0.0431	G	13.81	1	<0.001	Gr 92	0.25	G	0.36	1	0.55	Gr 92	0.7069	G	8.71	1	0.003
	Gr 04	0.0323					Gr 04	0.0645					Gr 04	0.9032				
Senna artemisioides	Un Gr 92	0.5367	GxY	0	1	0.985	Un Gr 92	0.2204	GxY	0.18	1	0.671	Un Gr 92	0.2429	GxY	0.14	1	0.705
ssp. × coriacea	Un Gr 04	0.5586	Y	0.04	1	0.834	Un Gr 04	0.167	Y	1.45	1	0.229	Un Gr 04	0.2744	Y	0.26	1	0.610
	Gr 92	0.2045	G	6.44	1	0.011	Gr 92	0.0909	G	3.21	1	0.073	Gr 92	0.7045	G	21.03	1	<0.001
	Gr 04	0.2164					Gr 04	0.0936					Gr 04	0.6901				
Senna atremisioides	Un Gr 92	0.3206	GxY	0.52	1	0.469	Un Gr 92	0.223	GxY	8.82	1	0.003	Un Gr 92	0.4564	GxY	11.95	1	<0.001
ssp. petiolaris	Un Gr 04	0.4648	Y	3.52	1	0.06	Un Gr 04	0.2114	Y	6.18	1	0.13	Un Gr 04	0.3238	Y	1.64	1	0.201
	Gr 92	0.2063	G	12.73	1	<0.001	Gr 92	0.3498	G	1.01	1	0.316	Gr 92	0.4439	G	47.25	1	<0.001
	Gr 04	0.3897					Gr 04	0.1385					Gr 04	0.4718				

Appendix II

REML analysis showing the significance between ICV of seedlings subjected to various grazing exclosure treatments in the plots located at the different distances from the watering point in Railway paddock at Middleback Field Station, Whyalla.

ICV at 0.5 km

	variances	std.error	z.ratio	constraint
Rep	1.3919	1.0940	1.2723	Positive
Rep:Treatment	2.4171	0.8497	2.8447	Positive
Treatment:spline(Day)	2.5613	0.8452	3.0303	Positive
Rep:Area_1.Treat_R:Day	0.3317	0.0588	5.6388	Positive
Rep:Area_1.Treat_S:Day	8.3232	0.9655	8.6204	Positive
Rep:Area_1.Treat_U:Day	5.9156	0.6977	8.4791	Positive

ICV at 1.5 km

	variances	std.error	z.ratio	constraint
Rep	0.5424	0.6164	0.8800	Positive
Rep:Treatment	1.9655	0.6751	2.9117	Positive
spline(Day)	0.1040	0.1341	0.7755	Positive
Treatment:spline(Day)	0.2342	0.1293	1.8118	Positive
Rep:Treatment:Day_R	0.5701	0.0726	7.8533	Positive
Rep:Treatment:Day_S	0.6624	0.0759	8.7249	Positive
Rep:Treatment:Day_U	0.7519	0.0952	7.9024	Positive

ICV at 3.0 km

	variances	std.error	z.ratio	constraint
Rep:Treatment	2.6727	0.7386	3.6188	Positive
spline(Day)	0.0224	0.1409	0.1588	Positive
Treatment:spline(Day)	0.4014	0.1955	2.0531	Positive
Rep:Treatment:Day_R	0.5267	0.077 6	6.7856	Positive
Rep:Treatment:Day_S	0.4909	0.0685	7.1687	Positive
Rep:Treatment:Day_U	0.5545	0.0786	7.0560	Positive

ICV at 5.0 km

	variances	std.error	z.ratio	constraint
Rep	0.4336	0.5706	0.7599	Positive
Rep:Treatment	1.9943	0.6755	2.9525	Positive
Treatment:spline(Day)	0.2244	0.0920	2.4379	Positive
Rep:Treatment:Day_R	0.6489	0.0807	8.0445	Positive
Rep:Treatment:Day_S	0.0231	0.0046	4.9974	Positive
Rep:Treatment:Day_U	0.8904	0.1049	8.4910	Positive

Appendix III

REML analysis showing the significance between seedlings in 3 different exclosure treatments in the open paddock (OP) and Sheep fenced plot (SF) in Railway paddock at Middleback Field Station, Whyalla.

ICV at SF plot

	variances	std.error	z.ratio	constraint
Rep:Area_1.Treat_R:Day	0.4203	0.0608	6.9071	Positive
Rep:Area_1.Treat_S:Day	2.5467	0.3051	8.3471	Positive
Rep:Area_1.Treat_U:Day	1.6258	0.2068	7.8633	Positive

ICV at OP plot

	variances	std.error	z.ratio	constraint
Rep:Area_2.Treat_R:Day	0.2703	0.0369	7.3213	Positive
Rep:Area_2.Treat_S:Day	3.3881	0.4101	8.2608	Positive
Rep:Area_2.Treat_U:Day	0.9391	0.1235	7.6017	Positive