Department of Environment and Agriculture
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A test of landscape function theory in the semi-arid shrublands of Western Australia

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STATEMENT OF ORIGINALITY

This thesis contains no material that has been accepted for the award of any other degree or diploma at any university. To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgement has been made.

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SYNOPSIS

Australia‟s rangelands encompass approximately 80% of the continent and generate significant wealth through a range of industries. The rangelands comprise four major ecosystem types, these are: grasslands, shrublands, woodlands and savanna. The ecological legacy of early pastoral development in most of Australia‟s semi-arid shrublands is largely one of degradation and desertification (Wilcox and McKinnon, 1974; Curry *et al.* 1994; McKeon *et al*. 2004; Mabbutt *et al.* 1963; Pringle and Tinley, 2001). Since the 1980‟s, there has been a slow and general shift by the pastoral industry towards sustainable stocking rates (Watson *et al.* 2007; Pringle and Tinley, 2001).

To implement grazing systems that better align stocking rates with carrying capacity in the semi-arid shrublands, pastoralists require a much more advanced understanding of patch patterning and ecological processes at a paddock scale. This understanding of theory could improve the management decisions made by pastoralists and other land managers (e.g. mining environmental officers, carbon offset developers, conservation park rangers, Indigenous communities) and assist them in their immediate challenge of cost-effective rehabilitation of degraded areas. Landscape function theory was largely developed for this purpose.

Landscape function theory was developed as a way to assess and interpret patch patterns and ecological processes that occur at a range of spatial scales (Ludwig *et al*. 1997). Landscape function theory is used to explain the concept of „functional heterogeneity‟ which is an information-rich phenomenon that has enabled the development of cross-scale metrics. Landscape function theory is based on four primary principles, these are:

1. Patchiness can be characterised by patch size, orientation, spacing and soil surface condition.
2. Natural landscapes have a characteristic spatial self-organisation, often expressed as patchiness.
3. Deviations from the „characteristics‟ or „natural‟ patchiness are seen as degrees of dysfunctionality and there is a long continuum from highly functional to highly dysfunctional patches.
4. Restoration or replacement of missing or ineffective processes in the landscape will improve soil surface conditions and soil habitat quality.

Landscape function theory and the associated landscape function analysis (LFA) methodology have become an accepted standard for the ecological assessment of rangeland environments. However, there have been a limited number of studies in Australia that have thoroughly examined the four principles that underpin the landscape function theory. Further interrogation of the principles that underpin the theory has the potential to enhance its utility and validate its assumptions. Therefore, the aim of this thesis was to test the four principles of landscape function theory in a semi-arid shrubland environment.

The overarching hypothesis of this thesis was that clear spatial patch patterns occur at a range of scales within the case study paddocks and these patterns determine the ecological functionality and resilience of the area. Specifically, I sought to find evidence of distinct patch-interpatch patterns and associations at a range of scales in the lower Murchison region of Western Australia (WA) and examined the impact that grazing and seasonal conditions can have on this natural patchiness. The study involved four components:

1. Empirical quantification of patch-scale heterogeneity and investigation into the existence of a gradient of functionality at a patch-scale.
2. Measurement of patch patterning at a paddock scale and an evaluation of sequences and associations of patch-interpatches in the context of their contribution to landscape functionality.
3. Investigation of the impact of grazing and seasonal conditions on perennial grass populations and the potential impacts of this on patch patterning and ecological processes.
4. Investigation of livestock grazing behaviour and its implications for patch patterning and ecological processes.

Significant variation was detected ($P<0.05$) between the physical and chemical properties of 11 different patch-interpatch subclasses. Heterogeneity within individual patches was also significant ($P<0.05$) and the greatest variation occurred within ecologically stable, high-order patches. Higher-order patch-interpatch subclasses were highly functional and when compared to the lower-order patch-interpatch subclasses, the former had: higher soil respiration rates ($>45\%$) ($P<0.05$), this indicates these subclasses are more biologically active; more than twice the number of perennial plant species within the patch ($P<0.05$); higher soil infiltration rates ($>70\%$ more rapid) ($P<0.05$), this indicates these subclasses can capture more rainfall and surface runoff when it occurs; and five times more carbon and nitrogen. A gradient of highly functional patches and highly dysfunctional interpatches was identified.

Distinct patch patterning between different land-types was found. The granitic shrubland land-type had a much greater proportion of the lower-order resource-shedding interpatch subclass ($>85\%$ of the area) compared to the other land-types. In contrast, *Acacia* sandplains had a higher proportion of the ecologically functional patches compared to granitic shrublands. Depending on the land-type, it was concluded that a functional ecosystem will generally have balanced proportions of particular patch-interpatch subclasses as this is likely to lead to the efficient capture and cycling of water and nutrients. In contrast, a degraded ecosystem will have higher proportions of ecologically dysfunctional patch-interpatch subclasses. A number of significant spatial associations and repeating sequences of individual patch-interpatch subclasses were found to occur in the study area. In the case study paddocks, distance-from-water did not have any significant effect on the relative proportions of the different patch-interpatch subclasses.

Native perennial grasses support perennial shrub patches in maintaining ecological stability and landscape processes in semi-arid shrublands. Perennial grasses were monitored over a 12 month period to determine whether summer rest from Merino sheep grazing had an impact on perennial grass populations. The change in the number of perennial grasses over the 12 month period was variable ranging from a 36.7% increase to mortality rates as high as 80.2%. There was evidence to suggest that the grasses in the exclosure treatments (i.e. no grazing) may have been conditioned by previous grazing events in such a way that made them highly susceptible to extended periods of moisture stress. Land-type, distance-from-water and stocking rate did not have a significant impact on the change in the number of perennial grasses over the 12 month period. Resting perennial grasses during the summer may be of benefit; however, given the high mortality rates in most of the paddocks, it was clear that seasonal conditions had a substantial overriding influence on the outcome.

Five major factors influenced sheep grazing behaviour in the study paddock; these include: land-type, greenness cover, time of day, air temperature and distance-from-water. The GPS-collared sheep demonstrated a clear grazing preference for the higher value land-types (i.e. alluvial plains and hardpan washplains). The results also indicated that the sheep were selectively grazing areas with high greenness cover (as expressed by Normalised Difference Vegetation Index [NDVI]). The results highlight the importance of understanding the selective grazing characteristics of Merino sheep when designing paddock layouts and developing management plans. This is because repetitive, selective grazing of high-value land-types has the potential to modify the natural patch patterning and ecological processes.

This study found empirical evidence which substantiates landscape function theory and concludes that it has significant application at a range of spatial scales in the semi-arid shrublands. The results explain why landscape function theory is the current standard for the assessment and interpretation of rangeland environments in Australia. Landscape function theory is the result of an evolutionary synthesis of earlier work, and it continues to be progressively refined as our knowledge of the complex patterns and ecological processes of the rangelands is improved.

Based on the findings of this study, I consider that there are three areas of further inquiry which could assist land managers to practically apply landscape function theory and contribute towards the restoration of degraded Australian rangelands, these are:

- determination of the „functional‟ composition of patch-interpatches subclasses for a range of land-types in the Australian rangelands that could be used as benchmarks for land managers;
- further empirical quantification of the ecological processes that drive landscape function to assist in simulation modeling and the estimation of cost / benefit of rehabilitation efforts; and
- the potential role that grazing management can play in the restoration of dysfunctional patch-interpatch patterns and ecological processes in the semi-arid shrublands.

PREFACE

During this project I designed the study with support from my previous supervisors Dr. Ben Norton and Dr. Don Burnside. Due to certain circumstances, Associate Professor Grant Wardell-Johnson became my supervisor and assisted in the final revisions of this thesis. I collected all data, sometimes with the assistance of colleagues (refer to Acknowledgments for details); I undertook statistical analyses with guidance from a biometrician; drafted and revised all chapters; co-authored a publication; and took all the photographs included in this thesis.

Some of the information contained within Chapter 6 was used to publish a paper which I co-authored, this was:

Thomas, D., Wilmot, M., Alchin, M. and Master, D. 2008, *Preliminary indications that Merino sheep graze different areas on cooler days in the Southern Rangelands of Western Australia*, Australian Journal of Experimental Agriculture, Vol. 48, No. 6/7, pp. 889-892.

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ACKNOWLEDGEMENTS

I commenced this study when I was living in Meekatharra and continued working on it whilst in Kununurra. The seven years I spent in the Gascoyne-Murchison and Kimberley regions ignited in me a strong affinity with the Western Australian rangelands and the people who passionately manage its vast expanses. The WA rangelands is truly one of the most remarkable regions in the world and it was a privilege to study a small part of it as a part of this thesis. In completion of this thesis I was supported by a comprehensive team of professionals, family and friends. I owe the highest gratitude to my wife Megan who endured the times when I was completely consumed with this manuscript. Megan‟s devotion and sincere encouragement was critical to my success; this thesis is dedicated to her.

A few different supervisors supported me in preparation of this thesis. Dr. Ben Norton was my supervisor from 2006 to 2009. Ben left for the USA in late 2009 and Dr. Graeme Robertson took over as my academic supervisor in 2010. Ben has an immense capacity to articulate complex concepts and I thank him for his dedication to meticulously edit my work. I am grateful for the number of insightful discussions I had with my other supervisor Dr. Don Burnside concerning the design of the study and the implications of my findings. Graeme also made a contribution to the structure and integrity of the thesis. Dr. Grant Wardell-Johnson took over as my sole supervisor in 2011 and provided invaluable advice in order to finalise this thesis.

I am thankful to my father Bruce Alchin and Dr. Ian Watson who were instrumental in the design and delivery of this study. I appreciated Ian‟s ruthless editor‟s „red pen‟ and the robust debates we shared concerning all aspects of rangeland ecology and management. Bruce spent countless hours reviewing my drafts, diligently forwarded relevant literature and acted as an invaluable sounding board for all my ideas.

There are numerous former colleagues within the Department of Agriculture and Food WA who assisted me in this study. Jane Speijers and Mario D‟Antuono provided assistance in the statistical analysis of data. John Bruce helped with the preparation of imagery and maps. Phil Thomas conscientiously provided data and useful information. Greg Brennan was very supportive throughout the PhD. Dr. Chris Chilcott provided me with encouragement towards the end of the thesis and I appreciated his support.

This research was funded by a Post-graduate „Top-Up Scholarship‟ from Australia Wool Innovation. I am very grateful for their financial support and the professional development that I obtained through involvement in their post-graduate network. This study would not have been possible without the active cooperation and partnership of Rob and Kathryn Mitchell (formerly of Barnong Station) and

Ellen and the late Bill Rowe (Carlaminda Station). I am very grateful of Rob and Kathryn‟s generous hospitality while I completed the field work and many discussions we shared well into the night. Similarly, Bill and Ellen generously assisted me in the field work of this study and their enthusiasm to acquire new knowledge was encouraging.

Fiona Brayshaw completed her PhD on the same two pastoral leases involved in this thesis and we provided each other with support and encouragement throughout. David Tongway provided technical information for sampling protocols. Jeremy Wallace provided advice concerning the use and application of remote sensing. David Wilcox gave me insights into historical management practices and forwarded relevant unpublished literature and anecdotes. Rosemary Bartle developed my understanding of business management and the drivers of profitability of pastoral businesses in the region.

Dr. Dean Thomas and Matt Wilmot from CSIRO were key partners in the grazing behaviour study. Dr. Hugh Pringle and Dr. Ken Tinley both acted as very knowledgeable sounding boards in relation to understanding landscape scale issues. Roderick O‟Connor, Dr. Alec Holm and many others of the „old guard‟ assisted me in understanding the historical context of management and rangeland science in the WA shrublands. Terry McCosker provided information and directed me to useful sources relating to grazing management. I would also like to thank Prof. Klaus Kellner who was an excellent host of the study tour I undertook in South Africa as a part of this thesis.

Finally, I am thankful to the many pastoralists who were very hospitable during my time in Meekatharra. They developed my understanding of rangeland ecology and management and kept me grounded on the major issues that affected the long-term sustainability of the industry.

Chapter 1

Landscape function theory in the semi-arid shrublands

Plate 1-1: *Acacia* sandplain, study area, July 2005

Photo: Mark Alchin

1.1 Introduction

Pastoralism was a major contributor to the development of Australia (McKeon *et al*. 2004; Bolton, 2008). Despite the economic contribution of the pastoral industry, the ecological legacy of early pastoral development in most of Australia"s semi-arid shrublands is largely one of degradation and desertification (Burnside *et al*. 1995; Curry *et al.* 1994; Mabbutt *et al.* 1963; McKeon *et al*. 2004; Pringle and Tinley 2001; Wilcox and McKinnon, 1974). Aided by the technology of windmills and fencing, livestock numbers in semi-arid shrublands were able to rise rapidly (Biswas and Biswas, 1980; Edwards, 1994).

In the Western Australian (WA) semi-arid shrublands, total livestock numbers reached five and half million sheep in 1934 and crashed to three million by 1941 following an extended dry period (Mabbutt *et al.* 1963; McKeon *et al.* 2004). Jennings *et al.* (1979) in a historic report commissioned by the WA Government commented that, "in the short-time (sic) which has elapsed since pastoral settlement, marked changes in carrying capacities made on the basis of the then present condition have occurred". Jennings *et al*. (1979) reported that livestock carrying capacities were reduced by at least one-third and these reductions were associated with a reduction in the ecological condition of the soil and the vegetation.

A detailed survey of the soil and vegetation in the Murchison region in WA found that, "approximately 42% by area of all vegetation was in poor to very poor condition, 37% was in fair condition and 21% was still in good to very good condition" (Curry *et al*. 1994, p. 1). Furthermore, a survey of the Yalgoo-Paynes Find region (i.e. Lower Murchison region) of WA found that, approximately 23% of the vegetation was in poor to very poor, 32% was in fair condition, and 45% was in good to very good condition (Payne *et al.* 1998).

It was estimated that 941,201 ha (or 13%) of the Gascoyne Catchment was "badly eroded" and was predicted to become "irreversibly degraded" unless the area was destocked (Wilcox and McKinnon, 1974, p. 1.1). A further 3.3 million hectares (or 48%) of the Gascoyne catchment was assessed as being degraded and it was recommended that the area needed to be managed carefully in order to stabilize it (Wilcox and McKinnon, 1974, p. 1.1). Despite some improvement in rangeland condition in selected areas (Watson *et al*. 2007), a significant proportion of the soils and vegetation within the WA rangelands remains in poor condition (**Figure 1-1**). This ecological degradation (see footnote[1]) poses a number of challenges for the sustainability of the region, regardless of its land-use (e.g. pastoralism, carbon sequestration, tourism, mining, Indigenous heritage, conservation).

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[1] The term „degradation" when used in rangeland survey reports (e.g. McKinnon and Wilcox 1974; Payne et al. 1998) generally refers to the loss of livestock pastoral potential due to the loss of topsoil and perennial vegetation. In this study, the term „ecological degradation" is used because the focus is on the „functionality" of ecosystems and not their land use. This concept is defined in more detail in this Chapter.

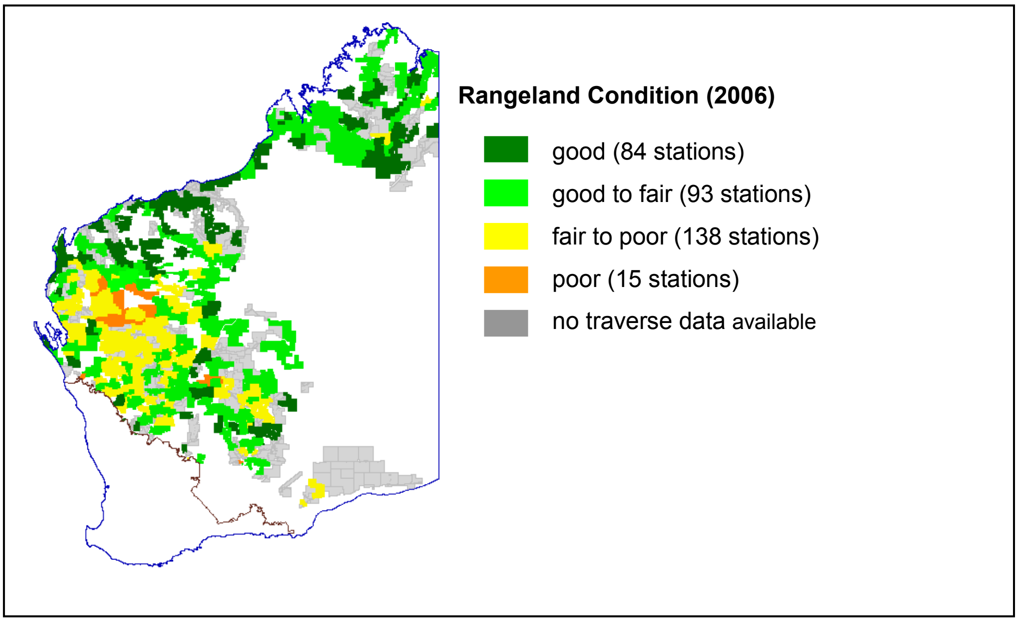


Figure 1-1: Rangeland condition of the WA rangelands as assessed by the Department of Agriculture and Food WA (Van Vreeswyk and Thomas, 2008)

1.2 Changes in land management and the need for new knowledge

Many pastoralists within the WA semi-arid shrublands have responded to the challenge of addressing the ecological degradation by adopting new management systems. During the 1900s, the predominant industry was wool from Merino sheep. The objective of most pastoral businesses was to run high numbers of large wethers with heavy wool cuts per head. In general, equal numbers of ewes and wethers were held by pastoral enterprises. If seasonal conditions permitted, wethers were sold at five or six years of age and ewes were held for longer (often ewes were never sold and died on the property). The low price of mutton in the earlier 1900s was a disincentive for many pastoralists to sell their older breeding ewes (Mabbutt *et al.* 1963). Despite the regular cycles of below-average rainfall, there tended to be no deliberate attempt to make any significant adjustments in stocking rates (Mabbutt *et al.* 1963).

The method by which stocking rates were set was rudimentary and based on a limited understanding of rangeland ecology and management (Mabbutt *et al.* 1963). In many cases, pastoralists set long-term stocking rates for paddocks during periods of above-average rainfall and this had obvious consequences when the seasonal cycle shifted. There was little recognition of the need for recruitment and establishment of perennial shrubs and grass patches to maintain functional landscapes (Mabbutt *et al.* 1963).

Since the 1980s, there has been a slow and general shift by industry towards systems which align livestock stocking rates with the sustainable carrying capacity (Pringle and Tinley, 2001; Smits, 1989; Watson *et al.* 2007). This is evident by the increasing level of participation in research and development efforts focused on natural resource management (NRM). A study found that many pastoralists from the region have become “more innovative, outward looking and more welcoming of new ideas" (URS, 2004). The majority of pastoral businesses now manage livestock numbers according to the seasonal feed supply, albeit in a delayed manner (Bartle, 2003; URS, 2002). This generally involves having a long-term, conservative stocking rate for certain paddocks or for the whole pastoral lease that pastoralists seek to maintain.

Some consider that the shift towards grazing systems that more effectively align livestock stocking rate with carrying capacity has the potential to deliver ecological improvement over large areas (Earl and Jones, 1996; Müller *et al*. 2007; Norton, 1998; Tainton, 1999; Taylor *et al*. 1993; Teague *et al*. 2004). However, to implement sustainable stocking rates with a high level of precision, pastoralists require a much more advanced understanding of patch patterning and ecological processes at a paddock scale. This understanding or theory could improve the management decisions made by pastoralists and other land managers and assist them in their immediate challenge of addressing the ecological degradation. Landscape function theory was primarily developed for this purpose.

1.3 Landscape function theory – interpretation of patch patterns and ecological processes

1.3.1 Landscape function theory defined

Landscape function theory has been developed as a way to assess and interpret patch patterns and ecological processes that occur at a range of spatial scales (Ludwig *et al*. 1997). The theory has been widely adopted by rangeland scientists and industry. The monitoring methodology which has been developed from the theory (i.e. Landscape Function Analysis or LFA) is used to assess the condition of the soil surface and perennial vegetation. LFA is currently used for a wide range of purposes, including the assessment of rangeland condition of pastoral leases and monitoring the relative success of rehabilitation of constructed mine waste landforms (Watson *et al*. 2007, Outback Ecology, 2010 respectively).

The LFA monitoring methodology was developed from a comprehensive study by CSIRO during the 1980s at Lake Mere, in western New South Wales (Ludwig *et al*. 1997). The purpose of this study was to elucidate the „internal workings" of a semi-arid landscape, and what happens to that landscape if it is being pushed too far by grazing pressure (Ludwig *et al*. 1997). The intended purpose of LFA was to provide a tool that could assist land managers to be able to measure changes in the ecological functionality of a landscape.

For the purposes of this thesis, landscape function theory is a collective description of the approach used to explain the biogeochemical processes, which capture and retain water and nutrients to produce biomass (Ludwig *et al*. 1997). Landscape function theory has taken some time to develop and is continuing to be refined (Ludwig *et al*. 1997). Ludwig *et al*. (1997) were arguably the first to clearly articulate and synthesise the theory of patch-interpatch patterns and processes by developing the Trigger-Transfer-Reserve-Pulse (TTRP) framework. The TTRP framework provided a conceptual structure to the landscape function theory. The work by Ludwig *et al*. (1997) was based on a body of research dating back to the 1950s.

Jim Charley is considered one of the pioneers investigating landscape function theory and patch dynamics with his PhD thesis in 1961; his work sought to understand how landscapes function at a patch scale (Charley, 1961). Following a student excursion to a property near Broken Hill, New South Wales (NSW), he observed distinct fence-line contrasts in the patch scale patterning of *Atriplex vesicaria* (bladder saltbush) which he presumed were the results of overgrazing. His research led him to investigate the impact that overgrazing had on soil, water and nutrient dynamics (Charley, 1961).

This early work was followed by key papers by Noy-Meir (1973) and Westoby *et al.* (1989) who presented conceptual frameworks that significantly advanced the thinking of landscape ecology. Noy-Meir (1973) described a pulse-and-reserve conceptual framework or model for how desert ecosystems function. This model is based on the premise that a rainfall event triggers a pulse of production some of which is returned into the reserve and the remainder is „lost" from the ecosystem. Westoby *et al*. (1989) built upon the conclusions from Noy-Meir"s (1973) work by emphasizing the dynamic nature of rangeland landscapes and challenged the traditional Clementsian succession model (Clements, 1916).

The Clementsian succession model suggested that vegetation communities operated within a linear continuum and grazing pressure and seasonal conditions were the main factors determining the relative position of the community on the continuum (Westoby *et al*. 1989). In contrast, Westoby *et al*. (1989) considered rangeland landscapes were far more complex than this simple model. They suggested that land managers and researchers could benefit by developing state-and-transition models appropriate for their environments.

Pickup"s (1985) work was also instrumental in the development of the landscape function theory and he demonstrated the value of assessing landscapes on the basis of their geomorphic characteristics (namely runoff, transfer and sink zones). Ludwig *et al.* (1997) view their TTRP framework and the associated LFA methodology as an integrative evolution of the earlier *reserve-pulse* and the *state-and-transition* models developed by Noy-Meir (1981) and Westoby *et al.* (1989) respectively. More recently, Holm *et al.* (2002a) made a valuable contribution to the landscape function theory by verifying the value of investigating landscape structure and the patchiness of semi-arid landscapes as a means of understanding ecological processes.

Landscape function theory is different compared to other earlier theories that were used to explain ecosystem dynamics (e.g. succession theory) because it does not classify landscapes based on „land condition". Classification of land condition is often intrinsically linked to a value judgment of land-use (**Figure 1-2**). For example, a nature conservationist may classify an area dominated by *Cenchrus ciliaris* (buffel grass) as „degraded" because there are few native plant species; however, a pastoralist may classify the area as being in good condition because it provides an abundant supply of livestock forage. Therefore, landscape function theory and the LFA methodology involve a purposeful change of focus from listing the simple presence / absence of plant species or biota, to an examination of the degree to which biophysical processes deal with vital resources with respect to stress arising from management and climatic events. This makes it significantly different, but complementary to traditional monitoring procedures (Tongway *et al*. 2003).

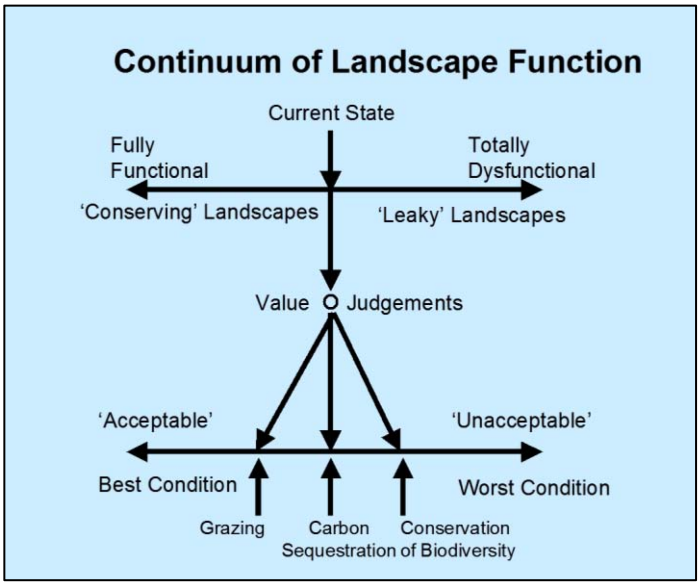
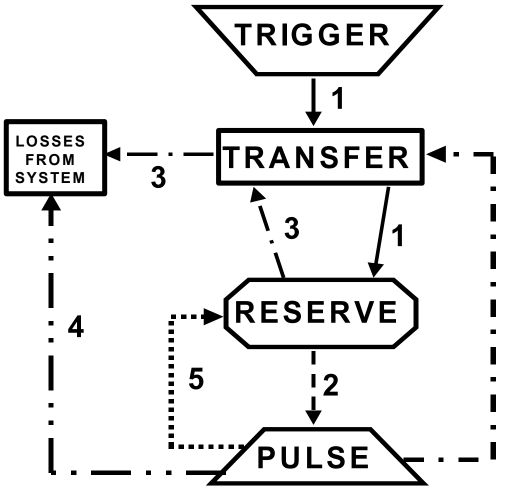


Figure 1-2: Continuum of landscape function (reproduced from Tongway *et al*. 2003)

The landscape function theory recognizes that whilst early pastoral development initiated marked changes in ecological processes, remnant areas still remain and these can be used as „analogues" or guidelines for the assessment of functionality and for designing rehabilitation. These analogue areas provide insight into the potential natural patchiness of a site. The LFA methodology integrates information about the soil surface conditions and vegetation components and thereby enables pastoralists, mining company environmental officers, conservation managers and those responsible for monitoring the condition of the soil and vegetation, to identify shifts in ecological functionality. An improvement in landscape functionality will generally result in an increase in vegetative biomass that could be used for various purposes depending on the land-use (e.g. pasture for livestock, habitat for short-range endemics, carbon sequestration).

Traditional rangeland assessment techniques based on Clements succession theory tended to monitor only vegetation characteristics which are usually less sensitive to change compared to the soil surface condition (e.g. perennial shrub density). In contrast, monitoring the size, stability and floristic diversity of individual patches may enable shifts in the ecological functionality of a landscape to be identified. Since one of the key determinants in landscape processes is rainfall-use efficiency, it is essential to be able to critically assess features that directly affect rainwater retention, such as patch quality and soil surface conditions.

To assess the status of the surface processes that regulate the availability of vital resources in space and time the TTRP framework was developed. The TTRP is a conceptual framework depicting sequences of landscape process operating in an explicitly spatial manner. The TTRP framework describes how limited water and nutrients are efficiently captured (process # 1), cycled through the ecosystem and used to generate a pulse of growth (process # 2) that is available for maintaining the ecological stability of a defined area (process # 5) (Ludwig *et al.* 1997) (**Figure 1-3**).



Ref	Process
1	• Run-on • Storage/Capture • Deposition • Saltation capture
2	• Plant germination, growth • Nutrient mineralisation • Uptake processes
3	• Run-off • Rill flow and erosion • Sheet erosion out of system • Wind erosion out of system
4	• Herbivory • Fire • Harvesting • Deep drainage
5	• Seed pool replenishment • Organic matter cycling/Decomposition processes • Harvest/Concentration by soil micro-fauna • Creation of habitat niches by soil fauna
6	• Physical obstruction/Absorption processes

Figure 1-3: Trigger-transfer-reserve-pulse conceptual framework. The table on the right lists the processes operating at different locations in the framework (Tongway *et al*. 2003)

Degradation of the land involves, “the reduction of the renewable resource potential by one or a combination of processes acting upon the land” (FAO UN, 2011). Degradation is a process, while the term „degraded‟ is typically used as a descriptor for a landscape that has crossed a certain threshold where excessive water and nutrients have been permanently removed. Therefore, a degraded landscape is often dysfunctional, likewise a non-degraded landscape is typically functional. There may be situations when a landscape may be impacted by the early phases of degradation, however it remains functional.

1.3.2 What are patches and interpatches?

The fundamental basis of the landscape function theory is that rangeland landscapes comprise both patch and interpatch areas and the ability of a landscape to capture and store water and nutrients is determined by the interactions between these two areas. Within this thesis, a patch is defined as a spatial area occupied by a dominant individual tree, shrub, or perennial grass that act as an obstruction to water flow. In this thesis, an interpatch is defined as a spatial area between patches occupied by varying amounts of organic debris (e.g. logs, litter) and typically acts as a run-off zone.

Some interpatches support biological soil crusts; in semi-arid areas these are often dominated by cyanobacteria (Ludwig *et al*. 1997). It is recognised that the term „interpatch" in this thesis is not used in exactly the same manner as defined by Ludwig *et al*. (1997) (namely that an interpatch may have organic matter and may not act strictly as a runoff area). The reason for this classification approach is explained in more detail in **Section 3.3.2**. Water and nutrients are generally captured and deposited within patches and used as a resource reserve by a number of organisms and plants (Ludwig *et al*. 1997; Pickup, 1985).

Reference to „patch scale" within this thesis refers to a spatial area occurred by one or more individual plant patches or interpatches. Reference to „paddock scale" refers to the size of a commercial sized paddock within semi-arid shrublands (approximately 5,000 ha).

Landscape function theory is used to explain that in the absence of degradation, patches of different sizes and shapes create distinct interlinked patterns and assemblages across landscapes which are highly efficient at capturing soil and litter materials being carried by wind and water (Ludwig *et al.* 1997). Efficient use of limited resources in semi-arid landscapes relies on a patterning characterised by an equitable composition of fertile patches and water-shedding interpatches. Patches encourage plant recruitment and establishment because they provide favourable moisture and nutrient conditions, seed supply and a stable soil temperature and surface (Pickup, 1985; Pressland *et al*. 1982).

The most important obstructions in semi-arid environments are shrub and perennial grass patches as they play a critical role in the cycling and distribution of nutrients. Fallen timber and organic debris are also an important component as they act as capture and retention sites of moisture and nutrients (Ludwig *et al*. 2005). Ephemeral herbage can contribute significant amounts of organic matter in degraded ecosystems where it may be the dominant form of plant life. However, herbage has little capacity to provide any stability and prevent excessive nutrient and water loss. Holm *et al*. (2003) found that herbage mass is more markedly affected by seasonal events and temporal variability. Further studies by Holm (2000) of degradation processes at a patch to a landscape scale concluded that a loss of vegetated patches from the landscape provided strong evidence to support a reduction of the functionality of a semi-arid landscape.

1.3.3 Patch patterning at a range of spatial scales

Landscape functional theory can be used to explain that the ecological functionality of a landscape within an area can be assessed at a range of spatial scales, ranging from an individual patch to a whole catchment. At the smallest scale, a land unit is an assemblage of patches and interpatches and has a recurring pattern of topography and soils. A land-system encompasses a number of land units and is classified by the recurring pattern of topography, soils and vegetation. These recurring patterns can be seen using aerial photography or other remotely sensed images.

At a larger spatial scale, land-systems are grouped into land-types according to a combination of landforms, soils, vegetation and drainage patterns (Payne *et al*. 1998). A catchment may involve a number of different land-types which collectively interact and determine the functionality of a landscape at very broad spatial scales.

1.3.4 The role of patches and interpatches in landscape function theory

Landscape function theory is based on the recognition that limited water and nutrients cause ecological processes to rely on the interactions of run-on (patch) and run-off (interpatch) areas. Any long-term disturbance that affects the proportional area that these categories occupy may result in excessive loss of water and nutrients. Tongway *et al.* (2003) reported that each natural landscape has a characteristic spatial self-organisation that reduces overall resource loss and optimises resource utilization and cycling. Patchiness can be characterized by patch size, orientation, spacing and soil surface condition. Deviations from the characteristic or natural patchiness are therefore seen as degrees of dysfunctionality that is a continuum from highly functional to highly dysfunctional (Tongway *et al*. 2003; Ludwig *et al.* 2002; Bastin *et al.* 2004).

Holm *et al.* (2002a) verified aspects of landscape function theory by investigating landscape structure and the patchiness of semi-arid landscapes. They demonstrated a general relationship between landscape patchiness, primary productivity and rainfall-use efficiency. In their study, which covered four sampling domains (25 x 25 km each) across the Murchison region and involved 100 sites, they found that generally there was less phytomass and poorer rainfall-use efficiency on dysfunctional or degraded landscapes than on functional or non-degraded landscapes.

The cause of this landscape dysfunction was primarily the reduction in patch size and an increase in interpatch size. Furthermore Williams *et al*. (1993) and Whitford (1995) reported a reduction in microbial respiration and water infiltration when the fertile vegetative patches necessary for a functional ecosystem were altered or completely removed. Similarly, Pressland (1973) found that the size of *Acacia aneura* trees was positively correlated with the stemflow and the amount of rainfall they could capture. **Figure 1-4** shows how the infiltration rate decreases at increasing distances from a woody patch (Pressland, 1976a).

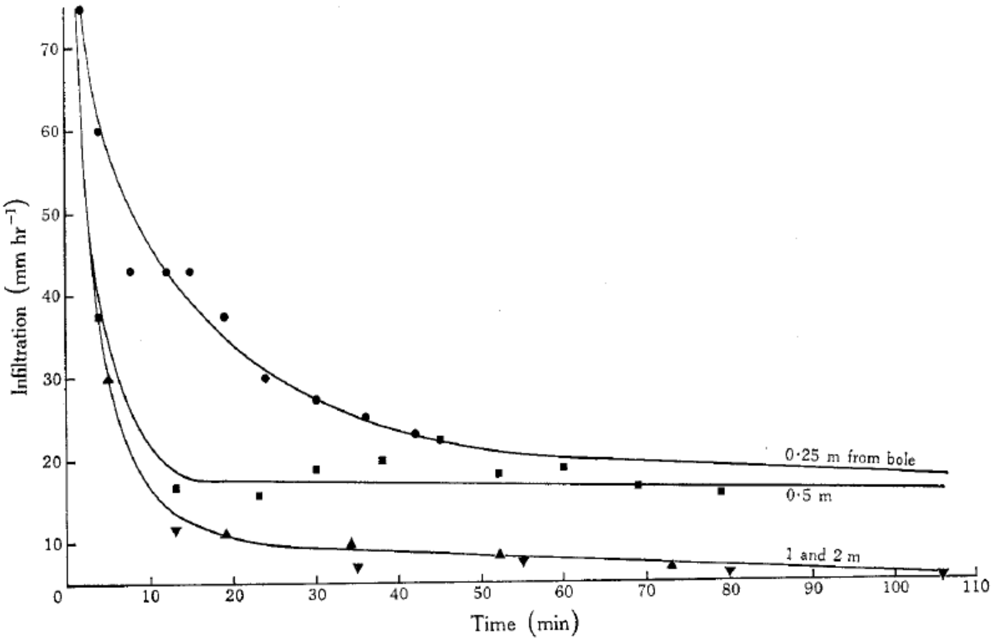


Fig. 2. Change in infiltration rate with time at distances of 0·25 m (●), 0·5 m (■), 1 m (▲) and 2 m (▼) from a mulga tree bole. (One infiltration curve is shown for the data taken at 1 and 2 m from the tree.)

Figure 1-4: Reduction in infiltration rates at increasing distances from a woody patch (Pressland 1976a)

Holm *et al*. (2002b) reported that the proportional areas of vegetated patches were positively correlated with oxidizable C and total N in surface soil in low woodland, but not in low-shrubland communities. Holm *et al*. (2002b) stated that the loss or disappearance of long-lived plants affects the physical obstruction to movement of resources around landscapes and reduces opportunities for nutrient cycling. Similarly, in a study of two central Australian *Acacia aneura* (mulga) shrublands, Friedel (1984) found that the herbage yield of a perennial community was higher than a community dominated by annuals. Hence, Holm *et al*. (2002b) concluded that the area occupied by vegetated patches and inter-patches, is an acceptable criterion against which to assess the ecological functionality of semi-arid environments.

The results from a 10-year grazing trial at Boolathana pastoral lease (24°39'S, 113°41'E) indicated that rainfall-use efficiency and net primary productivity were 29% and 15% higher on a non-degraded landscape than on a similar, but degraded landscape where there were far fewer shrubs (Holm *et al*. 2003). These findings support the principles underlying landscape function theory which state that in functional landscapes water and nutrients are retained and there is a close coupling between rainfall and net primary productivity (Ludwig and Tongway, 1995). In addition, the overall proportions of patches and interpatches, the size of individual patches and their localized patterning will also have an influence over the relative functionality of a landscape (Ludwig *et al*. 1997).

Ludwig *et al*. (2005) conducted a thorough review of the major studies that focused on how vegetation patches interact with ecohydrological processes. Specifically, they found that patches stored significantly more soil water, produced more growth, and had higher levels of infiltration than interpatches, and that run-off and erosion can markedly increase on disturbed hill-slopes.

Landscape function theory is also used to explain the concept of „functional heterogeneity", namely that landscape heterogeneity is not simply random variation that confounds robust statistical analyses. Instead, functional heterogeneity is an information-rich phenomenon that has enabled the development of cross-scale metrics. These cross-scale metrics recognize the role of surface and near surface processes in the allocation and re-allocation of resources in space and time (Tongway *et al*. 2003).

Soil surface conditions also play a major role in the development of patchiness and the functionality of an ecosystem. This is because soil is the growth medium for vegetation patches. The three key factors that will determine the capacity of the soil to support vegetation patches are (Tongway, 1994):

- infiltration rate (largely determined by soil morphology, structure and texture);
- soil stability (largely determined by exchangeable sodium percentage and soil texture); and
- nutrient cycling (largely determine by soil porosity, organic matter, moisture).

These factors can collectively be referred to as „soil quality" or „soil productive potential" (Tongway, 1994). There are a number of soil surface features that can be used to quantitatively assess soil quality, for example (Tongway, 1994): soil cover, crust brokenness, microtopography, cryptogram cover, erosion features. In general, a higher level of soil quality is generally associated with increased patchiness.

Spatial self-organisation is the main theoretical explanation for the occurrence of regular, coherent spatial patterns in ecosystems. It is a concept that is used to explain how natural landscapes have a natural pattern that serves to maintain adequate water and nutrients for the ecosystem. This chapter has shown that these patterns are a product of ecological processes and are also an important determinant of the functioning of landscapes at multiple scales. The role of the spatial self-organisation at fine scales has been investigated in other studies that have shown that fine-scale heterogeneity is critical to the ecological functioning of semi-arid landscapes (Ludwig *et al*. 2005). The concept of spatial self-organisation at landscape scales was developed by Ludwig *et al*. (1994), and its occurrence at smaller spatial scales has been investigated in part by Holm (2000).

In summary, landscape function theory is based on four primary principles that appear in the foundational text of Ludwig *et al*. (1997), these are:

1. Patchiness can be characterized by the patch size, orientation, spacing and soil surface condition.
2. Natural landscapes have a characteristic spatial self-organisation, often expressed as patchiness.
3. Deviations from the „characteristics" or „natural" patchiness are seen as degrees of dysfunctionality, and there is a long continuum from highly functional to highly dysfunctional patches and interpatches.
4. Restoration or replacement of missing or ineffective processes in the landscape will improve soil surface conditions and soil habitat quality.

To apply the landscape function theory, the LFA methodology is used to address three major questions:

1. What are the landscape components? (compile an inventory)
2. How do the landscape components fit together? (patch-interpatch patterning at a specified scale)
3. How do the landscape components work together? (ecological processes and function)

The landscape function theory and the associated LFA methodology have largely become an accepted standard for the ecological assessment of rangeland environments. However, there have been a limited number of studies that have thoroughly examined the four principles that underpin the landscape function theory. Further interrogation of the principles that underpin the theory in the field has the potential to enhance its utility and the robustness of its assumptions. This information would strengthen the empirical basis of the theory and potentially lead to improved management recommendations and decisions for rangeland landscapes.

1.4 Implications of grazing and climatic conditions on landscape function theory

Grazing and seasonal conditions are the two major factors that determine the trajectory of patch patterning and landscape function in the rangelands (Ludwig *et al*. 1997). In semi-arid rangelands grazing occurs from two primary sources: domestic livestock and non-domestic grazers (namely kangaroos, unmanaged goats, camels, horses, donkeys and rabbits). Non-domestic grazers are known to have a direct impact (usually adverse) on the soil and vegetation in semi-arid shrublands if left unmanaged (Fletcher, 1991; Gardiner, 1984; Norbury and Norbury, 1993). It is acknowledged that non-domestic grazers can have an impact on ground cover and associated landscape functionality (Wilson, 1991), however the focus in the experimental chapters of this thesis was on sheep grazing.

The relative impact of the disturbance is largely dependent on the inherent ecological resilience of the landscape (**Figure 1-5**). Ecological resilience is primarily determined by soil type, vegetation composition and topography. Topography in an *Acacia aneura* community has been reported to be one of the main factors that determined the difference in plant communities (flats *cf* ridges) and microtopography was important in determining plant species distribution.

A number of comprehensive studies and reviews have investigated the potential impact that grazing may have on vegetation dynamics in rangeland landscapes (Anderson *et al*. 1996; Ash and Stafford Smith, 1996; Barnes and Denny, 1991; Chaieb *et al.* 1996; Cipriotti and Aguiar, 2005; Danckwerts *et al*. 1991; Dowling *et al.* 2005; Earl and Jones, 1996; Fuhlendorf and Smeins, 1999; Graetz, 1986; Greene *et al*. 1994; Hart *et al.* 1993; Heitschmidt *et al*. 1989; Hodgkinson *et al*. 1989; Holm *et al.* 2003; Hunt, 2000; Jacobo *et al*. 2006; Knight *et al*. 1980; Taylor *et al*. 1997; Watson *et al.* 1997; Wilcox, 1973; Yan *et al*. 1996). As a general synthesis, these studies indicate that grazing in rangeland environments can have positive, negative or benign impacts on patch patterning and ecological processes depending on the intensity, frequency, type (domestic *cf* non-domestic grazing pressure) and timing of the grazing and resting periods.

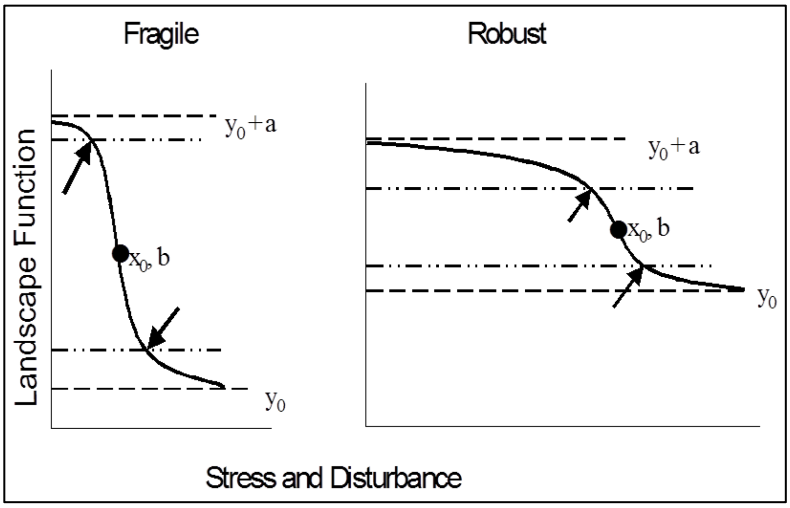


Figure 1-5: Predicted relationship between stress and disturbance on landscape function in both fragile and robust ecosystems (reproduced from Tongway *et al*. 2003)

For example, Hunt (2000) found that continuous grazing by sheep reduced the input into the seed-bank and caused a reduction in the number of established plant patches. In particular, at sites close to water, shrub patch density was reduced and grazing resulted in increased retrogression of shrub patches to a smaller, non-reproductive size-class (Hunt, 2000). Work by Anderson *et al*. (1996) indicated a similar interaction of very low levels of readily germinable seed in plant patches as a result of historical heavy grazing. These studies found that without adequate recruitment and establishment, semi-arid shrubland environments can deteriorate into a fragmented assemblage of isolated perennial patches with large, bare interpatch areas that facilitate significant outflows of water and nutrients (Danckwerts *et al*. 1991; Holm *et al*. 2002a). Similarly, Orr (1980) reported that increased grazing pressure reduced the projected foliar cover and basal area of *Astrebla* spp. (Mitchell grass).

In contrast, a study by Jacobo *et al*. (2006) showed that grazing could have a positive impact on the size and stability of perennial plant patches. The changes resulting from rotational grazing indicated an improvement in rangeland condition and in the livestock carrying capacity. Specifically, under rotational grazing, litter cover was higher in both the communities they studied while the size of the bare interpatches showed a significant reduction in the lowlands and a tendency to be smaller in the mid-slope areas (Jacobo *et al*. 2006). Burrows (1973) observed that regeneration of *Acacia aneura* (including the production of a large amount of surface litter) in western Queensland occurred in lightly stocked areas even in the absence of heavy summer rain.

Livestock grazing has also been reported to have affected the composition of plant patches. Taylor *et al*. (1993) investigated vegetation responses to increasing stocking rates under rotational grazing at a semi-arid location in Texas, USA. They concluded that the ecosystem was not able to sustain the initial plant species composition at any of the stocking rates tested. Over the 10-year study period it was observed that there was a reduction of highly preferred, perennial plant species and an associated increase in less desirable plants (Taylor *et al*. 1993).

Other long-term grazing trials have found that heavy, repeated defoliation and browsing on perennial grasses and shrubs led to decreased patch diversity and altered patch composition (Fuhlendorf and Smeins, 1999; Roux and Vorster, 1983). Studies on the impact of grazing intensity on palatable perennial patches also concluded that grazing can adversely affect their distribution, and this relationship is particularly accentuated in dry years (Cipriotti and Aguiar, 2005). These changes in species composition may be so extensive that semi-arid environments may not return to their original ecological states even after being rested for decades (O"Connor, 1991). Chapin *et al*. (1997) reported that floristic diversity is functionally important, because it increases the probability of including species that have strong ecosystem effects, and it can increase the efficiency of resource use.

Hacker (1984) also reported negative effects of heavy grazing on perennial grasses in a study of plant population dynamics in a mulga shrubland. While the frequency of annual forbs appeared to be influenced more by seasonal conditions, the perennial grass (*E. xerophila*) decreased under heavy grazing. Hacker (1984) inferred that the recovery of the grass was also inhibited by competition with annual plants in the immediate post-drought period.

While grazing is an important factor, rainfall can have an overriding influence on patch patterning and ecological processes in semi-arid environments. The effect of rainfall on patch patterning and ecological processes is determined by the following variables (Tainton, 1999):

- timing (namely what time of year does it occur; does it coincide with good growing conditions; what was the length of time since the last significant rainfall event; how long is each individual rainfall event);
- amount (how much rainfall occurred); and
- intensity (is the combination of timing and amount and it can have a significant impact on soil loss from erosion if a significant rainfall occurs over a short period of time).

When rainfall is above-average, the ecosystem typically produces larger „pulses" of growth which increases the organic matter within patches and interpatches (Ludwig *et al.* 1997). This positive feedback can enhance the functionality and relative stability of plant patches. Similarly, an extended period of below-average rainfall can deplete the moisture and nutrients within plant patches and increase their vulnerability to adverse processes such as wind erosion, grazing, solar radiation, fluctuations in soil temperatures and pests and diseases. The most effective rainfall in semi-arid shrublands typically occurs when air temperatures are adequate for plant growth and still cool enough to prevent excessive evaporation of moisture from the soil profile. Temperatures between 20 and 30°C are optimal for germination of *Acacia aneura* (Preece, 1971).

In summary, there is a substantial body of information that describes the potential impacts of grazing on patch patterning and ecological processes in the rangelands. This information is useful in understanding the application of the core principles of the landscape function theory. This thesis contributes to the present body of information by investigating the impact of sheep grazing on perennial grass populations. The focus on perennial grasses is important because they can play an important role in ecological processes in semi-arid environments (Anderson and Hodgkinson 1997). Finally, this thesis investigates sheep grazing behaviour and its implications for patch patterning and ecological processes.

1.5 The effect of sheep grazing behaviour on patch patterning

Key variables that can influence the effect of sheep grazing behaviour on patch patterning include: seasonal conditions; topography; forage availability and preferential grazing; time of day; distance-from-water; and competition with other grazers. This section outlines the nature of these effects.

1.5.1 Seasonal conditions effect

Seasonal conditions (temperature, humidity, wind direction and speed, day length, number of rain days, rainfall amount) are known to have a direct and tangible effect on animal grazing behaviour (Conradt *et al.* 2000; Orr, 1980; Owen-Smith, 1999). Seasonal conditions can cause localised concentrations of livestock with corresponding localised defoliation, trampling and deposition of dung and urine (Owen-Smith, 1999). Orr (1980) in a study of the effects of sheep grazing on *Astrebla* grasslands reported that wind direction, shade availability and watering facilities all resulted in heavy utilization of the grass population.

Summer temperatures regularly exceed 30°C in the study paddocks (Clewett *et al.* 2003). In these conditions, sheep will generally need to drink at least once a day (depending on water quality) and rest for a much larger portion of the day. This will concentrate grazing pressure close to watering points and local campsites (Dawson *et al.* 2009). Consequently, ground cover around the watering point will be reduced. The effect of the prevailing wind direction on livestock distribution is well recognized (Squires, 1981). Sheep prefer to graze into the wind and this can result in the southeast ends of paddocks being well-utilised with corresponding break-down in patches and disturbance to ecological processes.

1.5.2 Topography effect

The steepness and length of the topographic slope is known to influence the distribution of grazing animals and the consequent utilisation of forage (Mueggler, 1965). Sheep and goats are known to continue to utilise pastures even when the slope exceeds 30%; however, due to the nature of these areas, the time they spend foraging generally increases because the vegetation patches are sparser. Soil type (correlated to some degree with slope) may also play a role in animal behaviour as preferred grazing areas have been linked to certain soil types and associated vegetation cover and composition (Hinch, 1999).

1.5.3 Forage availability and preferential grazing

The high spatial variation in grazing distribution in semi-arid shrublands mirrors the significant patch patterning that characterise these areas (Adler *et al.* 2001). Sheep can travel long distances in search of forage (up to 25 km per day); however, they will usually seek to optimise the amount of time spent foraging (Hinch, 1999). The specific features of different land-types which can influence grazing behaviour include: topography, soil type, species composition of vegetation/land types and vegetation structure (height, density, morphology and species composition) (Brock and Owensby, 2000; Cook, 1966; Gillen *et al*. 1984; Harris *et al.* 2002; Hunt *et al*. 2007; Pinchak *et al*. 1991; Roath and Krueger, 1982).

The capacity for dietary selection is critical particular during dry times. McMeniman *et al*. (1986a) studied the botanical and nutrient content of diets selected by sheep grazing mulga associations in western Queensland. They found that the concentrations of nitrogen, phosphorus, sodium and copper decreased substantially when pastures dried out and that in drought conditions they may be insufficient to provide for the sheep"s theoretical requirements (McMeniman *et al*. 1986a). In these circumstances there will be an increased need for the sheep to be actively seeking out sources of nutrients in different land-types and perhaps rarely visited areas of a paddock.

Palmer *et al.* (2003) report that grazing pressure can be highly localised within the landscape, and it is these grazing „hot spots" which can act as the fulcrum for patch dynamics. Specifically, they found that there was a sharp decline in the utilisation of less desirable shrubs with increasing distances from the edges of grass patches (Palmer *et al.* 2003). Thus areas with desirable forage can be focal points for grazing activity and accentuate the innate heterogeneity at a fine scale (Adler *et al.* 2005; Chapman *et al*. 2007).

Initially, certain highly preferred plant species receive most of the grazing pressure, these tend to include the perennial grasses, namely: *Thyridolepis multiculmis*, *Eragrostis eripoda*, herbaceous *Maireana* species and *Enchylaena tomentosa*. Use of species of intermediate preference increases as ungrazed tussocks and browse of the preferred species become less available (Brown 1987; Freudenberger *et al*. 1999). Vegetative material of preferred plant species tends to be re-grazed before intermediate species become well grazed. Within patches, livestock tend to select tussocks of a particular grass species or a particular tree or shrub species of a certain size class.

Animals temporarily avoid patches contaminated by faeces (Tainton, 1999). Depending on the tolerance and resilience of plant species, selective grazing may decrease their relative distribution and density, since the preferred species must compete for growth resources against other species that have not been affected by defoliation (Papachristou *et al*. 2005). Defoliation may also kill adult plants and / or reduce the amount of seed produced and added to the soil seed bank.

In semi-arid shrublands, plant regrowth is low and in the absence of stored soil moisture, there can be an extended period before there is a minimum threshold quantity of forage required to re-attract grazers. This concept is valid until the total forage supply becomes highly limited and livestock are forced to compromise diet quality in an attempt to maintain their nutritional requirements. In these instances, patch grazing will occur as livestock selectively graze the available feed supply in a hierarchical manner (Adler *et al*. 2001; Turner *et al.* 1993). This was demonstrated by a study in central Australia by Low *et al.* (1981) who found that in drought conditions cattle utilised the less preferred areas and plants instead of the desirable but depleted floodplain communities.

Low *et al*. (1980) also demonstrated that open range cattle grazing in arid central Australia occurs in a highly preferential manner. Foothill fans, woodlands and gilgaied plains received about twice the mean grazing intensity compared to the less productive mulga-perennial grass community. Low *et al*. (1980) suggested that this information could be used to achieve more uniform utilisation of landscapes by controlling grazing distribution and thereby mitigate the adverse effects of localised grazing patterns.

1.5.4 Time of day effects

Most animals have a feeding pattern, with most feeding done in the early morning and the late afternoon to early evening (Squires, 1981). There is also a feeding period around midnight (Owen-Smith, 1999). Resting and ruminating are the predominant activities over midday and at night (Owen-Smith, 1999). Ruminants may reduce their daily grazing time in the non-growing season when food quality is poorest because of the effects of high fibre content on the rate of passage of food through the digestive tract (Owen-Smith, 1999). The total length of the grazing period is likely to have more of an impact on patch patterning than the timing of the feeding period.

1.5.5 Distance-from-water effects

The distance-from-water affects grazing distribution and associated forage removal (Hunt *et al*. 2007; Martin and Ward, 1970). Permanent watering points in most paddocks grazed by sheep in semi-arid shrublands are located at least three kilometres apart (Squires, 1978); sheep are able to walk approximately seven kilometres per day without seriously compromising performance (Squires, 1976). This is heavily dependent on a suite of underlying factors, including: the breed, age and physiological condition of the animal, water quality, feed availability and ambient temperature (Squires, 1976). For a substantial part of the year the total available grazing area is determined by the permanent watering point and consequently clear distance-from-water effects have been reported (Pringle and Landsberg, 2004). During the winter growing season in the study paddock, ephemeral surface water can be present and this will increase the total area available to sheep and may reduce distance-from-water effects.

Average water intake of sheep grazing a saltbush (*Atriplex vesicaria*) pasture in western NSW can almost treble during the later part of the summer period (Squires, 1976). Sheep alter their behaviour to drink twice a day instead of just once, and as a result the daily walking distance can almost double. Increased „transit" time to and from water reduces the amount of time available for foraging and imposes substantial metabolic energy costs (Osuji, 1974). Less available energy has a general impact on the physiological cycles, cognition and behavioural interactions of individual animals. Livestock need to „factor in" this energy cost of transit to and from drinking water and this will result in increased forage demand. The forage supply often limits the extent to which sheep can compensate for the increased demand. Interestingly, Hart *et al.* (1993) found that decreasing the size of a paddock and thus reducing the distance-from-water will reduce the amount of foraging time and can improve livestock productivity.

1.5.6 Competition with other grazers

Competition for the forage resource in the study paddocks can also occur with other sheep, kangaroos and, to a lesser extent, unmanaged goats. However, kangaroos and feral goats are known to prefer areas where sheep and cattle activity is limited (Andrew and Lange, 1986; Hacker and McLeod, 2003; Wilson, 1991). Therefore, significant competition between grazers in the study paddocks is likely to occur only when there are feed shortages on a regional basis (Pople *et al.* 2007). After localised thunderstorms, kangaroos and feral goats have been known to travel long distances and compete for limited forage resources with sheep (Norbury and Norbury, 1993). This is important because kangaroos and particularly feral goats repetitively defoliate decreaser species and can significantly reduce their vigour and density (Fletcher, 1995; Gardiner, 1984). While the presence and possible impacts of non-domestic grazers on the grazing behaviour of the sheep in the study paddock is acknowledged in this thesis, it was not the focus of this thesis.

1.6 Aims of this thesis

The landscape function theory and the associated LFA methodology have largely become an accepted standard for monitoring rangelands environments. However, there have been a limited number of studies that have thoroughly examined the four principles that underpin the landscape function theory (**Section 1.3.4**).

The aim of this thesis was to test these four principles in a semi-arid shrubland environment. The overarching hypothesis of this thesis was that clear spatial patch patterns occur at a range of scales within the case study paddocks and these patterns determine the ecological functionality and resilience of the area. The hypothesis will be tested by taking a similar „three-stage" approach to the LFA methodology, whereby the study will:

1. identify the patch-interpatch components;
2. evaluate how the patch-interpatch components „fit and work together"; and
3. investigate the impact of grazing disturbance on the different patch-interpatch components.

This study provides the present users of landscape function theory and the related LFA methodology with a greater understanding of the principles that underpin the theory and methodology and potentially lead to improved management decisions. This great understanding was sought through experiments conducted within four paddocks on two properties in the semi-arid shrublands of WA.

1.7 Content of this thesis

This thesis consists of seven chapters. **Chapter 2** introduces the rangelands and the specific study area in terms of its climatic conditions, soil and vegetation and grazing management history. **Chapters 3** to **6** present the results of the field work conducted in the four case study paddocks in the study area. **Chapter 7** concludes with an overall discussion of the key findings arising from this study and their implications for landscape function theory and sustainable management of the rangelands (**Figure 1-6**).

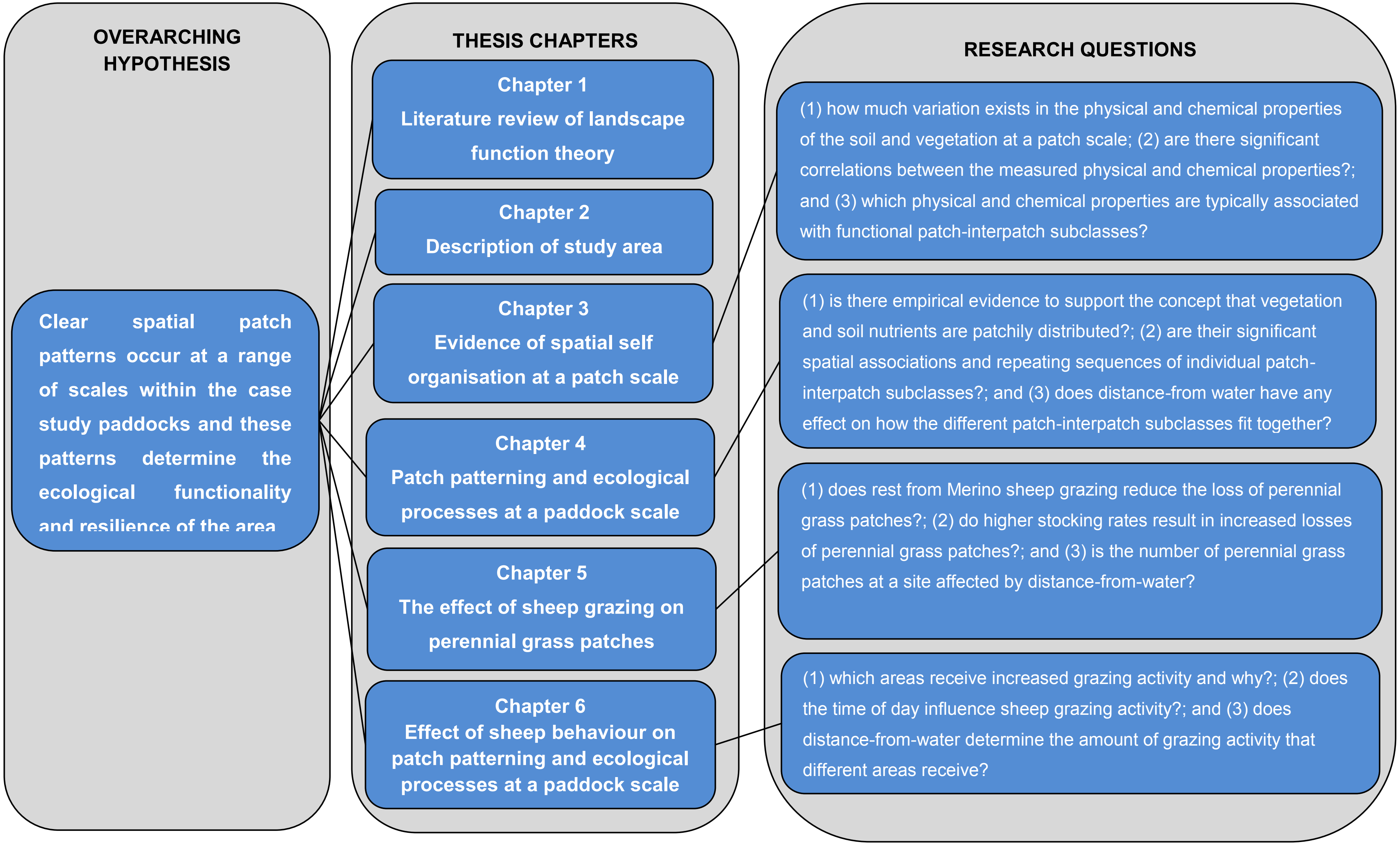
Chapter 3 investigates the components of the landscape and sought evidence of patchiness and a gradient of functional and dysfunctional patches. This was achieved by answering three main questions: (1) how much variation exists in the physical and chemical properties of the soil and vegetation at a patch scale; (2) are there significant correlations between the measured physical and chemical properties?; and (3) which physical and chemical properties are typically associated with functional patch-interpatch subclasses? The physical and chemical properties that were measured at a patch scale collectively indicate the relative capacity of a patch-interpatch to capture and retain water and nutrients.

Chapter 4 uses the information that was developed in Chapter 3 to examine how the landscape components (i.e. patches-interpatches) „fit and work" together. Chapter 4 investigates three specific questions: (1) is there empirical evidence to support the concept that vegetation and soil nutrients are patchily distributed; (2) are their significant spatial associations and repeating sequences of individual patch-interpatch subclasses?; and (3) does distance-from water have any effect on how the different patch-interpatch subclasses fit together? The chapter explores the implications of patch patterning in terms of the landscape"s relative capacity to efficiently capture, retain and cycle water and nutrients.

A fundamental assumption of landscape function theory is that adverse seasonal conditions and overgrazing are the two key factors which can drive an ecosystem towards the dysfunctional end of the gradient. Therefore, **Chapters 5** and **6** examine the impact of seasonal conditions and grazing by conducting two short-term studies. **Chapter 5** investigated the impact of sheep grazing on the mortality rate of perennial grasses. Perennial grass plants were selected due to the short timeframe available and their increased sensitivity to grazing compared to perennial shrub patches. Specifically, Chapter 5 answers three questions: (1) does rest from Merino sheep grazing during the 12-month period reduce the loss of perennial grass plants?; (2) do higher stocking rates result in increased losses of perennial grass plants?; and (3) is the number of perennial grass plants at a site affected by distance-from-water? Chapter 5 concludes by discussing the impacts of grazing pressure on the perennial grass populations in the context of the four principles of landscape function theory.

Limited information is available regarding the grazing behaviour of sheep in semi-arid environments. Understanding grazing behaviour will assist pastoralists to manage grazing pressure in a more precise and timely manner and thereby apply principle four of landscape function theory (i.e. restoration or replacement of missing or ineffective processes in the landscape will improve soil surface conditions and soil habitat quality). Therefore, **Chapter 6** investigates the grazing preferences of Merino sheep. Specifically, Chapter 6 answers three main questions: (1) which areas receive increased grazing activity and why; (2) does the time of day influence sheep grazing activity? and (3) does distance-from-water determine the amount of grazing activity that different areas receive?

The final Chapter (**Chapter 7**) synthesises the main results of **Chapters 3** to **6** and discusses them in the context of the suitability of the landscape function theory and the LFA methodology as a way to view and monitor the rangelands. This information will contribute to resolving the immediate challenge of the pastoral industry and other land managers have in rebuilding ecologically functional landscapes in the rangelands. To optimise the investment in any restoration effort, whether it is for pastoral production, nature conservation, or mine rehabilitation, it is critical that land managers / administrators are equipped with a detailed understanding of the inherent patch patterning and key drivers of ecological processes.



OVERARCHING HYPOTHESIS

Clear spatial patch patterns occur at a range of scales within the case study paddocks and these patterns determine the ecological functionality and resilience of the area

THESIS CHAPTERS

Chapter 1
Literature review of landscape function theory

Chapter 2
Description of study area

Chapter 3
Evidence of spatial self organisation at a patch scale

Chapter 4
Patch patterning and ecological processes at a paddock scale

Chapter 5
The effect of sheep grazing on perennial grass patches

Chapter 6
Effect of sheep behaviour on patch patterning and ecological processes at a paddock scale

RESEARCH QUESTIONS

(1) how much variation exists in the physical and chemical properties of the soil and vegetation at a patch scale; (2) are there significant correlations between the measured physical and chemical properties?; and (3) which physical and chemical properties are typically associated with functional patch-interpatch subclasses?

(1) is there empirical evidence to support the concept that vegetation and soil nutrients are patchily distributed?; (2) are their significant spatial associations and repeating sequences of individual patch-interpatch subclasses?; and (3) does distance-from water have any effect on how the different patch-interpatch subclasses fit together?

(1) does rest from Merino sheep grazing reduce the loss of perennial grass patches?; (2) do higher stocking rates result in increased losses of perennial grass patches?; and (3) is the number of perennial grass patches at a site affected by distance-from-water?

(1) which areas receive increased grazing activity and why?; (2) does the time of day influence sheep grazing activity?; and (3) does distance-from-water determine the amount of grazing activity that different areas receive?

Figure 1-6: Structural outline of thesis

Chapter 2

A description of the study area

Plate 2-1: Hardpan washplains, study area, March 2007

Photo: Mark Alchin

2.1 Abstract

Australia‟s rangelands encompass approximately 80% of the continent and generate significant wealth through a range of industries. The rangelands comprise four major ecosystem types, these are: grasslands, shrublands, woodlands and savanna. Landscape function theory is generally been adopted as the main approach used to interpret and assess patch patterning and ecological processes in the shrublands. The aim of this thesis was to test the four principles that underpin the landscape function theory in a semi-arid shrubland environment. This chapter comprises a review of the study area in terms of its climate, soils and vegetation and grazing management history. Four commercially grazed paddocks were selected for this study and were located in the lower Murchison region of WA. These paddocks ranged in size from 4,504 to 5,832 ha and comprised of *Acacia* sandplains, alluvial plains, hardpan washplains and granitic shrublands. The soil and vegetation in the paddocks was generally considered to be in fair to good condition.

2.2 Australia’s rangelands and the study area

Australia‟s rangelands encompass approximately 80% of the continent and generate over $90 billion per annum through a range of industries (Rangelands Australia, 2011) (**Figure 2-1**). Major industries include: mining, pastoralism, tourism, nature conservation, Indigenous heritage and training, defence training and carbon sequestration. Despite this large land mass, the rangelands are home to only 3% of Australia's total population. Pastoralism is the predominant land-use with approximately 6,000 pastoral enterprises which occupy 58% of the rangelands. Approximately 18% of the rangelands are under Aboriginal ownership and management (Rangelands Australia, 2011).

Australia's rangelands provide habitat to a significant number of rare, threatened and endangered flora and fauna species. The area has approximately 1,800 plant species and 605 vertebrate species, and includes five World Heritage sites (Rangelands Australia, 2011). The Australian rangelands comprise four broad ecosystem types: grasslands, shrublands, woodlands and savanna. Historical and current exploitation of the rangelands has led to substantial ecological degradation in many areas (McKeon *et al*. 2004). This has led to widespread erosion, soil salinity, loss and endangerment of plant and animal species, the spread of invasive species and a significant reduction in the productive potential of Australia‟s rangelands.

Figure 2-1: Geographical spread of Australia's rangelands (reproduced from Rangelands Australia, 2011)

Shrublands occupy approximately 23% of Australia‟s rangelands and are a major feature of the Gascoyne-Murchison region in Western Australia (WA) (Rangelands Australia, 2011). Large parts of the semi-arid shrublands of the Gascoyne-Murchison region are similar to Lake Mere in western New South Wales which is where the landscape function theory was developed (i.e. Mulga shrubland with < 400 mm rainfall) (Ludwig *et al*. 1997; Payne *et al*. 1998). It is for this reason that this region was selected as the study area for this thesis (**Figure 2-2**).

Figure 2-2: Gascoyne-Murchison region of Western Australia

This thesis took a case study approach and collaborated with two pastoral businesses (Barnong and Carlaminda Stations). Barnong Station (referred to as study site 1) and Carlaminda Station (referred to as study site 2) are located in the lower part of the Gascoyne-Murchison region and are approximately 500 km northeast of Perth (**Figure 2-3**). In consultation with the owners of each pastoral business, two case study paddocks were selected from each pastoral lease. The criteria for the selection of the study paddocks included: good vehicle access, secure stock-proof fencing, wellwatered, limited number of different land-systems, land-systems were representative of the region, and the management of these paddocks was similar to the approach applied across the whole pastoral lease.

Within the Sandstone-Yalgoo Paynes Find survey area there are 76 different land-systems. The majority of these land-systems represent less than 1% of the total survey area. Consequently, heterogeneity is an inherent feature of the region. The case study paddocks encompassed a maximum of six different land-systems some of which represent a comparatively high proportion of the survey area (namely Kalli, Tindalarra and Challenge represent 5.2%, 4.6% and 3.9% of the survey area respectively). The livestock carrying capacity of the paddocks were generally representative of the area (further detail provided in **Sections 2.5** and **2.6**).

A case study approach was taken instead of a replicated design because it was impossible to conduct a replicated experiment at a paddock scale due to the heterogeneity of the area. While acknowledging the statistical limitations of this approach, I envisaged that the results would make a meaningful contribution to the understanding of patch-interpatch heterogeneity at a paddock scale.

This thesis did not seek to draw any definitive comparisons between the four case study paddocks. Rather, the paddocks acted as individual case studies and provided an opportunity to test the four principles of the landscape function theory. A detailed description of the individual paddocks is provided in the following sections.

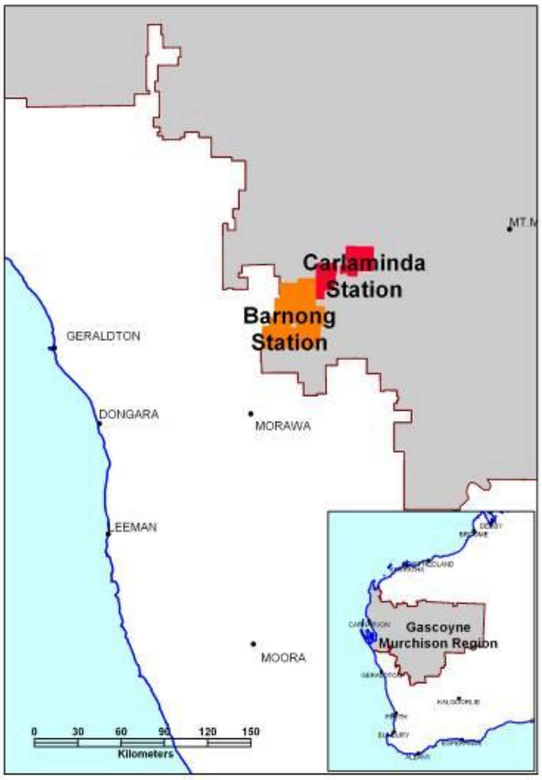
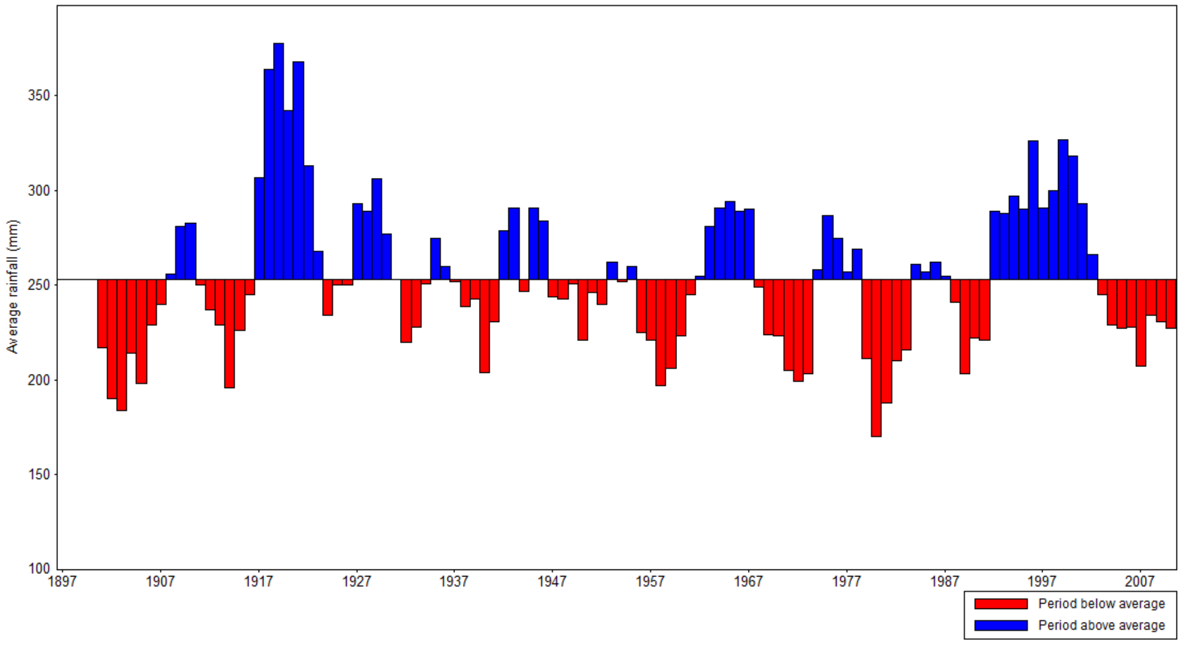


Figure 2-3: Location of study sites

2.3 Climate and seasonal conditions of the study area

The climate of the study area is semi-arid. The annual average rainfall is 253 mm and the area has an average of 50 rain days per year (Clewett *et al*. 2003). Summer rains associated with cyclonic disturbances occur infrequently and can generate significant amounts of vegetative biomass; however, the winter season is generally more reliable. Rainfall is very cyclical and transitions from extended periods of below-average to above-average rainfall (**Figure 2-4**).

Summers are usually dry and hot with mean temperatures ranging from 18 to 37°C and winters are usually cool with temperatures ranging from 6 to 24°C (Clewett *et al*. 2003). The mean relative humidity ranges between 17% (summer) and 49% (winter). By the end of the dominant winter growing season, there is a less than a 30% probability (3 out of 10 years) of receiving sufficient rainfall to generate a significant germination event (Clewett *et al*. 2003) (see footnote[2]). The rainfall during the field work component of this thesis (2006 to 2008) was generally below average and much of the study region was in drought conditions (**Figure 2-5**). February 2008 was the exception when 128 mm of rainfall was received by the study area.



Source: Rainman StreamFlow

Figure 2-4: Five year moving average of annual rainfall at Yalgoo Post Office (1897 to 2010) (Yalgoo is 15 km northeast of the northern boundary of study site 1) (Clewett *et al*. 2003)

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[2] A germination event was defined as receiving 50 mm rainfall over a 3 day period within one calendar year.

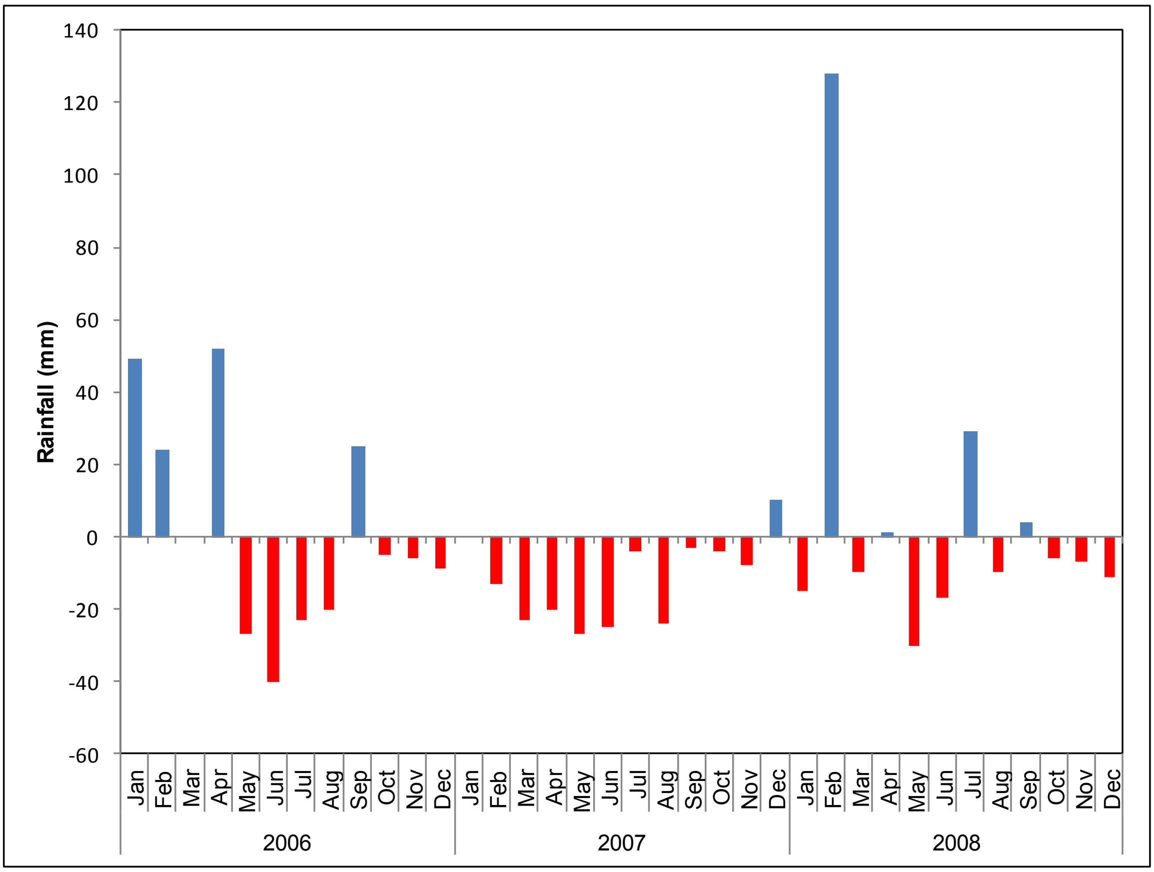

Figure 2-5: Monthly rainfall relative to the mean (+/-) at study area (Yalgoo Post Office) during the experimental period (2006 to 2008) (Clewett *et al*. 2003)

2.4 Soil and vegetation

The study paddocks were located within the Yalgoo-Paynes Find Area. An extensive survey of the soil and vegetation within this area was conducted by the Department of Agriculture WA between 1992 and 1993 (Van Vreeswyk *et al*. 1998). This survey mapped the region based on a number of land-systems. A land-system is a recurring pattern of soil, vegetation, and topography that can be distinguished from an aerial photograph or satellite imagery. The survey also assessed the condition of the soil and vegetation based on the occurrence of erosion, species diversity, projected foliar cover of the overstorey and understorey plants. Therefore, the land-system classifications that were developed by the Yalgoo-Paynes Find survey were used in this study.

2.5 Study site 1 (Barnong Station) - Case study paddocks 1 and 2

The two paddocks selected from study site 1 were Jacks Well (Paddock 1) and Five Mile (Paddock 2) (**Figure 2-6**).

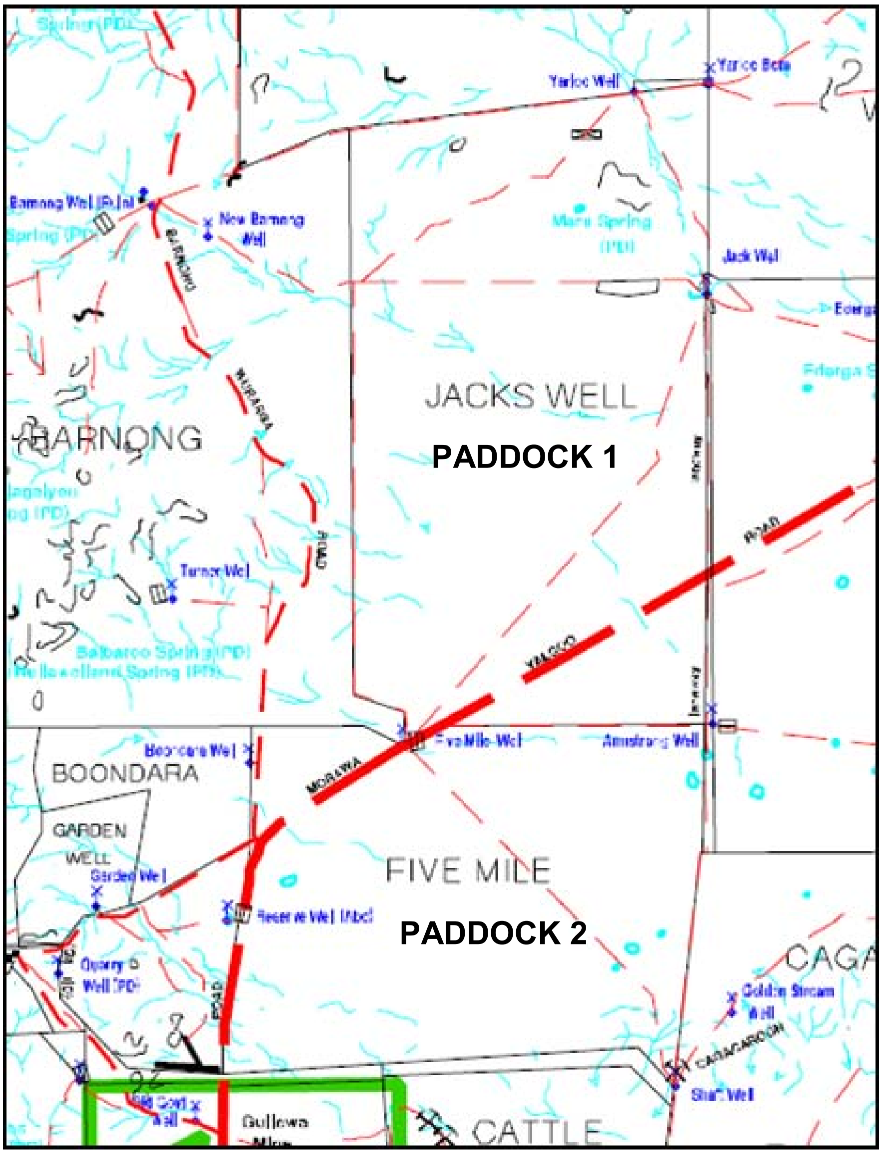

Figure 2-6: Layout of case study Paddocks 1 and 2

Paddock 1 is approximately 5,356 ha and contains four watering points that are equipped with self-mustering yards. Paddock 1 consists of four land-systems (listed in order of dominance):

- **Kalli** (red sandplains supporting *Acacia linophylla* [see footnote[3]] shrublands with perennial grasses);
- **Challenge** (gently, undulating gritty-surfaced plains, occasional granite hills, tors and low breakaways, with *Acacia* shrublands);
- **Tindalarra** (hardpan plains supporting *Acacia* shrublands with sparse drainage channels and associated drainage floors supporting *Atriplex* / *Maireana* shrubs under *Acacia xiphophylla*); and
- **Norie** (granite hills with exfoliating domes and extensive tor fields supporting *Acacia* shrublands).

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[3] Plant scientific names used throughout this thesis are based on the classification provided in Mitchell and Wilcox, 1994.

A summary of the land-systems in Paddock 1 based on the most recent land survey is provided (**Table 2-1**) (Van Vreeswyk and Godden, 1998). The topography of Paddock 1 is characterised by a gentle relief in most areas. The northern end of the paddock is slightly higher than the southern end. The paddock has good areas of shade for the sheep due to the high amount of shrub cover.

The recommended carrying capacity (RCC) is expressed in units of Dry Sheep Equivalent Days per hectare per 100 mm of rainfall (DDH/100 mm). DDH/100 mm is defined as the number of Dry Sheep Equivalent (DSE) Days per hectare that are available for every 100 mm of rainfall that is received. DDH/100 mm is a unit which is used to measure carrying capacity and stocking rate that attempts to take account of rainfall variability. To calculate the carrying capacity in DDH/100 mm on a per paddock basis the total number of DSEs that a paddock can sustainably carry was multiplied by 365 days (a whole year) and then divided by the size of the paddock (hectares) and then divided by the total annual rainfall and multiplied by 100 (e.g. 1000 DSEs multiplied by 365 days (for a whole year) divided by 15,000 ha paddock divided by 250 mm rainfall multiplied by 100 mm = 9.7 DDH/100 mm).

The recommended carrying capacity for each paddock is also provided in the more traditional unit of HA/DSE (the number of hectares required to support one dry sheep equivalent for one year) for the benefit of readers who are more familiar with this term.

Paddock 1 has traditionally been stocked with Merino ewes and lambs over the autumn-winter period (May to September) when the probability of rainfall and available forage is at its highest. The paddock has rarely been used over the summer period (November to February) because of the low incidence of summer rain and the inherently low availability of perennial forage. The vegetation in the paddock responds very well to late autumn and winter rains (May to August) and generates a large mass of annual forage in the form of everlasting daisies (e.g. *Angianthus milnei*, *Brachycome ciliocarpa* and *Cephalipterum drummondii*). Based on historical stocking rate records from 1991 to 2007, it was estimated Paddock 1 has maintained an annual average of 59% above its recommended livestock carrying capacity.

Table 2-1: Paddock 1 summary of land-systems and livestock carrying capacity

Land-system	**Paddock area (ha)**	**Proportion of paddock area (%)**	**Proportion of vegetation in fair to good condition (%)**	**Estimated area affected by erosion (%)**	**RCC (DDH/100 mm)***	**RCC (HA/ DSE)**
Kalli	3,789	70.7	100	0	6.3	20
Tindalarra	1,036	19.3	72	6	9.6	12
Challenge	469	8.8	100	0	7.6	16
Norie	62	1.2	100	0	6.3	20
TOTAL	**5,356**					

***RCC is recommended carrying capacity.**

Paddock 2 is very similar to Paddock 1 in terms of its soil and vegetation and infrastructure design. The paddock is well-fenced and has three watering points fitted with self-mustering yards. The paddock consists of five land-systems (listed in order of dominance):

- **Kalli** (red sandplains supporting *Acacia linophylla* shrublands with perennial grasses);
- **Violet** (undulating stony and gravelly plains and low rises supporting *Acacia* shrublands);
- **Tindalarra** (hardpan plains supporting *Acacia* shrublands with sparse drainage channels and associated drainage floors supporting saltbush-bluebush shrubs under *Acacia xiphophylla*);
- **Challenge** (gently, undulating gritty-surfaced plains, occasional granite hills, tors and low breakaways, with *Acacia* shrublands); and
- **Gabanintha** (greenstone ridges and hills supporting sparse *Acacia* shrublands).

A summary of the land-systems in Paddock 2 based on the most recent land survey is provided (**Table 2-2**) (Van Vreeswyk and Godden, 1998). The topography of Paddock 2 is characterised by a gentle to moderate relief. The eastern end of the paddock is generally higher than the western end due to a sloping granitic plain. The paddock has good areas of shade for the sheep due to the high amount of shrub cover.

The southeast corner of Paddock 2 is known to receive higher grazing pressure than the remainder of the paddock given the dominance of some highly preferred shrubs and, to a lesser extent, slightly higher number of perennial grasses. The prevailing southeast wind is also a factor. The paddock has been stocked in a similar manner to Paddock 1 with a winter-grazing regime. Based on historical stocking rate records from 1991 to 2007, it was estimated that the paddock has maintained an annual average of 100% above its recommended carrying capacity (**Figure 2-7**). The records indicate that stocking rate has generally been adjusted to the prevailing rainfall conditions over time, except for Paddock 1 between 2005 and 2006.

Table 2-2: Paddock 2 summary of land-systems and livestock carrying capacity

Land-system	Paddock area (ha)	Proportion of paddock area (%)	Proportion of vegetation in fair to good condition (%)	Estimated area affected by erosion (%)	RCC (DDH/100 mm)*	RCC (HA/ DSE)
Kalli	3,595	79.8	100	0	6.3	20
Violet	259	5.8	75	0	7.5	16
Tindalarra	249	5.5	72	6	9.6	12
Challenge	213	4.7	100	0	7.6	16
Gabanintha	188	4.2	67	0	5.8	20
TOTAL	**4,504**					

***RCC is recommended carrying capacity.**

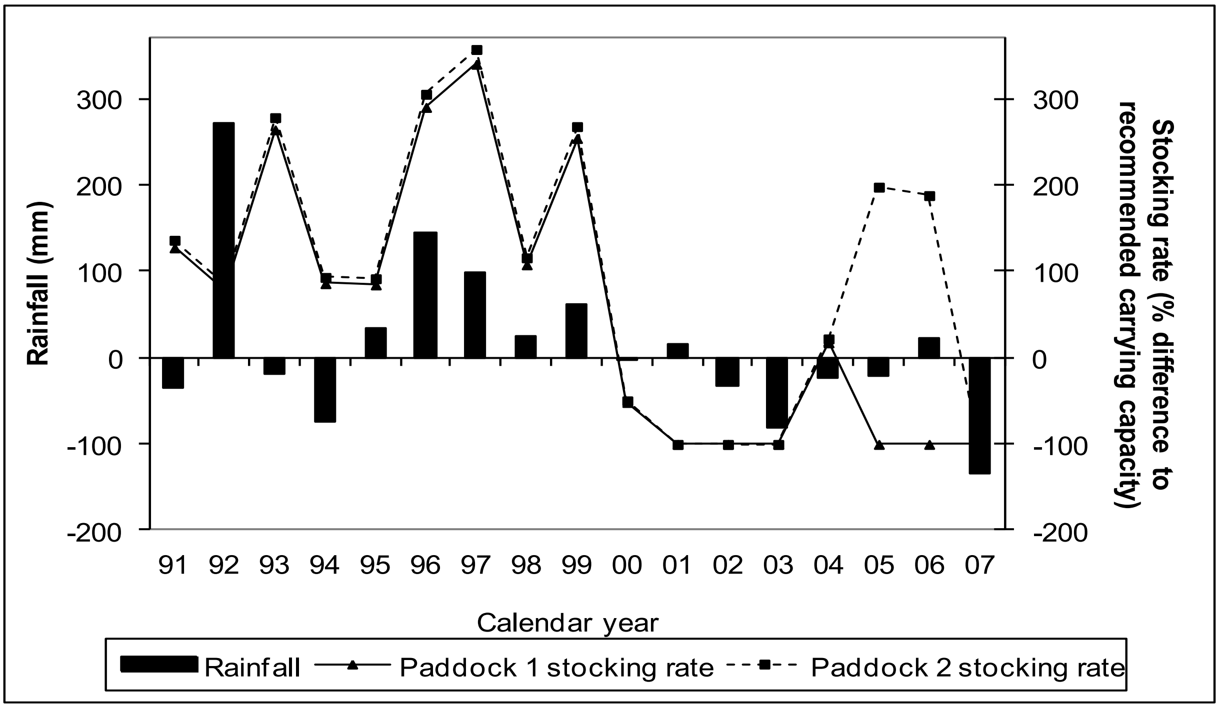

Figure 2-7: Stocking rate and rainfall relative to the long-term averages between 1991 and 2007

2.6 Study site 2 (Carlaminda Station) – Case study paddocks 3 and 4

The two paddocks selected from study site 2 were Walla Walla (Paddock 3) and Millegally (Paddock 4) (**Figure 2-8**).

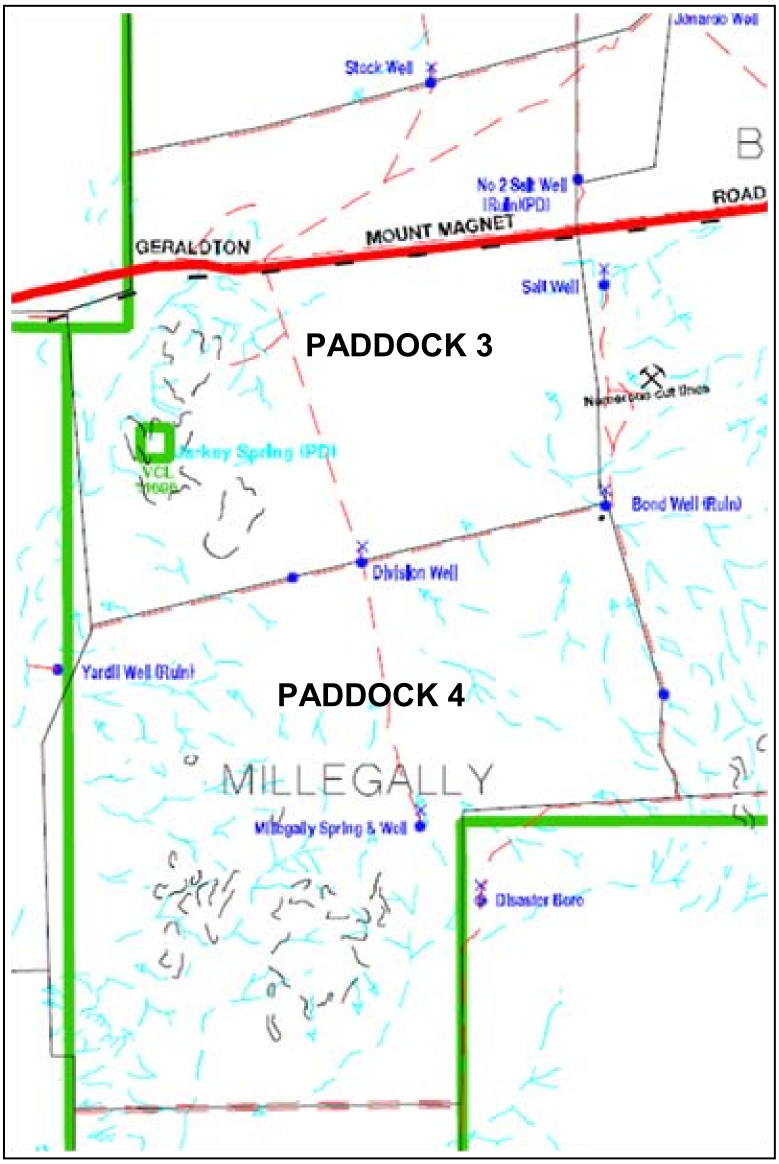

Figure 2-8: Layout of case study Paddocks 3 and 4

Paddock 3 (Walla Walla paddock) is approximately 5,575 ha, is well-fenced and contains four watering points that are fitted with self-mustering yards. In contrast to Paddocks 1 and 2, the large area of alluvial saltbush plains in Paddock 3 provides adequate forage for sheep over the summer period in years of above-average rainfall. The paddock consists of six different land-systems (listed in order of dominance):

- **Racecourse** (partly calcreted alluvial plains);
- **Monk** (very gently inclined wash plains with occasional wanderrie banks in lower areas);
- **Challenge** (gently, undulating gritty-surfaced plains, occasional granite hills, tors and low breakaways, with *Acacia* shrublands);
- **Mileura** (calcrete platforms and alluvial plains with saline soils);
- **Gabanintha** (greenstone ridges and hills supporting sparse *Acacia* shrublands); and
- **Nerramyne** (plains and low rises on weathered granite above sandy drainage plains).

A summary of the land-systems in Paddock 3 based on the most recent land survey is provided (**Table 2-3**) (Van Vreeswyk and Godden, 1998). The topography of Paddock 3 is characterised by a low relief. The area generally drains to the southern end of the paddock through diffuse, flat plains. Good shade cover is patchy throughout the paddock and is generally governed by the scattered groves of *Acacia* spp.

Paddock 3 has been continuously grazed and has generally maintained the same number of Merino sheep in the paddock from 1991 to 2007 (500 ewes and 300 lambs). Based on historical stocking rate records from 1991 to 2007, it was estimated that Paddock 3 has maintained an annual average of 28% above the recommended carrying capacity.

Table 2-3: Paddock 3 summary of land-systems and livestock carrying capacity

Land-system	Paddock area (ha)	Proportion of paddock area (%)	Proportion of vegetation in fair to good condition (%)	Estimated area affected by erosion (%)	RCC (DDH/100 mm)*	RCC (HA/ DSE)
Racecourse	2,693	48.3	100	0	17.8	7
Monk	1,026	18.4	90	0	7.8	16
Challenge	841	15.1	100	0	7.6	16
Mileura	680	12.2	100	0	13.8	7
Gabanintha	316	5.7	98	0	5.8	20
Nerramyne	19	0.3	100	0	6.1	20
TOTAL	**5,575**					

***RCC is recommended carrying capacity.**

Paddock 4 (Millegally paddock) is approximately 5,831 ha and is well-fenced and contains three watering points fitted with self-mustering yards. The paddock comprises of a number of land-systems that can provide adequate amounts of forage during both the summer and winter periods; however, it is generally more suited to winter-grazing due to the larger proportion of granitic undulating plains. The paddock comprises six different land-systems (listed in order of dominance):

- **Challenge** (gently, undulating gritty-surfaced plains, occasional granite hills, tors and low breakaways, with *Acacia* shrublands);
- **Nerramyne** (plains and low rises on weathered granite above sandy drainage plains);
- **Monk** (very gently inclined wash plains with occasional wanderrie banks in lower areas);
- **Kalli** (red sandplains supporting *Acacia linophylla* shrublands with perennial grasses);
- **Gabanintha** (greenstone ridges and hills supporting sparse *Acacia* shrublands); and
- **Tindalarra** (hardpan plains supporting *Acacia* shrublands with sparse drainage channels and associated drainage floors supporting saltbush-bluebush shrubs under *Acacia xiphophylla*).

A summary of the proportional area of the land-systems in Paddock 4 based on the most recent land survey is provided (**Table 2-4**) (Van Vreeswyk and Godden, 1998). The topography of Paddock 4 is perhaps the most variable compared to the other paddocks. A raised granite dome is located near to the centre of the paddock and the remaining area is characterised by sloping plains with low relief. The paddock has large areas with good shade, except for on the granite dome, where shrub cover is low.

Paddock 4 has been continuously grazed with approximately the same number of Merino sheep in the paddock from 1991 to 2007 (350 ewes and 210 lambs). Based on these historical stocking rate records, it was estimated that Paddock 4 has maintained an annual average of 58% above the recommended carrying capacity (**Figure 2-9**).

Table 2-4: **Paddock 4 summary of land-systems and livestock carrying capacity**

Land-system	Paddock area (ha)	Proportion of paddock area (%)	Proportion of vegetation in fair to good condition (%)	Estimated area affected by erosion (%)	RCC (DDH/100 mm)*	RCC (HA/ DSE)
Challenge	2,355	40.4	100	0	7.6	16
Monk	954	16.4	90	0	7.8	16
Gabanintha	782	13.4	98	0	5.8	20
Nerramyne	754	12.9	100	0	6.1	20
Tindalarra	529	9.0	78	6	9.6	12
Kalli	457	7.9	100	0	6.7	20
TOTAL	**5,831**					

***RCC is recommended carrying capacity.**

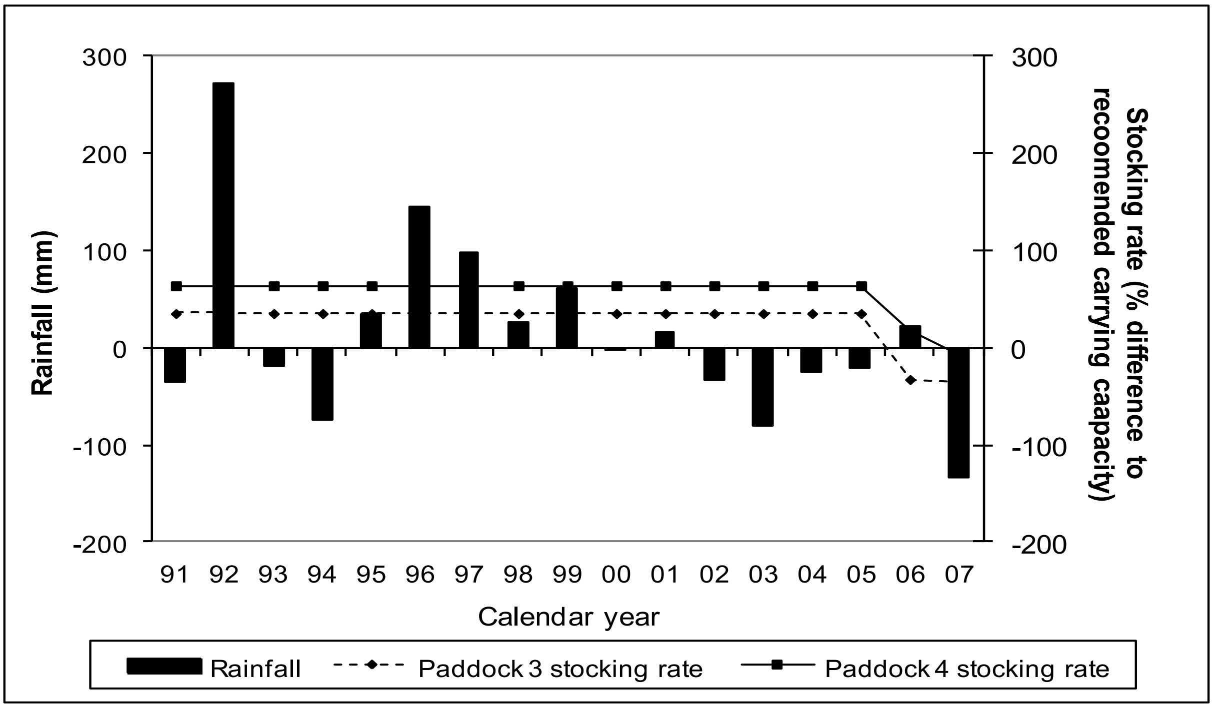

Figure 2-9: Stocking rate and rainfall relative to the long-term averages between 1991 and 2007

2.7 Grouping of land-systems within the study paddocks based on land-type

For the purposes of data analysis in Chapters 3 to 6, the 10 different land-systems within the study paddocks were grouped into four major land-types. This grouping into land-types was done on the basis of the similarities in landforms, soils, vegetation and drainage patterns between the different land-systems (**Table 2-5**) (based on information from Burnside, *et al.* 1995; Payne, *et al.* 1998).

Table 2-5: Grouping of land-systems into land-types

Study land-types	Study paddock land-systems
Granitic shrublands (GS)	Challenge, Norie, Gabanintha, Nerrayme, Violet
Acacia sandplains (SP)	Kalli
Hardpan washplains (HP)	Tindalarra, Monk
Alluvial plains (AP)	Racecourse, Mileura

2.8 Summary of case study paddocks

Paddock sizes and rangeland condition were similar among them all (**Table 2-6**). There were substantial differences in the recommended carrying capacities as well as the actual averaged annual stocking rates that were maintained from 1991 to 2007. **Chapter 3** investigates the components of the landscape within these case study paddocks and sought evidence of self-organisation and a gradient of functional and dysfunctional patches.

Table 2-6: Summary table of case study paddocks

Study site	Study paddock	Paddock size (ha)	Dominant land-type	% of paddock in fair-good condition	Recommended carrying capacity (DDH/100 mm)*	% above the recommended carrying capacity 1991 to 2007**
1 (Barnong)	Paddock 1 (Jacks Well)	5,356	*Acacia* sandplains	95	7.1	59
	Paddock 2 (Five Mile)	4,504	*Acacia* sandplains	96	6.6	100
2 (Carlaminda)	Paddock 3 (Walla Walla)	5,575	Alluvial plains	98	13.2	28
	Paddock 4 (Millegally)	5,832	Granitic shrublands	96	7.3	58

***Based on a weighted average of the proportional areas of each land-system.**

****Based on a weighted average of the individual carrying capacities of each land-system in the paddock.**

*****The period from 1991 to 2007 was selected as it was the period within which stocking rate figures obtained from the pastoralists were the most accurate. Prior to 1991 business records were less detailed.**

Chapter 3

Evidence of patchiness and a gradient of ecological functionality at a patch-scale

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Plate 3-1: Granitic shrublands, study area, September 2006
Photo: Mark Alchin

3.1 Abstract

The first and third principles of landscape function theory state that patchiness can be characterized by the patch size, orientation, spacing and soil surface condition and deviations from the „characteristics" or „natural" patchiness are seen as degrees of dysfunctionality. To test these principles, this chapter examined the landscape components in the case study paddocks to find evidence of patchiness and a gradient of highly functional and highly dysfunctional patches. This was achieved by measuring a number of physical and chemical properties within a range of different patch-interpatch subclasses.

A total of 11 different patch-interpatch subclasses were selected (P1 to P11). These patch-interpatch subclasses were selected because they represented a hypothetical gradient of ecological functionality at a patch-scale. The properties that were measured within each of the patch-interpatch subclasses were: soil respiration (n = 16), soil carbon (n = 4), soil nitrogen (n = 4), soil bulk density (n = 8), soil infiltration (n = 3), plant species richness (n = 7,887) and patch size (n = 7,887). These properties were chosen because they are indicators of the relative capacity of the different patch-interpatch subclasses to capture and retain water and nutrients.

The results in this chapter substantiate the first, second and third principles of landscape function theory. Significant variation ($P<0.05$) between the measured properties of the 11 different patch-interpatch subclasses was detected. Heterogeneity within individual patches was also significant ($P<0.05$) and the greatest variation occurred within highly functional patches (i.e. P1). Highly functional patch subclasses (P1, P2) had:

- higher soil respiration rates (> 45%) ($P<0.05$), this indicates these subclasses are more biologically active;
- more than twice the number of perennial plant species within the patch ($P<0.05$);
- higher soil infiltration rates (> 70% more rapid) ($P<0.05$), this indicates these subclasses can capture more rainfall and surface runoff when it occurs; and
- five times more carbon and nitrogen, this indicates these subclasses have a disproportionate amount of the available nutrients.

3.2 Introduction

Semi-arid landscapes are biologically active and require all of their components, at a range of spatial scales, to relate efficiently in order to remain ecologically functional. Patch patterns are influenced by a number of biogeochemical processes (e.g. photosynthesis, soil respiration, litter fall and decay, aeolian and fluvial erosion, mineralization) that can alter the local edaphic and vegetative state and structure of a patch or an interpatch zone. Local biogeochemical processes and interactions between patches and interpatches may have a cumulative impact on ecosystems as the scale becomes increasingly coarse. Hence, patch-scale heterogeneity or patchiness is the first step towards investigating the patterns and processes that occur within the study paddocks.

Within this thesis, a patch is defined as a spatial area occupied by a dominant individual tree, shrub, or perennial grass that act as an obstruction to water flow. In this thesis, an interpatch is defined as a spatial area between patches occupied by varying amounts of organic debris (e.g. logs, litter) and typically acts as a run-off zone.

This chapter sought to examine the components of the landscape and find evidence of patchiness at a patch-scale. It also sought to find a gradient of highly functional and highly dysfunctional patches. The chapter addressed three main questions: (1) how much variation exists in the physical and chemical properties of the soil and vegetation at a patch-scale; (2) are there significant correlations between the measured physical and chemical properties?; and (3) which physical and chemical properties are typically associated with functional patch-interpatch types?

The physical and chemical properties that were measured at a patch-scale collectively indicate the relative capacity of a patch-interpatch to capture and retain water and nutrients. Therefore, this information identifies the differences in ecological functionality at a patch-scale and will be used to test the application of the first and third principle of landscape function theory in the study area:

First principle: Patchiness can be characterized by the patch size, orientation, spacing and soil surface condition.

Third principle: Deviations from the „characteristics" or „natural" patchiness are seen as degrees of dysfunctionality, and there is a long gradient from highly functional to highly dysfunctional patches.

3.3 Methods

3.3.1 Study area

The measurement of the physical and chemical properties on the different patches-interpatches subclasses was conducted in four study paddocks (refer to **Sections 2.5** and **2.6** for a description of the study paddocks).

3.3.2 Classification approach for patch-interpatch subclasses

Hierarchical theory is used to explain the concept that ecosystems function at a range of spatial scales and it suggests that processes and corresponding outcomes (e.g. loss of topsoil) are slower at higher levels than at lower levels of scale (O"Neill *et al*. 1989). Researchers have found that disturbances that occur at an individual patch-scale have the potential to collectively impact on processes on a patch mosaic (unit of land containing contiguous patches), landscape, regional, national and even at a global scale (Holm, 2000; O"Neill, 1988; Schlesinger and Pilmanis, 1998).

Studies focusing on landscape processes at a patch-scale tend to broadly classify the individual components of the landscape as either patches or interpatches (Aguiar and Sala, 1999; Holm *et al*. 2002; Ludwig *et al.* 2005; Ludwig *et al*. 1997). Pickup (1985) was instrumental in highlighting a more detailed stratification of the land surface based on geomorphic characteristics. These included six different types of runoff zones, four different types of transfer zones and three different types of sink zones (Pickup, 1985). The monitoring framework of LFA classifies patches and interpatches based on soil surface condition (Tongway *et al*. 2003). Patch types are then assessed based on 11 characteristics that are used to provide a relative ranking of patches" surface stability, water infiltration and nutrient cycling capacities (see footnote[4]). Burrow (1972) also made a contribution to understanding the spatial patterns of semiarid communities.

Not all patches capture and retain water and nutrients in the same way. Therefore, they are unlikely to make equal contributions to the ecological processes. Any reporting on the simple proportions of patches to interpatches in the study paddocks may provide a less precise assessment than if further subclasses of patches and interpatches are recorded. The creation of more specific subclasses of patches-interpatches may provide enhanced insight into the structure of communities and their ecological processes. In this context, after I completed an initial visual reconnaissance of the four study paddocks, I created a total of eleven different subclasses of patches and interpatches (**Table 3-1**). These were stratified into four key categories:

(1) woody vegetation > three metres in height,
(2) woody vegetation < three metres in height,
(3) perennial grass tussocks, and
(4) interpatch areas.

These categories were intended to represent four intuitive „subgradients" of functionality at a patch-scale, namely: P1 to P3; P4 to P6; P7 to P8; and P9 to P11.

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[4] These characteristics are: rain-splash protection; perennial vegetation cover; litter; cryptogam cover, crust brokenness, soil erosion type and severity; soil erosion type and severity; deposited materials; soil surface roughness; surface nature; slake test; and soil surface texture.

The parameters used in the classification of the patches and interpatches were:

- the height of the dominant perennial plant species;
- the percentage of bare ground beneath the dominant species crown;
- the density and diversity of other perennial plants within the same patch;
- the presence / absence of cryptogamic cover; and
- the presence / absence, type and degree of erosion.

If more than one type of vegetation occurred within a patch (i.e. perennial grass *cf* perennial shrub) the vegetation which was the „dominant" feature of the patch would determine its patch-interpatch subclass classification. The individual size of a total of 7,887 patches was measured and the mean values for each of the subclasses were calculated.

Table 3-1: **Classification of the different patch- interpatch subclasses**

Patch-interpatch category	Patch- interpatch subclass ID code	Patch-interpatch description	Representative plate
Woody shrub > 3 metres in height	**P1**	High order patch. Tall shrub > 3 metres in height. Soil surface below crown is < 25% bare-ground. Two or more perennial plant species within the patch. Nil erosion. Cryptogams present.	
	P2	High order patch. Tall shrub > 3 metres in height. Soil surface below crown is 25 to 75% bare-ground. Two or more perennial plant species within the patch. Minor erosion may be present Cryptogams may be present.	
	P3	Low order patch. Tall shrub > 3 metres in height. Soil surface below crown is > 75% bare-ground. Less than two perennial plant species within the patch. Signs of active erosion present/hardened stripped soil surface. Cryptogams generally absent.	
Woody shrub < 3 metres in height	**P4**	High order patch. Shrub < 3 metres in height. Soil surface below crown is < 25% bare-ground. Two or more perennial plant species within the patch. Nil erosion. Cryptogams present.	

Patch-interpatch category	**Patch- interpatch subclass ID code**	**Patch-interpatch description**	**Representative plate**
	P5	High order patch. Shrub < 3 metres in height. Soil surface below crown is 25 to 75% bare-ground. Two or more perennial plant species within the patch. Minor erosion may be present. Cryptogams may be present.	
	P6	Low order. Shrub < 3 metres in height. Soil surface below crown is > 75% bare-ground. Less than two perennial plant species within the patch. Signs of active erosion present/hardened stripped soil surface. Cryptogams generally absent.	
Perennial grass tussocks	**P7**	High order patch. Groups of perennial grass tussocks (> 5 individual plants) which are approximately < 20 cm apart. > 50% of the area between tussocks is covered with litter. Nil erosion present. Limited cryptogam cover.	
	P8	Low order patch. Isolated perennial grass tussocks. Basal areas are > 20 cm apart. < 50% of the area between tussocks is covered with litter. Signs active erosion present. Cryptogams present.	

Patch-interpatch category	Patch- interpatch subclass ID code	Patch-interpatch description	Representative plate
Interpatch areas	**P9**	High order interpatch. Interpatch with > 50% of area covered with litter, which may include: tree branches and leaves, annual plant litter, cryptogams and new recruits of perennial plants; erosion not evident.	
	P10	High order interpatch. Interpatch with 10 to 50% of area covered with litter, which may include: tree branches and leaves, annual plant litter and cryptogams. Limited erosion.	
	P11	Low order interpatch. Interpatch with < 10% herbaceous litter covering the area. Active erosion present. Stripped, hardened soil surface. Cryptogams present.	

3.3.3 Measurement of physical and chemical properties of patch-interpatch subclasses

There are a number of properties that can be used to measure ecological functionality (Eldridge and Mensinga, 2007; Holm *et al.* 2002). Six properties were selected for the purpose of this study, these were: soil respiration, soil carbon and nitrogen ratio, soil bulk density, soil water infiltration, plant species richness, and patch size. These properties were considered to provide a sound empirical basis on which to evaluate the functionality of the patch and interpatch subclasses. They were also chosen because of the comparative ease at which they could be repetitively measured in the field. These measurements were replicated on the 11 different subclasses of patches and interpatches. The results of these measurements were then integrated and analysed.

The measurements for soil respiration, soil C:N ratio, soil bulk density and soil infiltration were all conducted in Paddock 1 at Study Site 1 on randomly selected individual patch-interpatches that represented the 11 different subclasses. The methods for the measurement of the six parameters are outlined in the following sections.

3.3.3.1 Soil respiration

Soil respiration can be described as the efflux of carbon dioxide (CO_2) from the soil (Cooper, 2000). Specifically, the term soil respiration is used to denote the amount of CO_2 which evolves from a square metre of soil *in situ* in an hour (Hartigan, 1980). The measure of CO_2 evolution can be a sensitive indicator of several essential ecosystem processes, including: metabolic activity in the soil, persistence and decomposition of plant residues in soil, and conversion of soil organic carbon to atmospheric CO_2 (Cooper, 2000; Hartigan, 1980). The main source of CO_2 evolved from the soil of most terrestrial ecosystems is microbial respiration during the decomposition of detrital litter and roots. Live root respiration can also form a large component of the evolved CO_2 (Cooper, 2000; Hartigan, 1980). Measurement of soil respiration is a useful approach for studying not only the factors governing soil biological activity but also the carbon and associated energy flow. As a general rule, the higher the respiration rate, the higher the biological activity in the soil.

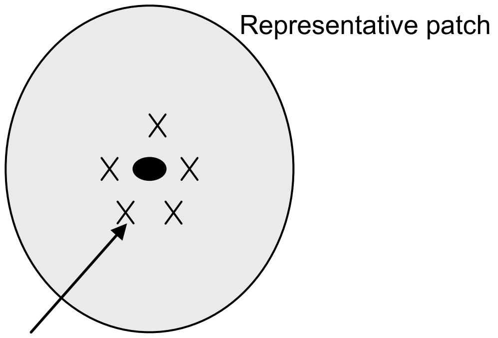
There are a number of ways to measure soil respiration and the method selected for this study was the static alkali absorption method which is done *in situ* (Hartigan, 1980). The advantage of this method is that it preserves the natural bulk density and ambient soil temperature of the soil. It also avoids the exposure of subsoil materials to unnatural levels of oxygen and uses a large soil sample (200 mm diameter x 100 mm depth). CO_2 evolved from soil biota diffuses into the airspace inside the respiration ring and is collected in a solution of alkali ($CO_2 + 2KOH \rightarrow K_2CO_3 + H_2O$). The objective was to obtain the mean soil respiration value and its variance for each subclass

Soil respiration was measured on the 11 different subclasses. Four representative patch-interpatches from each of the subclasses were selected and soil respiration was measured on each with four replicates per individual (a total of 16 samples of soil respiration were recorded for each subclass, n=16). Refer to **Appendix 1** for a detailed description of the method.

3.3.3.2 Soil carbon and nitrogen

Four soil samples from each of the 11 different patch and interpatch subclasses were collected and analysed for carbon and nitrogen (a total of 44 samples; n = 4). Soil samples were taken from randomly selected representative patch-interpatch individuals within the study paddocks (Holm, 2000). Any surface litter was carefully swept away from the soil surface before a soil sample (depth 0 to 20 mm x width 100 mm) was taken with a paint scraper and bulked and thoroughly mixed.

Samples were only taken at a depth interval of 0 to 20 mm because it is known that this is where the vast majority of the soil carbon and nitrogen is stored (Brady and Weil, 2002). Therefore, any variation between the different patch-interpatch subclasses is likely to be detected within this depth interval. It is recognised that sampling additional soil profile intervals would have been beneficial, however financial constraints for soil analysis prevented this from occurring. Five samples of each patch subclass were taken in a concentric pattern at a radius of 10 cm around the stem or trunk of the plants (Holm, 2000) (**Figure 3-1**). The sampling procedure was the same for the three interpatch subclasses, except the five individual soil samples were taken from the middle of the interpatch area.



Five samples taken from an equal distance of 10 cm from the centre of the patch / interpatch and bulked and mixed for testing; repeated on 4 patches/interpatches of the same subclass (n = 4).

Figure 3-1: Layout for soil carbon and nitrogen sampling

Total Nitrogen was determined using a Leco Truspec® instrument. This method quantitatively determines the amount of nitrogen in all forms (ammonium, nitrate and organic nitrogen) in materials using an induction furnace and a thermal conductivity detector (AOAC, 1990). Prepared (dried and ground) samples were ignited in an induction furnace at approximately 1000°C in a pure oxygen environment within a quartz tube that is purged with pure helium. An aliquot of the combustion gases was passed through a copper catalyst to remove oxygen and convert nitrous oxides to N_2, the sample was scrubbed of moisture and carbon dioxide, and nitrogen content was determined by thermal conductivity.

The total carbon content was determined in prepared materials using a Leco SC444 instrument. The samples were combusted in a pure oxygen atmosphere, purged with helium and any carbon present was converted to CO_2. The sample gas flowed into a non-dispersive infrared (NDIR) detection cell where the CO_2 was measured.

3.3.3.3 Soil bulk density

Soil bulk density refers to the oven dry weight of soil per unit volume, and reflects soil porosity and soil strength (Hazelton and Murphy, 2007). Soil bulk density values which may „inhibit‟ or „restrict‟ root growth of agricultural species are suggested to range from approximately 1.66 g/cm^3 for sands and up to 1.58 g/cm^3 for sandy clay loams (Moore, 1998). Bulk densities that may „prevent‟ root growth have been estimated at 1.85 g/cm^3 for sands and 1.8 g/cm^3 for sandy clay loams (Moore, 1998). Bulk density results can provide an indication of potential root restrictions. Eight soil bulk density samples were taken from each of the 11 different patch-interpatch subclasses (a total of 88 samples; n = 8).

Soil samples were taken from representative individual patches and interpatches. Samples were taken in the same layout to the soil carbon and nitrogen measurements (**Figure 3-1**). Numbered aluminum cans (55 mm diameter, 20 mm height) were gently driven into the soil upside down using a rubber mallet and a striking plate. A paint scraper was used to gently excavate around the dish; it was then slid under the can‟s open end and lifted to remove an intact soil core. Any excess soil was sheered of the top using a fine piece of wire. Attention was paid to ensure the soil structure was not disturbed and the can was completely filled with soil.

The soil sample cans were placed in a drying oven at 105°C for 48 hours and then weighed (W_2). Every can after being emptied of soil was cleaned and weighed in grams (W_1) using electronic scales with two decimal point accuracy. The volume of the cans was calculated. The following formula was then used to calculate the bulk density of the samples:

Bulk Density: D (g/cm^3) = ($W_2 – W_1$) / V

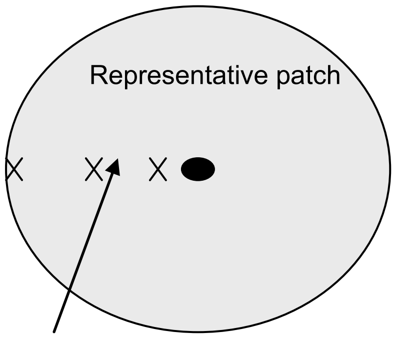
where

W_2 (g) = weight of oven dried soil and can

W_1 (g) = weight of can

V (cm^3) = volume of can

To determine whether the bulk density samples taken from the centre of the patches and interpatches were representative of each subclass, the intra-variation was examined. This meant that three representative individuals from each subclass had samples taken from the inner, middle and outer zones of the patch-interpatch area (a total of 99 samples; n = 3) (**Figure 3-2**). Soil bulk density was the only property that was measured to investigate intra-variation due to constraints of time and financial resources for analysis.



Three samples taken 10 cm from the inner, middle and outer zones of the patch and pooled for testing; repeated on 3 patches/interpatches of the same subclass (n=3).

Figure 3-2: Layout of sampling for intra-variation of soil bulk density

3.3.3.4 Soil water infiltration

The steady state infiltration rate (Cooper, 2000) of the 11 different subclasses was measured. Three measures were taken in each of the different subclasses (33 samples in total; n = 3). Single infiltration rings (200 mm diameter) were hammered 40 mm into the soil profile using a circular striking plate at a distance of 10 cm from the stem of the plant patches. In the case of the interpatches the infiltration rings were hammered into the centre of the interpatch zone. The soil was pressed around the outside perimeter of the rings. Rings were initially filled to a level of 40 mm (3,140 ml) and were continually refilled to maintain this level over a period of an hour to calculate the steady state infiltration. At intervals of 5, 15, 30, 45 and 60 minutes, the total amount that had infiltrated into the soil was recorded. The infiltration rate was calculated using the following formula:

$$\text{Infiltration rate (mm/hr)} = \text{Intake (mm)} / \text{time (min)} * 60$$

The mean and the variance were calculated and reported for each subclass.

3.3.3.5 Plant species richness

Curry *et al*. (1994) concluded that the best indicators of a grazing gradient were the density of woody perennials and palatable perennial species, as both parameters increased with distance-from-water. Therefore, plant species richness in this study was defined as the number of perennial plant species that occur within an individual patch or interpatch. It is an important ecological parameter as it can indicate the structural stability and the evolutionary state of a patch or interpatch. Species richness was measured for the 11 different subclasses. The species richness of a total of 7,887 individual patches and interpatches was recorded.

The number of perennial plant species within the individual patches and interpatches was measured by using a series of line intercept transects located in each of the four study paddocks. It involved identification and recording of all the mature plant species (stem > 10 mm diameter) that occurred within individual patch and interpatches from the various subclasses. The results from the line intercept transects is the focus of **Chapter 4** and it is for this reason that a full description of the methodology used to calculate plant species richness is provided in **Chapter 4**.

3.3.3.6 Patch size

In this study, patch size was defined as the intercept length of a patch-interpatch along a transect. The patch size values were calculated based on the data obtained from the transects (refer to **Chapter 4**). The outskirts of a patch was generally demarcated by the outer edge of an accretionary mound, woody debris, surface litter apron and the canopy of a tree or shrub perpendicular to the transect. A total of 7,887 patches and interpatches were individually measured and the mean values for each of the subclasses were calculated.

3.3.4 Statistical analysis

A summary table of the hypotheses and the statistical approaches used to test each one is provided (**Table 3-2**).

Table 3-2: Summary table of statistical approach used to test the Chapter 3 hypotheses

Hypothesis	Approach used to test null hypothesis	Factors (F) and Variates (V)	Outcome of analysis
1. There was significant variation in soil respiration between the different patch-interpatch subclasses.	Analysis of variance (ANOVA) with blocking at ($P<0.05$) between the patch and interpatch subclasses.	Soil respiration (V)	Mean soil respiration values of patch-interpatch subclasses and LSD.
2. There was significant variation in soil carbon and nitrogen between the different patch-interpatch subclasses.	Analysis of variance (ANOVA) with blocking at ($P<0.05$) between the patch and interpatch subclasses.	Soil carbon (V) Soil nitrogen (V) Soil carbon:nitrogen ratio (V)	Mean soil carbon, nitrogen, carbon:nitrogen values of patch-interpatch subclasses and LSD.
3. There was significant variation in soil bulk density between the different patch-interpatch subclasses.	Analysis of variance (ANOVA) with blocking at ($P<0.05$) between the patch and interpatch subclasses. Intra-variation within patches and interpatches was analysed using a split plot ANOVA that separates the variance between and within patches.	Soil bulk density (V)	Mean soil bulk density values of patch-interpatch subclasses and LSD.
4. There was significant variation in soil water infiltration between the different patch-interpatch subclasses.	Analysis of variance (ANOVA) with blocking at ($P<0.05$) between the patch and interpatch subclasses.	Soil water infiltration (V)	Mean soil water infiltration values of patch-interpatch subclasses and LSD.

Hypothesis	Approach used to test null hypothesis	Factors (F) and Variates (V)	Outcome of analysis
5. There was significant variation in species richness between the different patch-interpatch subclasses.	A linear mixed model (REML) was used because there was more than one variance component.	Patch-interpatch subclass (F) Land-type (F) Dominant plant type (F) Line transect number (F) Patch size (F) Watershed effect (F) Species richness (V)	Mean species richness and standard error of patch-interpatch subclasses.
6. There was significant variation in patch size between the different patch-interpatch subclasses.	Linear mixed model (REML) was used to test for significant differences ($P<0.05$) because there was more than one source of variation.	Patch-interpatch subclass (F) Land-type (F) Dominant plant type (F) Line transect number (F) Watershed effect (F) Species richness (F) Patch size (V)	Mean patch size and standard error of patch-interpatch subclasses.
7. There will be strong correlations between the measured physical and chemical properties.	Two-sided test of correlations different from zero probabilities. A trellis plot was used to output the data.	All six measured properties (V)	R^2 and significance levels of all potential correlations.
8. There is a functionality gradient for the patch-interpatch subclasses.	The 11 different patch-interpatch subclasses were used as variates in a principal component analysis (PCA). Correlations between the parameters were investigated using the output from the PCA and a trellis scatter plot.	All six measured properties (V)	Development of a functionality gradient for the subclasses.

3.3.4.1 Hypothesis 1: Soil respiration

An analysis of variance (ANOVA) with blocking was run to determine whether there was a significant difference ($P<0.05$) between the patch and interpatch subclasses. The individual patches-interpatches of each sampled subclass were regarded as plots and the replications were a part of the blocking structure. Subclass means were displayed in figures with a 5% least significant difference (LSD) to compare the means.

3.3.4.2 Hypothesis 2: Soil carbon and nitrogen

An ANOVA was conducted in order to test for significant differences in the carbon and nitrogen (C:N) ratio between the patch-interpatch subclasses. The source of the variation was examined and discussed. The LSD of the means ($P<0.05$) was calculated and used to determine significance of the differences between the means.

3.3.4.3 Hypothesis 3 and 4: Soil bulk density and soil water infiltration

An ANOVA was conducted in order to test for significant differences in both soil bulk density and soil water infiltration between subclasses. For bulk density and infiltration, five and three replicates were used respectively, for each subclass. The LSD of the means ($P<0.05$) was calculated and used to determine the significance of the differences between the means.

Based on results from preliminary analyses, bulk density was found to be highly correlated with a number of the other measured parameters. Hence, bulk density was selected to investigate the amount of intra-variation that may occur within patches and interpatches. These results were analysed using a split plot ANOVA that separates the variance between and within patches. It examined the effect of patch subclass, location of sample within the patch (inner, middle and outer) and the interactions between these two factors. The particular interest for this analysis was the interaction effects. The differences between the means were calculated using an LSD ($P<0.05$).

3.3.4.4 Hypothesis 5: Plant species richness

To test for differences ($P<0.05$) in species richness between the patch-interpatch subclasses a linear mixed model (REML) was used (Genstat, 2007) because there was more than one variance component. Patch-interpatch subclass, land-type, patch size, watershed effect, line transect number and dominant plant species were all used as factors in the model. Non-significant terms (apart from patch-interpatch subclass) were removed from the model. The raw data was heavily skewed left and therefore it was log-transformed prior to analysis.

The watershed effect was calculated by cumulating the total length of the preceding interpatch of each patch along the transect. The watershed effect was included because it was inferred that the size of the preceding interpatch may influence the amount of water and nutrients a patch may receive. The effect of distance from watering points on species richness in the different patch subclasses was tested separately (P<0.05). The final linear mixed model included the following fixed and random effects:

Fixed model: Constant + logPatch size

Random model: Dominant species + Patch subclass + Dominant species.Patch subclass + Land type + Land type.Transect number

3.3.4.5 Hypothesis 6: Patch Size

A linear mixed model (REML) was used to test for significant differences (P<0.05) in patch size of the various subclasses (Genstat, 2007) because there was more than one source of variation. The model included the effects of the following factors: transect number, land-type, patch subclass, watershed effect, the dominant plant species of each patch, distance-from-water and patch size. Non-significant terms (apart from patch-type) were removed from the model.

The model was run once and the residual values were checked to determine whether the data were normally distributed. The data was heavily skewed left and therefore the linear mixed model fitted the log of patch size in order to stabilize the variance. The model was used to determine the relationship between patch size and patch-interpatch subclass. The final linear mixed model included the following fixed and random effects:

Fixed model: Constant + Distance water + Patch subclass

Random model: Land type + Land type.Transect number

The model was used to test whether the relative distance from a permanent watering point has an effect on patch size. Factors of patch subclass, distance-from-water, land type and transect number were all used in the analysis as a part of either the fixed or random components of the model.

3.3.4.6 Hypothesis 7: Correlations between physical and chemical properties

A two-sided test of correlations different from zero probabilities was conducted to determine the correlations between the different physical and chemical properties (Genstat, 2007). A trellis plot was used to output the data.

3.3.4.7 Hypothesis 8: Summary of physical and chemical properties – principal component analysis

To examine the similarities between the 11 different patch-interpatch subclasses, the physical and chemical properties of each of the 11 different patch-interpatch subclasses were used as variates in a principal component analysis (PCA). Mean values for each subclass were used in the PCA because the measurements of the individual parameters were made on different samples of patches and interpatches. A PCA based on a correlation matrix was used as it effectively standardises the variables prior to running the analysis (Gabriel, 1971; Gower and Digby, 1981). The correlations between the parameters were also investigated using the output from the PCA and a trellis scatter plot.

3.4 Results

3.4.1 Soil respiration

There was a highly significant difference ($P<0.001$) in soil respiration between a number of the different patch-interpatch subclasses (**Figure 3-3**). A large proportion of the total variance (91.3%) was attributed to the differences between the subclasses. Much smaller variation was detected between individual patches of the same subclass (7.6%) and between the replications within the individual patches (1%). The LSD ($P<0.05$) used to compare the means was 43.4 CO_2/m^2/hr. Based on this result, the 11 different subclasses can essentially be grouped into two statistically significant ($P<0.05$) groups: (P3, P6, P8, P9, P10, P11) and (P1, P2, P4, P5, P7) with the exception that P9 is different ($P<0.05$) to P3 and P11. There was a 46.4% difference between the highest recorded value (P1) and the lowest recorded value (P3).

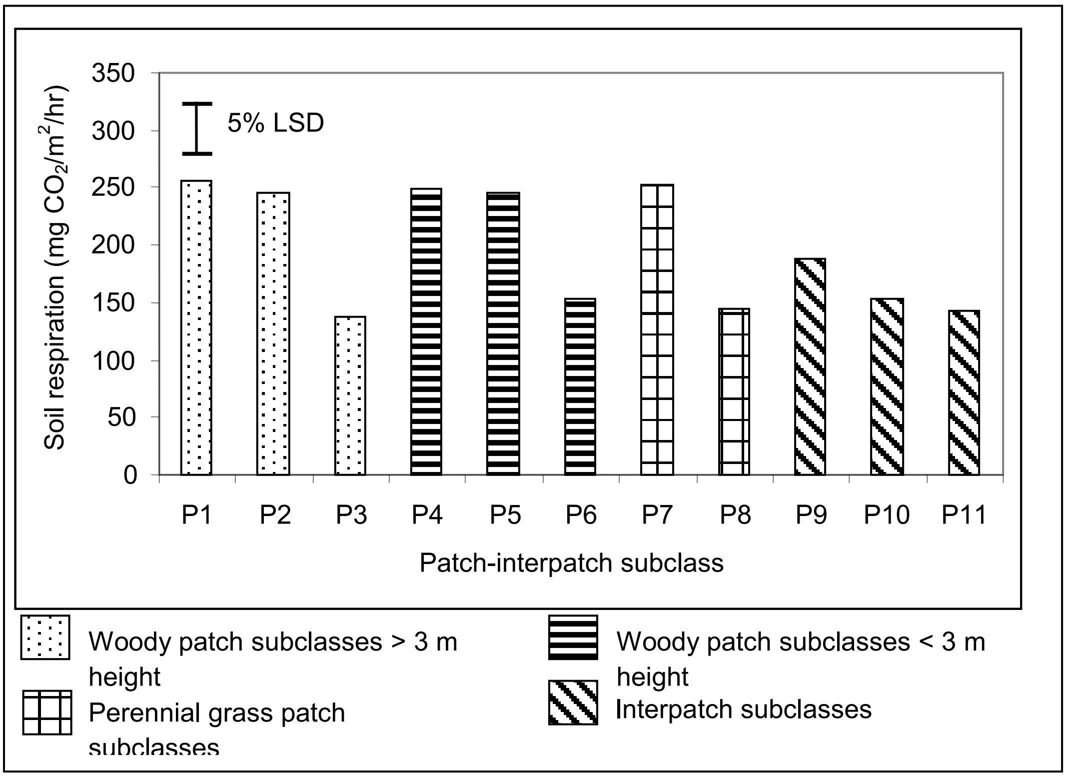


Figure 3-3: Soil respiration mean values of the different patch-interpatch subclasses with 5% LSD

3.4.2 Soil C:N ratio

There was a highly significant difference ($P<0.001$) in total soil carbon between various subclasses. High-order patches (P1 and P2) had up to 85% more soil carbon than bare interpatches (P11) **Figure 3-4**). The trend for higher order patches exhibiting more nutrients was also demonstrated by the differences in total nitrogen between the patch-interpatch subclasses (**Figure 3-5**). Interpatch subclasses P9, P10 and P11 and patch subclasses P3, P6 and P8 all had low soil respiration and low soil carbon and nitrogen suggesting that all these subclasses represent harsh, relatively biologically inactive environments.

There was less difference between the patch-interpatch subclasses in terms of their C:N ratios. This is because the proportional amount of carbon and nitrogen at each subclass was relatively similar. The only significant difference ($P<0.05$) in soil C:N ratios was between P3 and P4 (a difference of 38.5%) (**Figure 3-6**). When the subclasses were averaged into two broad groupings (patch and interpatch subclasses), the mean C:N ratio of the interpatch subclasses was 13.9% lower than the mean ratio of the patch subclasses. This indicates that the soil nitrogen levels of the patch areas are lower in proportion to the soil carbon content. P1, P2, and P3 patches had substantially more carbon relative to the amount of nitrogen compared to the other subclasses.

Increased amounts of soil carbon should typically be associated with higher soil respiration rates provided nitrogen is not limiting. The results reflect this general relationship (R=0.66).

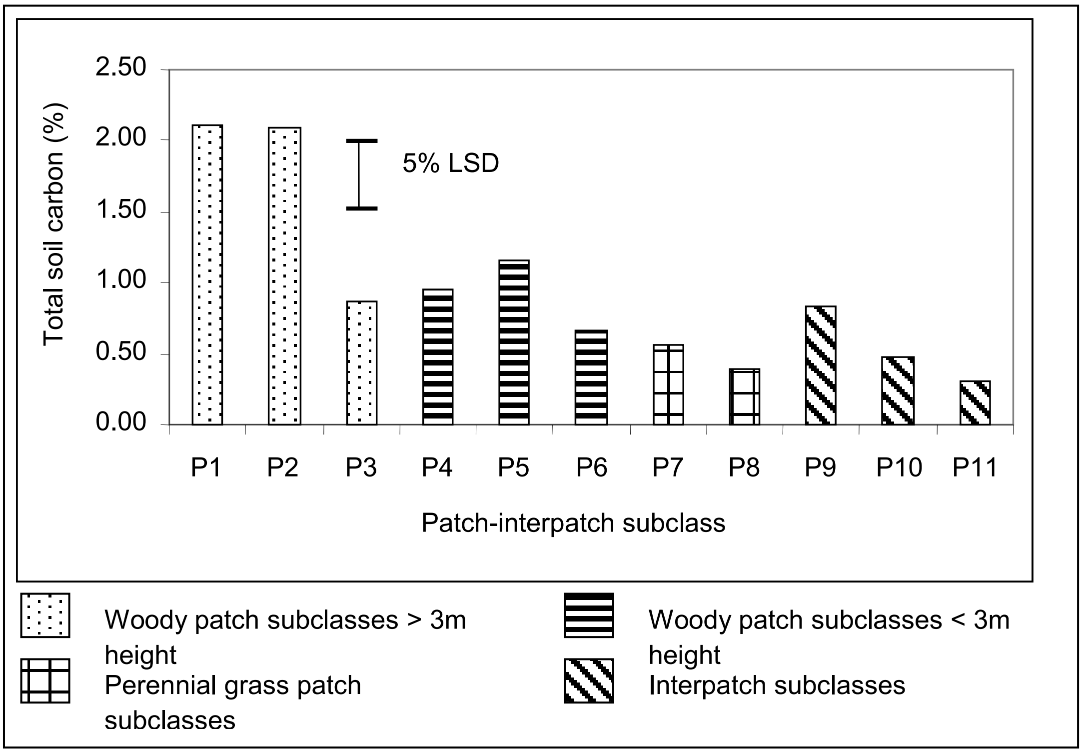


Figure 3-4: Total soil carbon mean values (profile depth 20 mm) of the different patch-interpatch subclasses

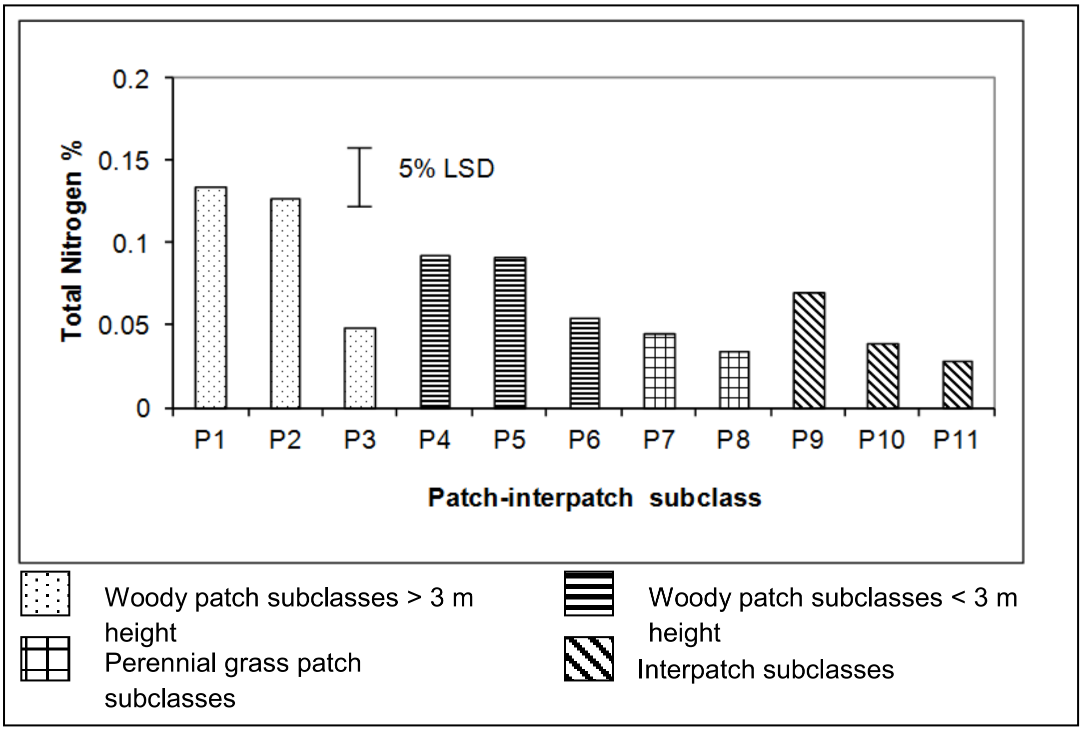


Figure 3-5: Total soil nitrogen mean values (profile depth 20 mm) of the different patch-interpatch subclasses

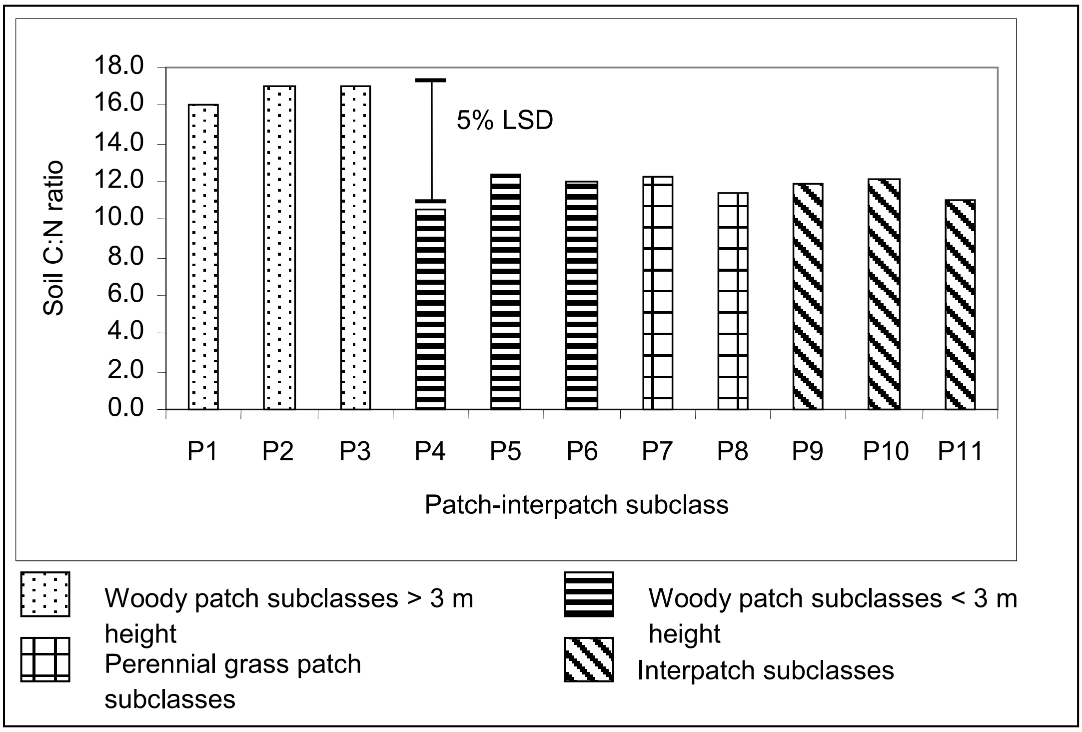


Figure 3-6: Soil C:N ratio mean values (profile depth 20 mm) of the different patch-interpatch subclasses

3.4.3 Soil bulk density

There were highly significant differences ($P<0.001$) in soil bulk density between a number of the patch-interpatch subclasses (**Figure 3-7**). Specifically, high order patches P1 and P4 had significantly lower soil bulk densities than the lower order patches within their equivalent categories. There was a 31% difference in bulk density between the highest (P11) and the lowest (P1) subclass. A significant proportion of the variance (95%) was accounted for by the differences between the subclasses, whilst a minor proportion resulted from differences between the replicates (5%). The LSD ($P<0.05$) value was 0.094. The results indicate that soil bulk density decreased as patches become more ecologically stable.

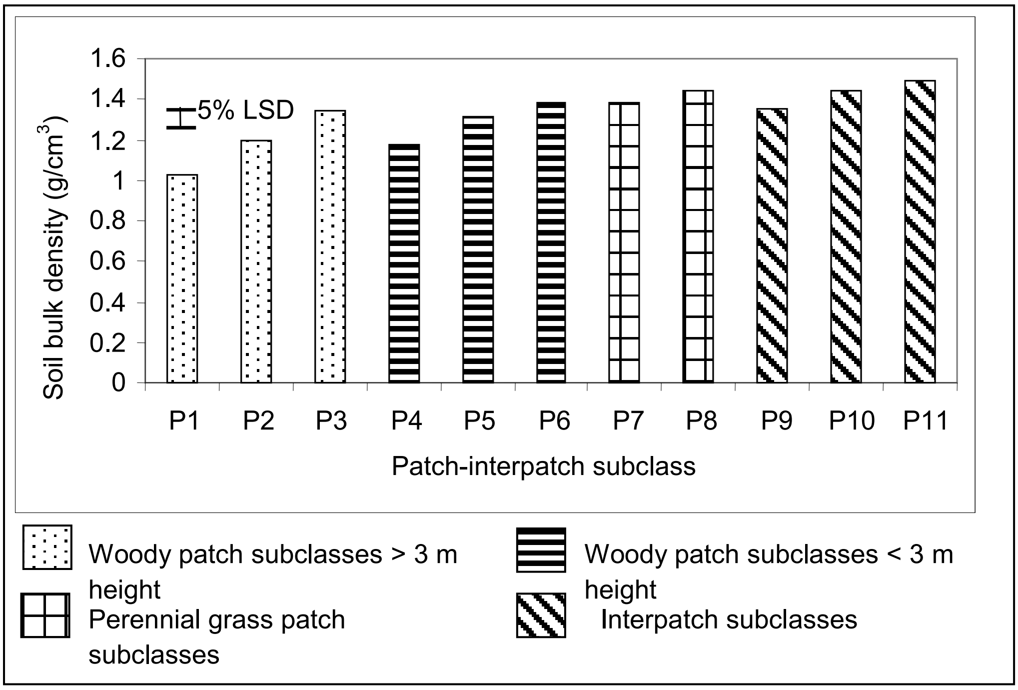


Figure 3-7: Mean values of soil bulk density (profile depth 20 mm) mean values of the different patch-interpatch subclasses

Additional samples were taken from the inner, middle and outer zones of the patches and interpatches to examine consistency of soil bulk density values. The results indicated that there was highly significant ($P<0.001$) variation between these zones of patches-interpatches of particular subclasses (**Figure 3-8**). The variation between the zones was the highest in P1 and P4. The majority of the subclasses had a general trend of increasing bulk density away from the centre of the patch or interpatch.

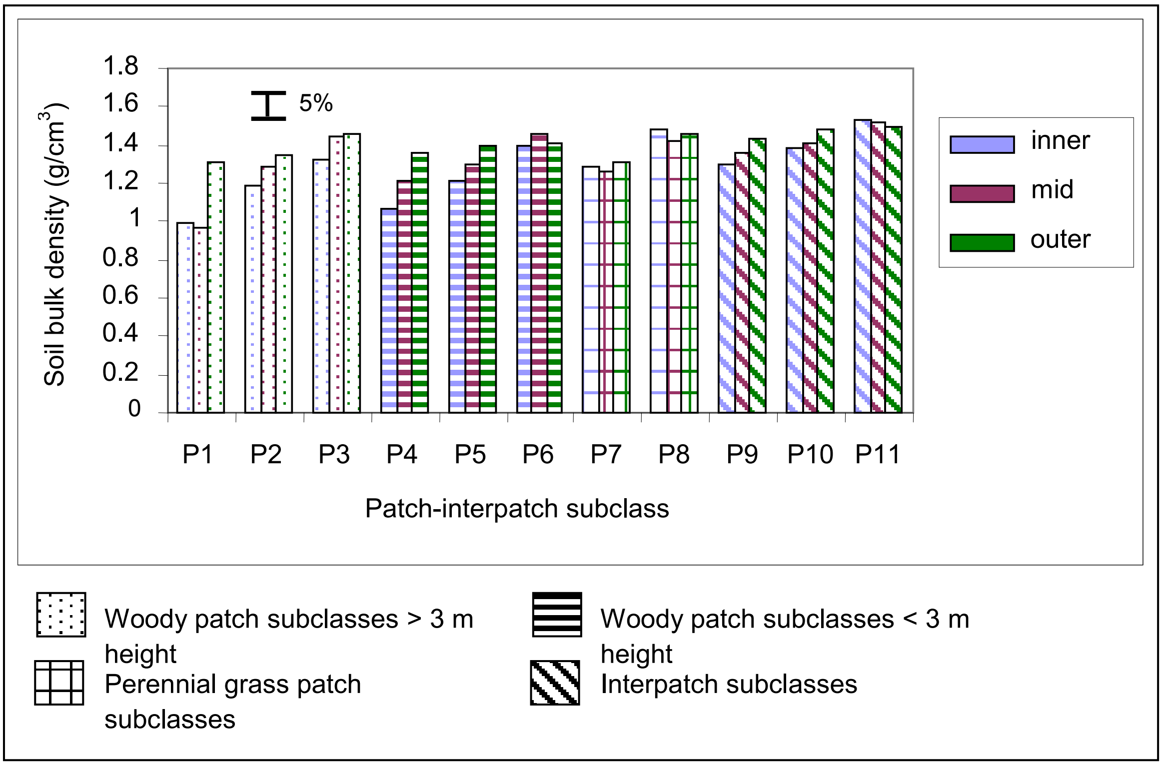


Figure 3-8: Mean values of soil bulk density (profile depth 20 mm) between the inner, middle and outer zones of patches and interpatches (LSD based on the within and between patch interaction).

3.4.4 Soil water infiltration

There was highly significant variation (P<0.001) in water infiltration between various subclasses (**Figure 3-9**). The LSD (P<0.05) value was 2.51 mm/hr. Three major groupings based on the LSD were identified: high infiltration (P1; 13.28 mm/min), moderate infiltration (P4, P5, P9; with a range of 9.44 and 10.02 mm/min) and low infiltration (P2, P3, P6, P7, P8, P10, P11; with a range of 3.82 and 7.33 mm/min). These results suggest that high-order patches and interpatches have higher infiltration potentials.

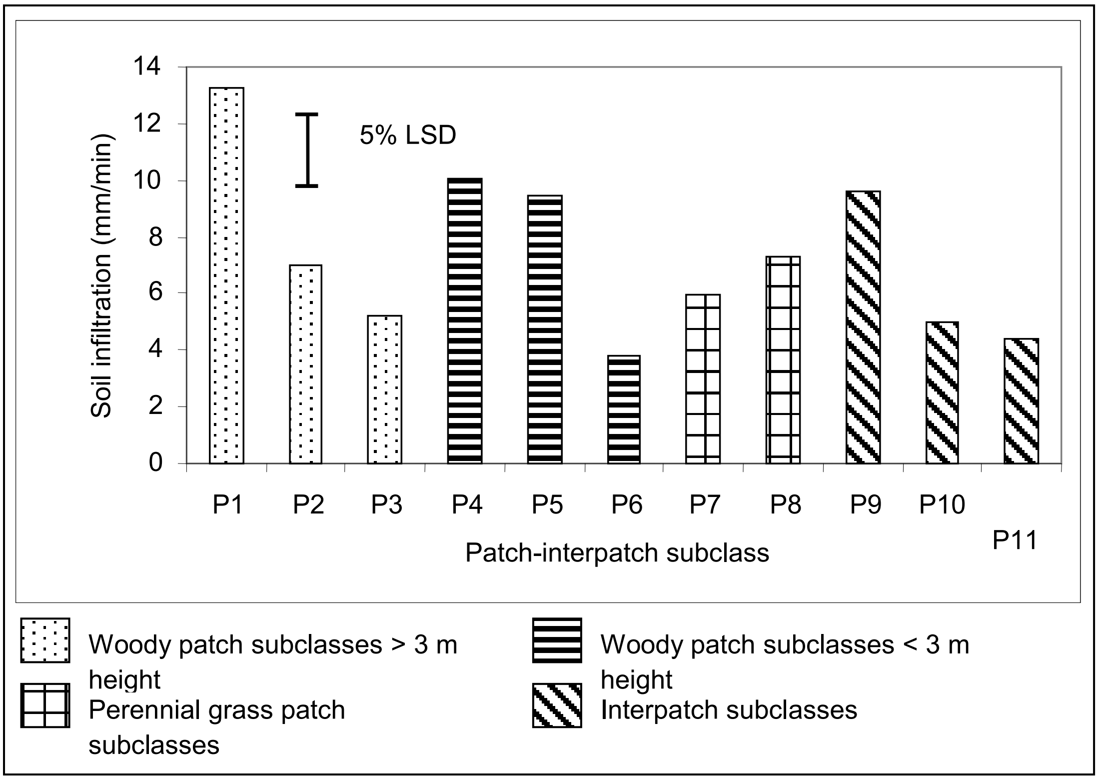


Figure 3-9: Mean soil water infiltration rates of different patch-interpatch subclasses

3.4.5 Plant species richness

The linear mixed model used for the analysis indicated that there were highly significant differences (P<0.001) in species richness between the various patch-interpatch subclasses. A large proportion (42.7%) of the variation in species richness was attributed to the differences in the subclasses (**Figure 3-10**). Land-type and scientific error (variance between transects) both accounted for low to moderate amounts of variation, 0.4% and 12.4% respectively. The high-order subclasses typically had a greater number of plant species than the low-order subclasses. The majority of patch subclasses had two to three plant species, the maximum number of species in an individual patch was nine (P1 patch).

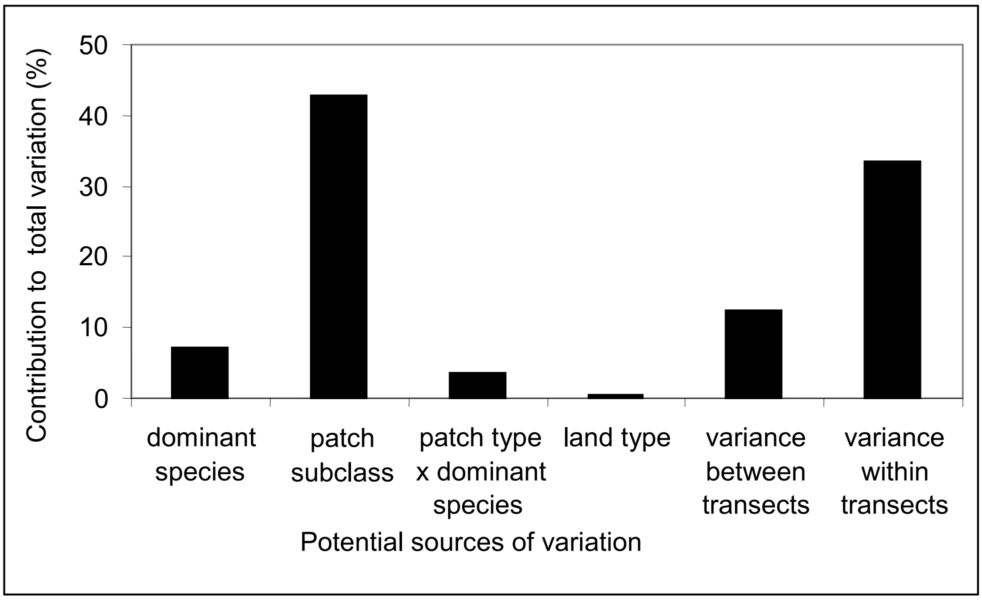


Figure 3-10: Potential sources of variation in the differences in mean plant species richness between the different patch-interpatch subclasses

The model suggested that patch size had a highly significant effect ($P<0.001$) on species richness. The number of plant species within a patch-interpatch generally increased with patch size. Interpatch subclasses P9, P10 and P11 did not have any established perennial plant species present (i.e. species count is zero) and were dropped from some of the later analyses because they were heavily skewing the data. Distance-from-water had no significant effect ($P<0.05$) on species richness within patches of the same subclass.

There were significant differences (LSD 5%) between almost all the individual subclasses. Based on the 5% LSD, three general groupings can be made, these include: P1; P2 and P4; and P3, P5, P6, P7 and P8 (**Figure 3-11**). These results indicate that high-order patches (namely. P1, P2 and P4) generally have greater plant species richness.

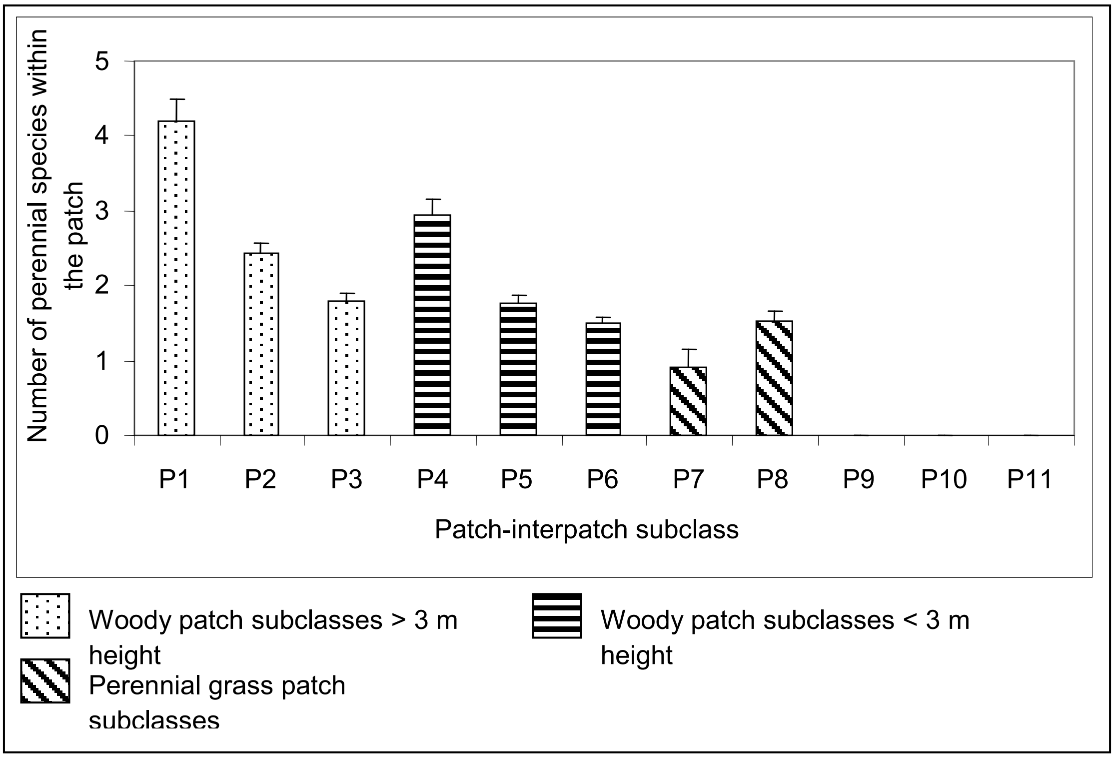


Figure 3-11: Mean plant species richness between patch-interpatch subclasses (Note: standard error bars are present because the sample sizes for each subclass were not equal in number)

Species richness was determined by how many different types of perennial plant species that were present in a subclass (**Table 3-3**). There was typically one plant species that dominated certain subclasses. In addition, some species only occurred in specific subclasses (namely *Acacia acuminata*, *Acacia aneura, Acacia linophylla*). These species tended to be decreaser perennial shrubs and grasses (see footnote[5]). Similarly, unfavourable, increaser species were more common with particular subclasses. Subclasses P7 and P8 are not shown because, by definition, they were completely dominated by perennial grasses. Likewise P9 to P11 are not shown as no perennial plant species were recorded in these subclasses (because they were primarily run-off areas). For analysis purposes the individual plant species were grouped according to their functional groups (refer to **Appendix 2** for a full listing of individual plant species based on the functional groups)

The results suggested that in the lower order P3 and P6 subclasses, palatable tall shrubs (e.g. *Acacia aneura*) were still present in high proportions in comparison to the other subclasses (particularly P1 and P4). *Acacia aneura* and *Eremophila forrestii* made up a high proportion of the P3 and P6 subtotals. Interestingly, P3 and P6 also had the highest proportions of unpalatable tall shrubs (namely *A. grasbyi, A. tetragonaphylla, Hakea preissii, A. acuminata*). There was a marked difference in the occurrence of palatable tall shrubs and palatable small shrubs: between the P1 and P3 subclasses, and between the P4 and P6 subclasses.

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[5] A decreaser species is a plant that decreases under increasing grazing pressure.

In comparing the high and low-order patch sub-classes, it may be important that there was little variation between the occurrences of unpalatable tall shrubs and unpalatable small shrubs. Subclasses P3 and P6 patches had substantially less grass and palatable small shrub species and moderately fewer palatable shrubs compared to P1, P2 and P4 patches. There appeared to be a clear gradient of the frequency of palatable sub-shrubs with patch subclass. The significantly higher occurrence of perennial grasses with subclasses P1, P2, P4, and P5 compared to the ecologically dysfunctional P3 and P6 subclasses suggests that perennial grasses may require a much more ecologically functional site in order to establish.

Table 3-3: Frequency (%) of plant functional groups within woody shrub patches

Functional Group*	Frequency of plant functional groups (%)					
	P1 (n=39)	P2 (n=748)	P3 (n=126)	P4 (n=37)	P5 (n=2169)	P6 (n=474)
Tree	12.3	9.5	3.0	2.5	4.4	1.0
Palatable tall shrub	8.2	10.9	11.3	2.5	6.2	5.2
Unpalatable tall shrub	23.8	32.7	42.2	32.6	39.7	45.1
Palatable sub-shrub	17.5	10.6	8.3	22.7	18.6	14.1
Unpalatable sub-shrub	1.9	0.7	0.4	0.8	2.1	0.2
Palatable small shrub	14.5	14.1	8.1	13.6	12.0	4.4
Unpalatable small shrub	1.9	0.7	0.4	0.8	2.1	0.2
Perennial grass	19.7	20.0	4.1	23.6	16.5	3.1

***Plant functional groups are based on classifications in Mitchell and Wilcox *et al*. 1994). Patch subclasses P7 and P8 are not included as they by definition are completely dominated by perennial grasses. Subclasses P9, P10 and P11 are not included as they are interpatches and dominated by annual species**

3.4.6 Patch size

The linear mixed model indicated that there were highly significant differences (P<0.001) between patch sizes of various subclasses. The model calculated the main sources of the fixed variation in patch size (**Figure 3-12**). A moderate component (31%) of the variation was a result of the dominant plant species that occupied each patch. There is a natural interrelation between the dominant plant species and patch subclass (i.e. different subclasses were usually associated with one or two dominant plant species). Hence, when these factors are combined, they accounted for over half of the variance. The influence of the land-type in which the patch was measured, did not appear to have a significant effect (3.3%) on patch size. The differences in patch size of the subclasses is large within transects, but there is little additional variance (2.7%) between transects. A potential watershed effect on patch-interpatch size was not significant (P = 0.572).

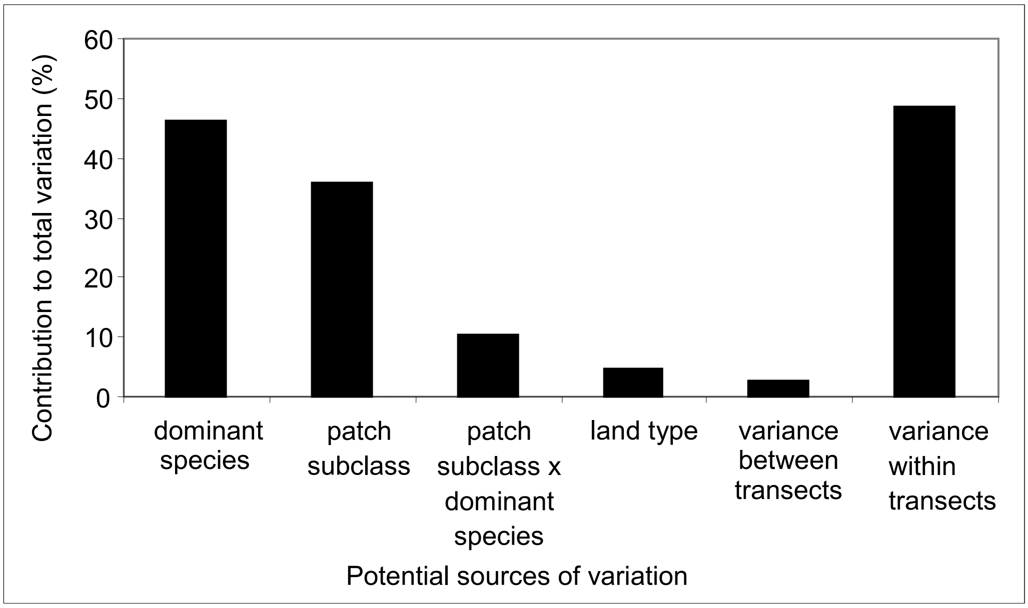


Figure 3-12: Sources of variation in the differences in mean patch size of the patch-interpatch subclasses

The results from the model suggest that there were highly significant differences (P<0.001) in patch sizes between several patch-interpatch subclasses (**Figure 3-13**). Based on a 5% LSD there were four distinct groupings. In order of decreasing size, these included: (P1 and P11; P2, P3, P4, P7 and P10); (P5 and P9); and (P6 and P8).

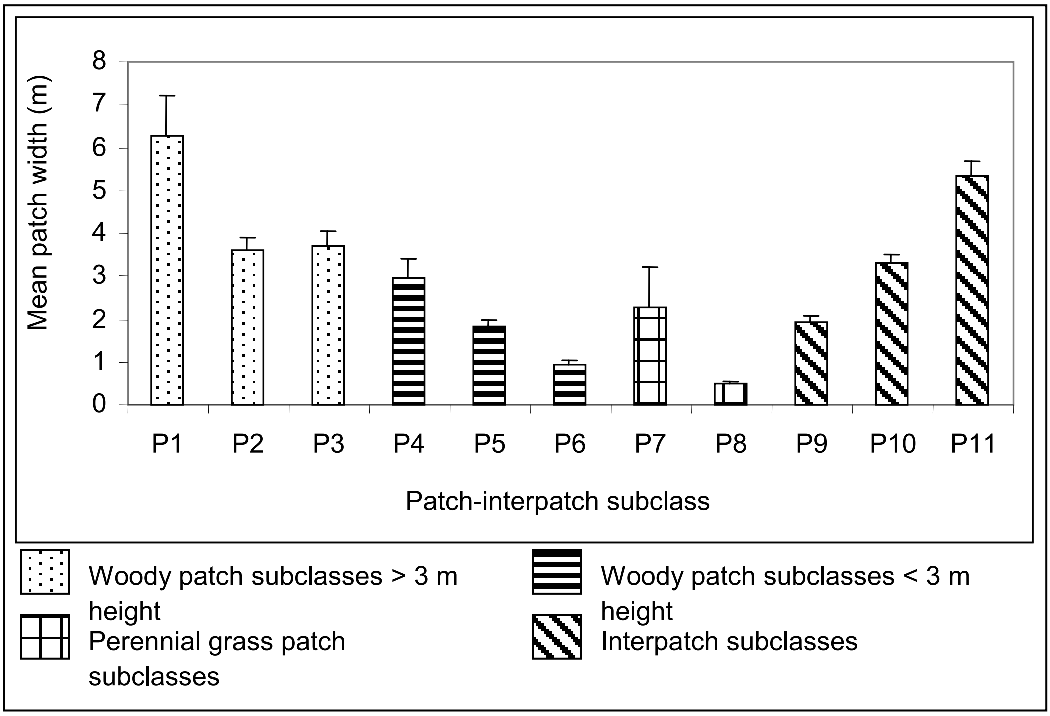


Figure 3-13: Mean patch size of the different patch-interpatch subclasses (Note: standard error bars are present because the sample sizes for each subclass were not equal in number)

A highly significant interaction ($P<0.001$) was found between the patch size of the patch-interpatch subclasses and distances-from-water. However, the variation was largely the result of subclasses P4 and P8 as they were operating at opposite ends of the gradient (P4 decreasing, and P8 increasing in patch size at greater distances-from-water).

The results suggested that subclass P4 decreased in size (0.16 m per km) at increasing distances-from-water, whilst subclass P8 increased in size (0.10 m per km) at increasing distance-from-water. It was considered that the result from subclass P4 was explained by the dominant species factor. The larger P4 patches closer to water were dominated mainly by increaser plant species such as *Acacia tetragonaphylla*, which can become quite large woody shrubs as they are rarely heavily browsed. Therefore, the analysis was repeated with the inclusion of dominant species as a random factor. In this analysis the patch subclass by distance-from-water interaction was no longer significant ($P=0.273$). Hence I could not detect any significant evidence ($P>0.05$) across all the subclasses to support the theory that favourable patch subclasses become larger at increasing distances-to-water and interpatches, particularly the lower order ones (such as P11), become smaller.

3.4.7 Correlations between physical and chemical properties measured at a patch-scale

There were significant positive and negative correlations ($R^2 >0.60$) between a number of the measured physical and chemical properties (**Table 3-4**). I found that soil bulk density was correlated with every other property except for patch size. The strongest positive correlation ($R^2 >0.95$) was between total soil carbon and total soil nitrogen ($P<0.001$). Soil respiration and water infiltration were also positively correlated ($R^2=0.67$). Patch size was the only property that was not significantly correlated (positive or negative) with any other property which means that it was independent (**Figure 3-14**).

Species richness was expected to increase as the size of a patch increases, particularly given that larger patches tend to attract and retain a greater share of water and nutrients (Pickup, 1985). The results were unable to demonstrate this potential relationship ($R^2 = 0.031$ $P>0.05$). It was inferred that this might be because there was a significant proportion of large interpatch areas that usually have no perennial species present. However, when the correlations were rerun based on individual patch-interpatch subclasses, the positive correlation between patch size and species richness was not any stronger or significant. It is acknowledged that in this study species richness was limited only to perennial plants, it is possible that differences may occur if annual plants were measured and analysed.

Table 3-4: Correlations between measured properties of the 11 patch-interpatch subclasses

	Soil respiration	Total soil carbon	Total soil nitrogen	Soil bulk Density	Water infiltration	Species richness within patch
Total soil carbon	0.6625*					
Total soil nitrogen	0.7684*	0.9596**				
Soil bulk density	-0.7374*	-0.8900**	-0.9298**			
Water infiltration	0.6678*	0.6301*	0.7448*	-0.7901*		
Species richness within patch	0.5431	0.6851*	0.6948*	-0.7915*	0.5209	
Patch size	0.2910	0.4392	0.3793	-0.4350	0.2061	0.6625

Note: Significance levels: *(P<0.05) and **(P<0.001).

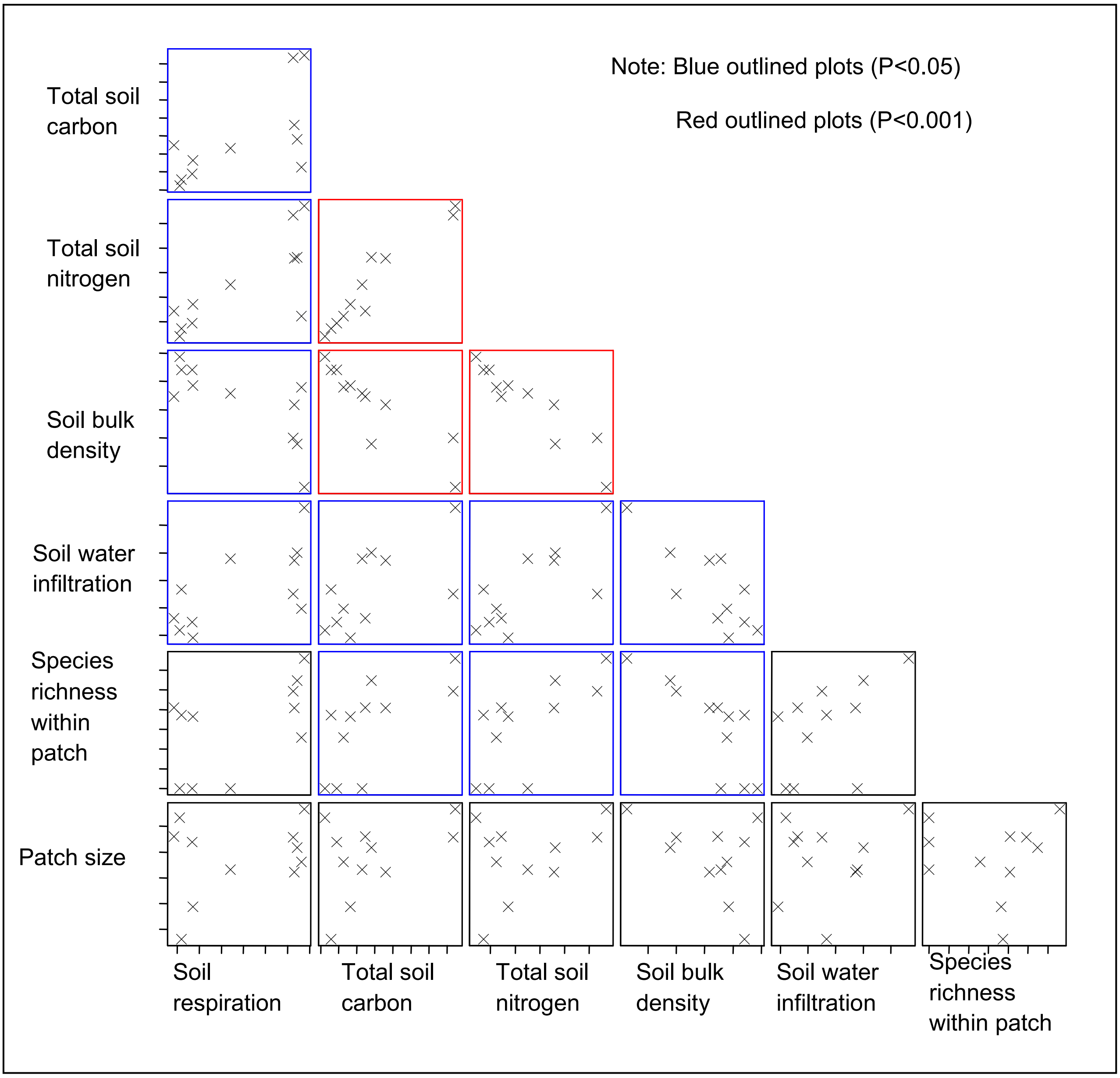


Figure 3-14: Relationships between measured properties of the patch-interpatch subclasses

3.4.8 Summary of parameters using a principal component analysis

With a few exceptions, the results indicated that high-order patch and interpatch subclasses had higher soil respiration and infiltration, more total soil carbon and nitrogen and greater plant species richness compared to lower order subclasses. This trend was largely independent of land-type and the distance-from-water. Patch size was removed after an initial principal component analysis (PCA) was conducted because it was skewing the results and it was considered an ancillary indicator of ecological functionality compared to the other parameters. With the removal of patch size as a variate, the first, second and third principal components accounted for 99.8%, 0.17%, and 0.01% of the variation between the subclasses, respectively. The biplot of the first two principal components accounted for 99.9% of the variance and shows the relationships between the measured properties and the patch-interpatch subclasses (**Figure 3-15**).

The biplot illustrates the existence of a gradient of functionality at a patch-scale between the four categories of subclasses (patches > 3 m in height; patches < 3 m in height; perennial grasses; interpatches). The gradient within each group is outlined on the biplot (coloured dotted lines). The position of subclass P1 and P2 indicated that were not significantly different, although the results suggest that there is a substantial reduction in ecological functionality when a patch is reduced to a subclass P3. Similar trends were found with subclasses P4, P5, and P6, although P5 appeared to be slightly out of alignment that could be caused by the limited variation between P4 and P5 for most of the measured properties.

There appeared to be a clear subgradient between the interpatch subclasses P9, P10, and P11 that all represented a lower functional state compared to the patch subclasses. There was a distinct difference between perennial grass clumps (P7) and isolated tussocks (P8) on Axis 2 not Axis 1.

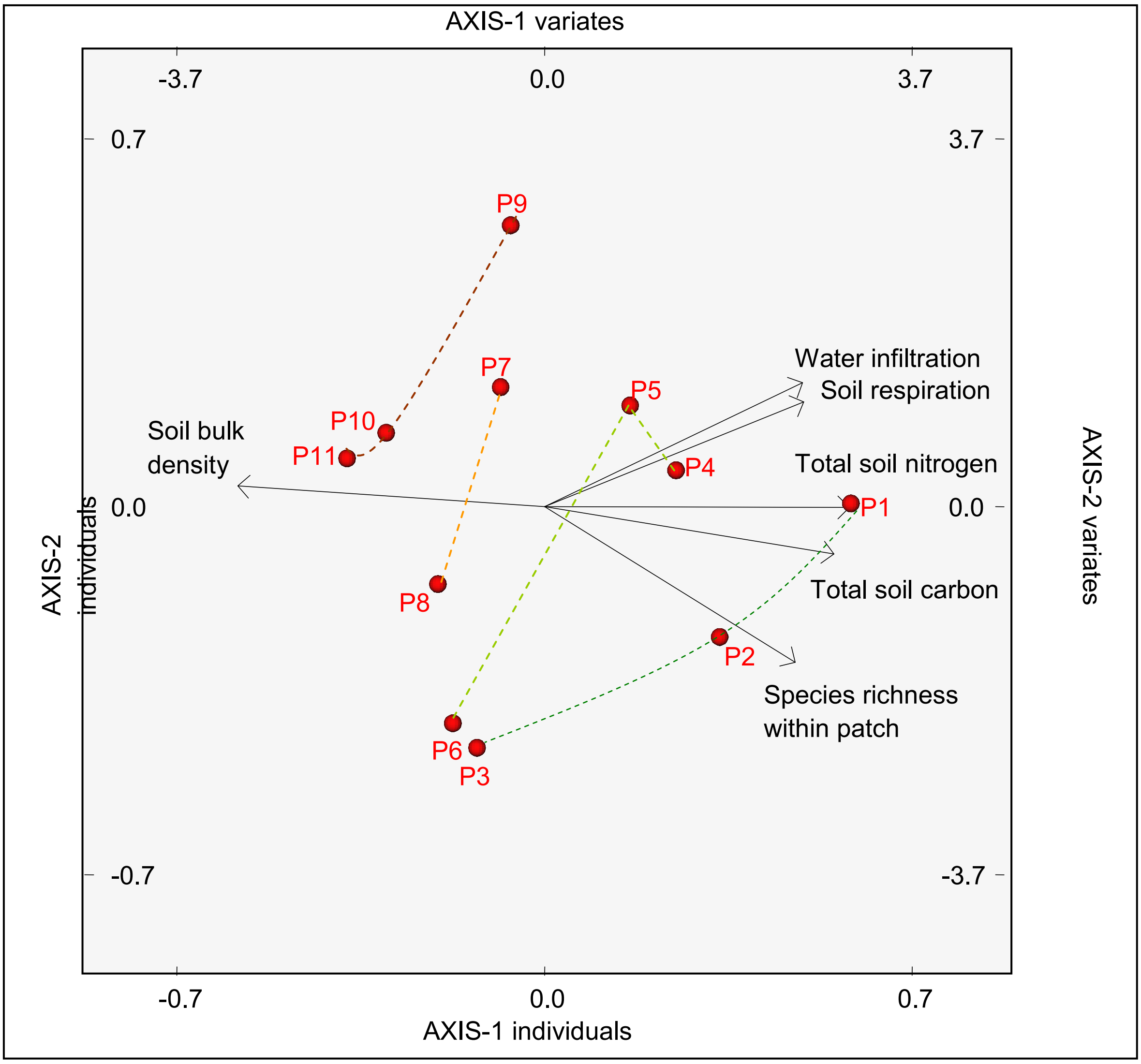


Figure 3-15: Principal component analysis biplot displaying the gradient of functionality between patch-interpatch subclasses (dotted, coloured lines highlight the proposed gradients between subclasses within the same category [i.e. trees and shrubs >3 m – dark green; trees and shrubs < 3 m - light green; perennial grasses - orange; interpatch zones – brown]).

3.5 Discussion

3.5.1 Evidence of patchiness at a patch-scale

The results clearly demonstrate that there is significant patchiness at a patch-scale in the study area and that there was a gradient of functionality. The significant variation ($P<0.05$) that was present between the 11 patch-interpatch subclasses validates the approach that was intuitively developed to stratify the study paddocks at a patch-scale. In the study paddocks, highly functional patch subclasses (e.g. P1 subclass) were more biologically active, had more than twice the number of perennial species, soil infiltration rates were 50% higher, and they had up to five times more carbon and nitrogen than low-order, dysfunctional interpatches ($P<0.05$). Therefore, the results support the third principle of landscape function theory principle that a gradient in functionality exists between the different patch-interpatch subclasses.

Patch subclasses in this study were proven more functional than interpatch subclasses; however, the latter are an integral component to landscape processes. For example, Eldridge and Freudenberger (2005) reported that at the scale of individual grass tussocks, cryptogams provide an ecological service by redistributing rainfall and organic material to productive grassy patches without contributing to sediment yields. The partitioning of limited resources between patches and interpatches is a key feature that assists in the stability of semi-arid landscapes. This indicates that a functional ecosystem requires a balanced composition of patch-interpatch subclasses.

Burrows (1973) investigated regeneration and spatial patterns of *Acacia aneura* (mulga) in south west Queensland and found that an optimum balance between maintaining adequate drought reserves (mulga trees) and ground forage production would require a mulga tree density (or P1 patch) of approximately 160 trees per ha. High tree densities are known to suppress herbaceous shrubs and grasses (Beale, 1971). Mulga seedling regeneration may be significantly depressed if tree densities exceed 640 trees per ha. Given the role grass tussocks can play in decreasing excessive runoff, it was recommended that they should comprise >2% of the landscape (Pressland and Lehane, 1982). A suitable balance of patch-interpatch subclasses in the study paddocks is explored in more detail in **Chapter 4**.

I found that patchiness also occurs at a finer scale and that there is significant intra-variation within individual patches. There can be significant variation ($P<0.05$) between the inner, middle and outer zones of individual mature trees and shrubs. There was a general linear trend of decreasing intra-variation of soil bulk density from the high to low-order subclasses. Hence, the water and nutrients within more stable, fertile patches were more heterogeneously distributed compared to intermediary and low-order patches. It would appear that, as individual patches are disturbed over extended periods, this homogenizes soil surface conditions. This is evident at the extreme of subclass P11 (> 75% bare-ground) in which there was virtually no difference in edaphic conditions between the inner, middle and outer zones of the interpatch.

The role of patchiness at fine scales has been investigated in other studies that have shown that fine-scale heterogeneity is critical to the ecological functioning of semi-arid landscapes (Ludwig *et al*. 2005). Aguiar and Sala (1999) found that in semi-arid environments there is a precipitation threshold below which primary production will be zero. In a homogeneous ecosystem, production will be zero if precipitation is below this threshold. In contrast, in a spatially and ecologically heterogeneous ecosystem, the redistribution of water and nutrients allows the ecosystem to concentrate the resources and hence generate a pulse of production with less total precipitation (Aguiar and Sala, 1999).

The results suggest that there is a baseline for soil respiration (approximately 135 mg $CO_2/m^2/hr$) in which a residual amount of soil biological activity continues to occur even in the least functional subclasses. This highlights that even in degraded interpatch areas, the soil environment is not completely biologically „sterile". The roots of woody plants can extend some distances from the main stem of the plant. *Acacia Karoo* is reported to be able to exploit the soil profile up to a distance of at least nine metres from the main stem (Stuart-Hill and Tainton, 1989). The majority of tree roots of mulga are located in the top 30 cm of soil, although some roots can still be present to a depth of 120 cm (Pressland, 1975). Hence, this „baseline effect" is largely explained by the distribution of tree and shrub roots which can extend into the degraded interpatch areas (except when the interpatch is relatively large, approximately >20 metres). I considered that this adequately explains the similarities in the soil respiration values for subclasses P3, P6, and P11.

Trees and shrub patches with minimal cover and approximately >75% bare-ground (subclasses P3 and P6) had soil respiration rates similar to highly dysfunctional interpatches (P11). The mean length of the P11 subclass was only 5.7 metres, hence these interpatches are well within the potential rooting radius of many mature trees and shrubs. Consequently, it was inferred that the main contributor to the baseline soil respiration rate measured in dysfunctional patches and interpatches was tree and shrub roots from surrounding tree patches.

It is suggested that the higher fertility of highly functional tree and shrub patches (subclasses P1 and P2) may be partially caused by the increased moisture holding capacities, which enable micro-organisms and plants to continue to be active for much longer during dry periods. During dry periods, the moisture reserves of dysfunctional patches would become depleted more rapidly and some micro-organisms may enter into a cryptobiosis and plants would enter into a period of dormancy or may die. This could have a potentially cumulative, long-term impact on the fertility of the patch and its surrounding area.

Perennial grass patches (subclass P7) had high soil respiration rates but low soil carbon and water infiltration. The role of perennial grasses in the study paddocks is likely to be highly dependent on seasonal conditions (this topic is explored further in **Chapter 5**). Due to the low to moderate functionality of the perennial grass patches in this study, I consider that perennial shrubs are likely to play a minor role in maintaining long-term ecological stability of the study paddocks. Previous work has demonstrated that grass-mediated capture of overland flows of water improved the supply of water to mulga shrubs, trapped litter and reduced the number of rainfall events that generate run-off from red earth soils (Anderson and Hodgkinson, 1997). Therefore, there is an obvious plant-plant dependency. Perennial grasses actively recruit within the stable zone that shrub patches generally provide and in turn they may influence the local hydrology and fertility of shrub patches (Anderson and Hodgkinson, 1997; Freudenberger *et al.* 1999).

The study found that distance-from-water had no significant effect ($P<0.05$) on plant species richness within patches of the same subclass. This means that the number of different plant species within a patch of a particular subclass is not influenced by its distance from a permanent watering point (which is a surrogate for livestock grazing pressure). This result was expected because I did not consider that the characteristics of individual subclasses would change in response to distance-from-water. However, I did anticipate that the relative proportions of the different subclasses would vary in response to distance-from-water. For example, I would expect a higher number of highly functional patches to occur at greater distances-from-water because of the reduced grazing pressure (this issue is investigated in **Chapter 4**).

It is acknowledged that this study did not explore the variation that may occur within the patch and interpatch subclasses across the landscape (i.e. differences between paddock and properties). The research methodology was designed on the assumption that patch and interpatches within the same subclass are likely to have similar physical and chemical properties within the study area. It is possible that variation between patches and interpatches of the same subclass may occur depending on their location in the paddock or area of the different properties.

3.5.2 Correlations between physical and chemical properties at a patch-scale

The results clearly showed that patches that have a low soil bulk density are also likely to have high soil carbon, high soil nitrogen and high soil infiltration. One of the strongest correlations between the six measured properties was that between soil respiration and water infiltration. This correlation is likely to exist because of macropores (>0.75 mm in size) that are created by invertebrates, microbial activity and both living and decaying roots (Eldridge and Freudenberger, 2005; Greenwood and McKenzie, 2001). Macropores contribute to improving soil structure that is critical to good soil infiltration (Greenwood and McKenzie, 2001). How does soil infiltration increase soil respiration?

The infiltration process influences the source, timing, volume, and peak rate of run-off (Stenfield *et al*. 2006). When precipitation is able to enter the soil surface at manageable rates, as is the case with these patches, the soil is protected against accelerated erosion and soil fertility is maintained (Stenfield *et al*. 2006). It is also known that roots increase the structural stability of the soil through enmeshment of soil aggregates by fine roots and root hairs and binding of soil aggregates by associated fungal hyphae and organic residues (Goss, 1987). Hence, a stable soil environment will encourage increased soil infiltration, plant growth and microbial activity and thereby exhibit greater rates of soil respiration.

There was a significant, positive correlation between soil carbon and soil respiration. However, there was a much greater difference in soil carbon between the high-order patches (P1 and P2) and the low-order interpatches (P10 and P11), than between the soil respiration values. The results indicated that there was adequate nitrogen supply to generate a growth pulse should adequate moisture become available (Silcock, 1976). Therefore, this suggests that a substantial component of the soil carbon may have been unavailable for microbial decomposition.

A strong correlation was found between soil carbon and soil nitrogen. This result was similar to that observed by Holm *et al.* (2002b). Holm *et al.* (2002b) reported that resilience of landscapes depends on the success of colonizing species to rapidly revegetate bare-soil areas that result from loss of vegetated patches. Low soil C:N ratios (< 10:1) ensures rapid mineralization of organic nitrogen and thus provides an available pool of nitrogen, at least in the short-term, for rapid plant growth particularly during favourable seasons (Holm *et al*. 2002).

3.5.3 Physical and chemical properties that characterise highly functional patch-interpatch subclasses

The amount of bare-ground within an individual patch-interpatch is considered one of the key properties that characterise its present ecological functionality. A large amount of surface litter within patches from the highly functional P1 subclass was observed. Litter is known to play an important role in maintaining the water dynamics, nutrient cycling and other biotic interactions at a patch-scale (Aguiar and Sala, 1999; Eldridge and Freudenberger, 2005; Moore and Biddiscombe, 1964; Schlesinger and Pilmanis, 1998). Litter provides a stable, moist soil environment that may foster microbial activity (as indicated by the high soil respiration rates that were recorded) and possesses a higher capacity to act as an ideal seed incubator and growing environment for vascular plants (Ludwig *et al.* 2005).

Based on my visual observations during the field survey, the majority of the litter present in the highly functional P1 subclass patches was generally detached herbaceous and woody material from the dominant tree or shrub that occurs within the patch. Lesser amounts of deposited herbaceous litter were evident, generally on the outer rim of the accretionary platform of the patches that was probably the result of aeolian and alluvial transportation from local, less stable sites.

The significant load of litter within the patch can provide an ample feed source for a suite of diverse micro-organisms (Chartier and Rostagno, 2006; Ludwig *et al.* 2005). The litter will be cycled and incorporated into the soil and this was evident from the significantly higher soil respiration rates and total carbon and nitrogen levels recorded within these patches ($P<0.05$). The contribution that plant litter can make in improving the supply of soil nutrients has been investigated by Burrows (1972). Burrows (1972) found that litter production and decomposition from an arid zone shrub (*Eremophila* *gilesii*) community accounted for the release of up to 0.33 kg organic phosphorus per hectare per year and the average litter break-down time was 20 months. The slow breakdown period highlights the need to have a continuous supply of litter in different phases of decomposition to ensure soil fertility is maintained.

The activity of the micro-organisms plays a dual role within the patch by enriching nutrient levels and reducing bulk density ($P<0.05$) through bioengineering (Eldridge and Mensinga, 2007). A nutrient-enriched, porous, moist, stable soil environment facilitates the active recruitment and establishment of a diverse range of vascular plants (Schlesinger and Pilmanis, 1998). This explains why subclass P1 had the highest species richness ($P<0.05$) as well as having higher proportions of favourable plant functional groups.

Plant species are known to differ in their rates and pathways by which they process resources, in their effects on the physical environment, and in their interactions with other species (Chapin *et al.* 1997). Therefore, higher numbers of a diverse range of plant species within a patch provide stability to ecosystem processes. The increased amount of soil carbon within P1 patches suggests that the plants deposit surface litter and the action of micro-organisms decomposes and incorporates the litter into the soil, which reduces bulk density ($P<0.05$) through increasing the soil humus. The reduced soil bulk density improves the soil‟s infiltration rate. These higher order patches (P1) have the capacity to infiltrate water at least 50% faster compared to lower order patches and up to 72% faster compared to lower order interpatch zones (P11). In water-constrained environments, it is important to maintain a balanced composition between higher order patches and resource-shedding interpatches.

In the study region, rainfall is highly variable (CV ≥34%) and major events are often separated by extended dry periods. Hence, the ability of an individual patch to capture the maximum amount of rainfall during an event and retain it until the next event may well determine its present stability and eventual longevity. The dominant tree or shrub species of the patch may have an important function in enhancing infiltration rates within the patch as it may be acting as an ecosystem „wick‟, whereby the existence of many macropores within the confines of the patch substantially increases the uptake of captured water (Eldridge and Freudenberger, 2005). Slatyer (1965) and Anderson and Hodgkinson (1997) also highlight that the near-vertical architecture of Mulga (*A. aneura*) branches and stems promotes efficient channeling of rainfall to stem bases which increases the amount of water captured.

The infiltration rates of higher order patches (namely subclasses P1, P2, P4, and P5) from this study were consistent with trends observed by other studies that investigated the relationship between patches and infiltration rates (Eldridge and Freudenberger, 2005; Greene, 1992; Pressland, 1973).

The highly functional patch (subclass P1) and the most dysfunctional interpatch (subclass P11) both had larger diameters ($P<0.05$) compared to all the other subclasses. This suggests that at either end of a gradient of functionality, the ecological processes may provide an opportunity to build-up existing favourable patches (subclass P1) or conversely wind and water erosion may result in the expansion of degraded, sealed areas (subclass P11). Studies have shown that increasing size of fertile patches is known to contribute to species richness in local communities (Da-yong *et al*. 2008). The results concurred with this observation as high-order patches (subclass P1, P2 and P4) had a greater diversity and larger number of preferred plant species.

In summary, based on the results in this study, the properties that characterise highly functional patches are:

- < 25% bare-ground and a substantial amount of surface litter that is at varying stages of decomposition;
- elevated soil respiration rates (> 200 mg $CO_2/m^2/hr$);
- moderate to high amounts of soil carbon and nitrogen (soil carbon > 1.5%; C:N ratio > 10:1);
- moderate to high water infiltration rates (> 10 mm/hr);
- moderate plant species richness (> 3 plant species within the patch area); and
- moderate patch size (> 4 m width).

A qualitative ranking of the relative11 patch-interpatch subclasses identified in this study was compiled based on the empirical evidence reported in this chapter (**Table 3-5**). This information is used to assess landscape functionality at a paddock scale in **Chapter 4**.

Table 3-5: Qualitative ranking of ecological functionality of the patch-interpatch subclasses

Functionality gradient category	Patch-interpatch subclass
Highly functional	P1 (high order), P2 (high order)
Functional	P4 (high order), P5 (high order), P7 (high order), P8 (low order), P9 (high order),
Dysfunctional	P3 (low order), P6 (low order),
Highly dysfunctional	P10 (high order), P11 (low order)

3.6 Conclusion

The results in this chapter validate the first and third principles of landscape function theory. Significant patchiness at a patch-scale was found within the study paddocks. This heterogeneity reflects the variation in ecologically functionality that exists at a patch-scale and supports the third principle of the theory that a gradient of functionality exists within landscapes. The empirical results from this chapter support the approach that was taken to intuitively stratify the study paddocks based on 11 different patch-interpatch subclasses.

It was found that highly functional patches (i.e. subclasses P1 and P2) had higher soil respiration rates, elevated amounts of soil carbon and nitrogen, lower soil bulk densities, higher infiltration rates and greater plant species diversity compared to dysfunctional patches and interpatches ($P<0.05$). The results support previous studies that suggest that factors that increase the amount of bare-ground and increase the soil bulk density may reduce the capacity of patches and interpatches to capture and retain water and nutrients.

Chapter 4 uses the information that was developed in **Chapter 3** to examine how the landscape components (i.e. patches-interpatches) „fit and work" together.

Chapter 4
The role of patch patterning in ecological processes at a paddock scale

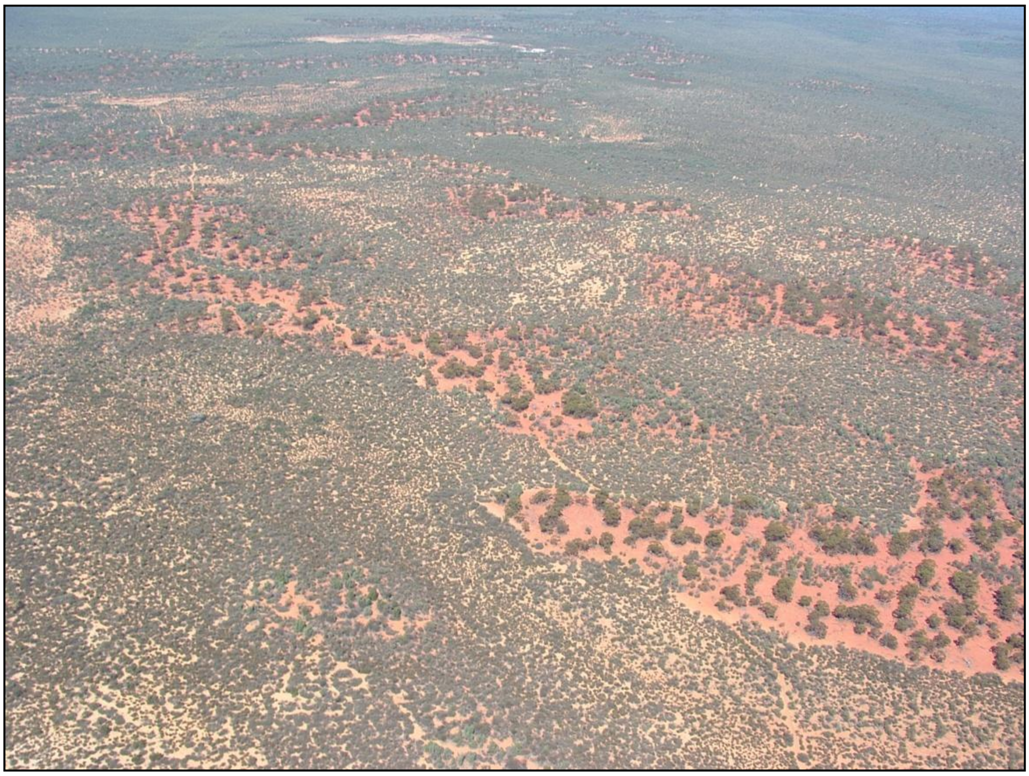


Plate 4-1: Patch patterning at a landscape scale in the lower Murchison region, April 2004
Photo: Mark Alchin

4.1 Abstract

Patches and interpatches maximise primary productivity by distributing and cycling scarce water and nutrients through specific sequences and associations with each other. Homogenisation of this innate patch patterning may lead to suboptimal or, in extreme situations, zero productivity. This chapter found that the second and third principles of landscape function theory could be applied at large spatial scales within semi-arid shrublands. This was achieved by measuring the proportions of the eleven different patch-interpatch subclasses within four study paddocks. Empirical evidence substantiated the first principle of landscape function theory that vegetation and soil nutrients are patchily distributed and demonstrate a distinct level of patchiness. Patch-interpatch subclasses P2, P5, P10 and P11 occurred most frequently and dominated the length of the transects.

Distinct patch patterning between the different land-types was also found. The granitic shrubland land-type had a much greater proportion of the high resource-shedding interpatch P11 subclass (> 85% of the area) compared to the other land-types. In contrast, *Acacia* sandplains had a higher proportion of functional patch subclasses (P1, P5 and P4) compared to granitic shrublands. Depending on the land-type, it was concluded that a functional ecosystem will generally have balanced proportions of P1, P2, P4, P5, P7 and P9 subclasses as these will be the most effective at capturing and retaining water and nutrients. In contrast, a degraded ecosystem will have higher proportions of the ecologically dysfunctional P3, P6 and P11 subclasses. This evidence substantiated the third principle of landscape function regarding dysfunctionality. A number of significant spatial associations and repeating sequences of individual patch-interpatch subclasses were found to occur in the study area. These associations and repeating sequences provided evidence of spatial self-organisation and thereby substantiated the second principle of the landscape function theory. Distance-from-water did not have any significant effect on the relative proportions of the different patch-interpatch subclasses at a paddock scale.

4.2 Introduction

Plant cover in ecosystems that are severely water-constrained is not continuous and is typically less than 60% (Aguiar and Sala, 1999). The low amount of total plant cover is an adaptation to optimise the use of limited water and nutrients. In a homogenous ecosystem, water and nutrients are distributed evenly and if the amount of resources is limited, it will affect the ecosystem‟s ability to maintain soil biological processes and plant growth. Noy-Meir (1973) named this dynamic the „ineffective precipitation‟ or „zero yield‟ intercept.

In ecosystems with homogeneous plant cover, which receive precipitation equal to P_a, plant production will be zero because it is below the production threshold (**Figure 4-1**). In contrast, plant production in ecosystems with heterogeneous plant cover may be determined by a different equation (dashed line in **Figure 4-1**). According to the Noy-Meir (1973) model, dysfunctional patches-interpatches will lose water, causing a shift in status from P_a to P_o without changing their production which is already zero. As a consequence, functional patch-interpatch subclasses may have a higher water availability, P_i resulting from the water that falls directly on them, in addition to the run-on transported from the dysfunctional subclasses. Therefore, plant production in ecosystems with a high amount of patchiness may be greater. This highlights how patch-interpatch subclasses „fit and work‟ together to maintain ecological processes in semi-arid shrubland environments.

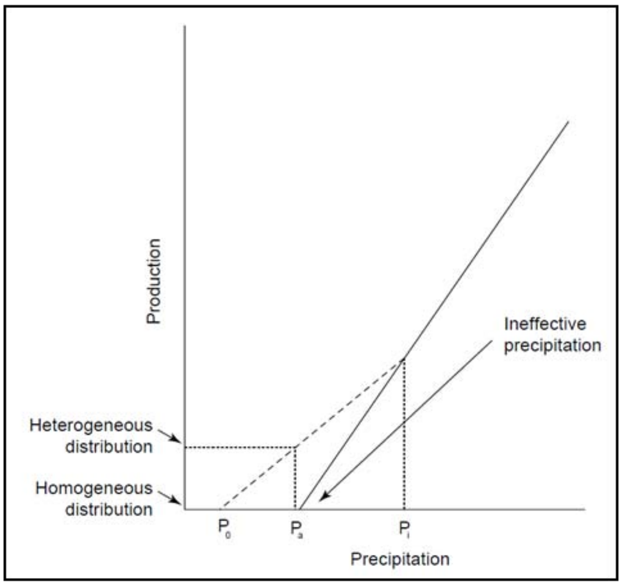


Figure 4-1: Hypothetical relationship between mean annual precipitation and production for arid and semi-arid ecosystems (unbroken line) (reproduced from Noy-Meir, 1973)

Studies have shown that water and nutrients are unlikely to be evenly distributed at large spatial scales (Pickup, 1985). Furthermore, highly functional patches are likely to be the products of a process of „self-enhancement‟ whereby these patch subclasses capture and retain additional water and nutrients (Pickup, 1985). These processes are critical to optimise the use of limited moisture and nutrients in semi-arid shrublands. Based on previous research, high levels of self-organisation and spatial patterning are likely to occur at large spatial scales (Aguiar and Sala, 1999; Holm *et al.* 2002a;

Ludwig *et al*. 2005; Ludwig *et al*. 2002; Rietkerk *et al.* 2000; Schlesinger and Pilmanis, 1998; Tongway *et al*. 2003). Therefore, if there are clear associations between different patch-interpatch subclasses then this will provide evidence of the landscape components „working together" to optimise the use of water and nutrients.

Pringle *et al*. (2006) demonstrated that the innate patch-interpatch patterning of semi-arid landscapes could be radically altered when excessive grazing occurs and initiates degradation processes. These degradation processes can be self-perpetuating even if grazing is subsequently eliminated. This issue will be investigated in this chapter by exploring the effect of distance-from-water on the proportions of the patch-interpatch subclasses. Distance-from-water is often used as a surrogate measure to estimate grazing pressure within a paddock (Pringle and Landsberg, 2004). This is because it can be difficult to obtain an accurate estimate of total sheep and non-domestic grazers (i.e. kangaroos and feral goats) numbers. However, studies have found that the location of watering points affects grazing distribution and associated forage removal (Hunt *et al*. 2007; Martin and Ward, 1970).

It is expected that the level of grazing pressure close to a watering point would be higher because grazers will spend a disproportionate amount of their time in this area. Topography, shade cover and wind speed and direction are also important factors that can influence the impact of grazing on the natural patchiness of an ecosystem (Brock and Owensby, 2000; Cook, 1966; Gillen *et al*. 1984; Harris *et al.* 2002; Orr 1980).

The four primary principles that underpin landscape function theory are:

1. Patchiness can be characterized by the patch size, orientation, spacing and soil surface condition.
2. Natural landscapes have a characteristic spatial self-organisation, often expressed as patchiness.
3. Deviations from the „characteristics" or „natural" patchiness are seen as degrees of dysfunctionality, and there is a long gradient from highly functional to highly dysfunctional patches.
4. Restoration or replacement of missing or ineffective processes in the landscape will improve soil surface conditions and soil habitat quality (Ludwig *et al*. 1997).

In **Chapter 3**, clear evidence of the first and third principles of landscape function theory was found at a patch scale in the study area. This chapter sought to test if principles two and three apply in the study paddocks. This chapter uses the information about the characteristics of the patch-interpatch subclasses that was developed in **Chapter 3** to examine how the landscape components (i.e. patches-interpatch subclasses) fit and work together. It investigates three specific questions: (1) is there empirical evidence to support the concept that vegetation and soil nutrients are patchily distributed at a paddock scale?; (2) are their significant spatial associations and repeating sequences of individual patch-interpatch subclasses at a paddock scale?; and (3) does distance-from-water have any effect on how the different patch-interpatch subclasses fit together?

The chapter explores the implications of patch patterning in terms of the relative capacity of semi-arid shrubland environments to efficiently capture, retain and cycle water and nutrients and thus tests principle 2 of the landscape function theory.

4.3 Methods

A description of the soil and vegetation of the four case study paddocks is presented in **Sections 2.5** to **2.6**. Assessments on transects were conducted to measure the degree of patch-scale heterogeneity and determine the level of patch patterning within the four study paddocks. This information was used to evaluate the relative proportions of the patch-interpatches subclasses within the paddocks and their associations with each other (refer to **Chapter 3**, **Table 3-1** for a description of the 11 patch-interpatch subclasses).

4.3.1 Line intercept transect site selection

A minimum of six line intercept transects were located in each study paddock (**Figure 4-2**). The line intercept transects were a minimum of 900 m in length. Each study paddock had a minimum number of six transects, and the larger paddocks had up to nine (a total of 30 transects were measured). The number of transects in each paddock was guided by the objective of achieving adequate representation of the dominant land-system in each paddock. The criteria used to determine the specific location of the seven transects were:

- at least two transects in the dominant land-type in each paddock (based on the categories in **Table 2-5**);
- approximately one kilometre intervals from permanent watering;
- transects were generally located to avoid intersecting the ecotones; and
- the starting point of transects was generally at close proximity to existing access tracks.

The dominant land-type of study paddocks 1 and 2 was *Acacia* sandplains, with less than 20% of the paddocks‟ areas consisting mainly of hardpan plains and granitic shrublands. Consequently, all of the transects in study paddocks 1 and 2 were located in *Acacia* sandplains. In contrast, study paddocks 3 and 4 had a more diverse mix of land-types. Therefore, transects were located in *Acacia* sandplains, hardpan washplains, granitic shrublands and alluvial plains.

The first of the seven transects in each paddock commenced at a distance of one kilometre from a permanent watering point (**Figure 4-2**). Depending on the layout of the access tracks and the associations of the land-types, successive transects were located at approximately one kilometre intervals from water. Access to some areas of the paddocks was severely limited and hence sampling throughout all areas of the paddock could not be achieved. Transects were started at least 100 metres from the access track to avoid disturbance and edge effects.

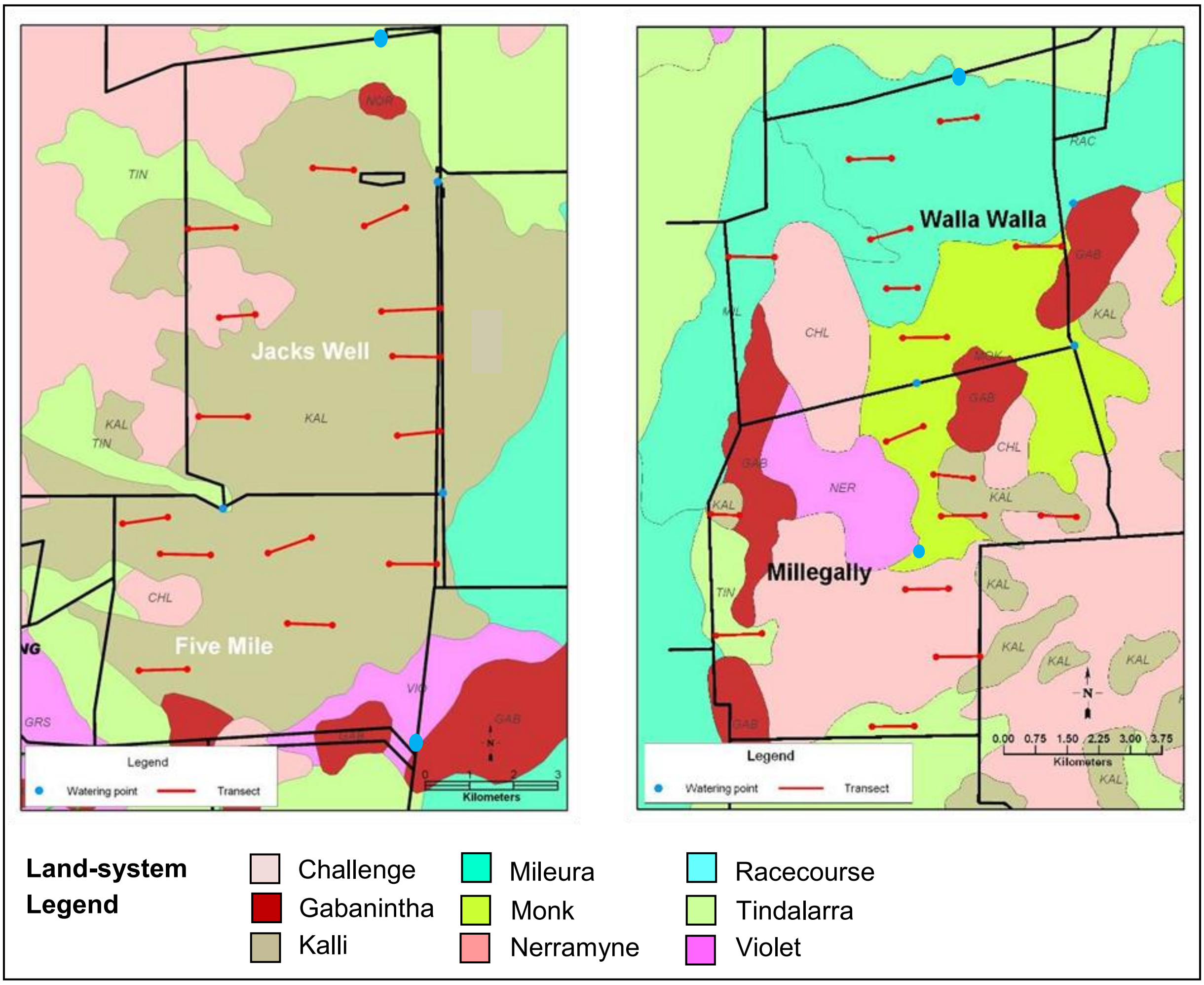


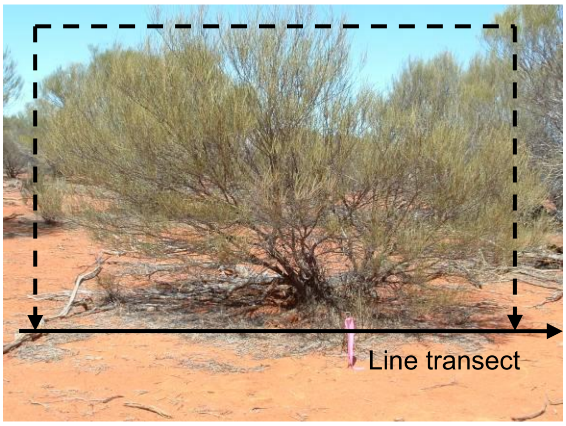
Figure 4-2: Location of line intercept transects in study paddocks 1 and 2 (left) and study paddocks 3 and 4 (right). Note: The colour coding and corresponding three-letter prefix shows the patterning of the different land-systems in the study paddocks (see Payne *et al.* 1998 for a full description)

4.3.2 Line intercept transect method

After taking a GPS waypoint at the start of each transect, a second waypoint was marked at a minimum distance of one kilometre either directly west or east from the original starting point. Using the GPS beeline tracking feature, I traversed towards the second waypoint and monitored the distance travelled. The orientation of some of the transects was not precisely due east or west. This was only discovered once the transects were mapped digitally and it is likely to be caused by the strength of the satellite signal at the time those transects were completed.

The data from the line intercept transects provided the proportion (%) of the transect that each of the 11 different patch-interpatch subclasses comprised (refer to **Table 3-1** for description of patch-interpatch subclasses). Guided by a GPS, the length along the intercept line for each patch and interpatch subclass encountered was recorded (measured by the number of steps to 0.25 fractions).

The boundaries of vegetation patch subclasses began and ended were defined at the outermost limits of its crown (**Plate 4-2**).



The actual length that would be recorded as a part of the transect was determined by the outreaches of the shrub‟s crown intersecting the transect line

Plate 4-2: Example of the spatial limits of a patch along a line line intercept transect

In situations where it was physically impossible to ingress through the middle of a shrub patch due to extremely thick vegetation, I made a mark on the line intercept transect line and moved a perpendicular distance to the left-hand side of the patch and continued with the intercept-distance measurement until the patch ceased. At the end of the patch intercept, I returned to the line intercept transect line position and continued following the transect line (**Figure 4-3**).

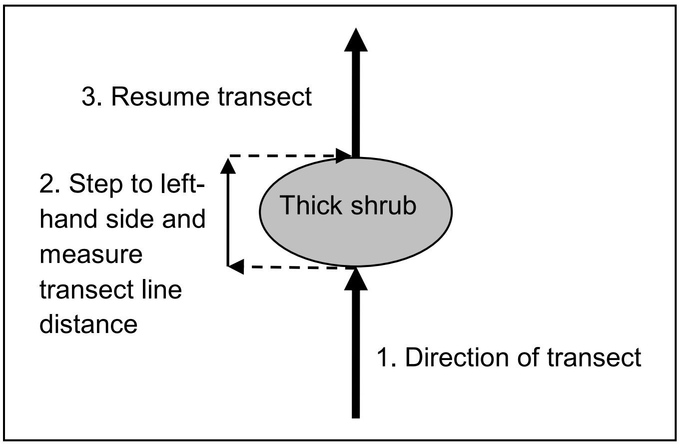


Figure 4-3: Approach used to maintain the line intercept transect line when navigating around thick shrubs

Where multiple patches (generally P1, P2, P4 and P5 subclasses) were adjacent to one another without intervening interpatches, these were recorded as separate entities based on the outer limits of their crown intercepts (**Plate 4-3**).

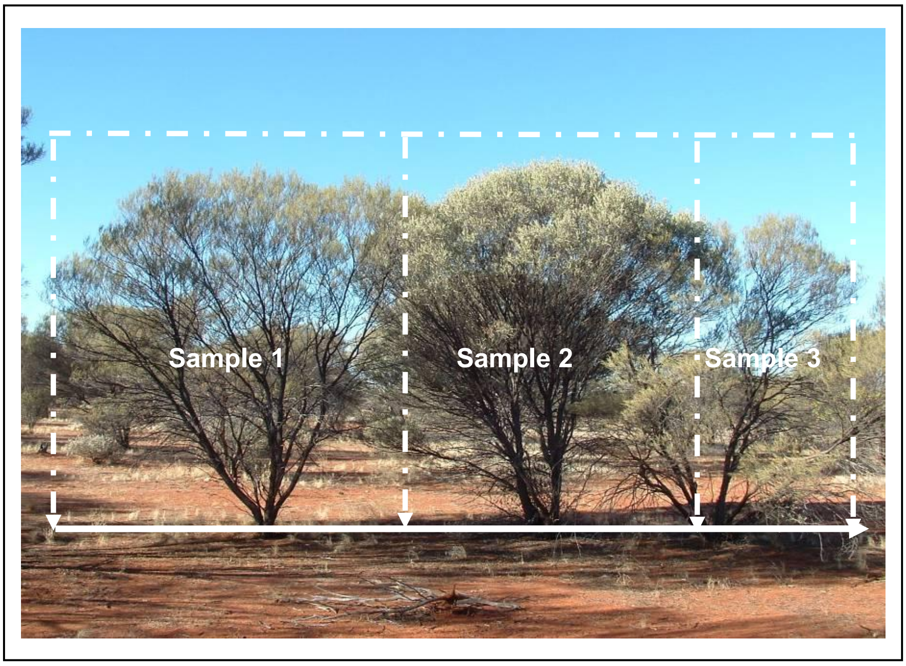


Plate 4-3: Example of recording individual patches based on limits of their crown intercepts

For each patch-interpatch subclass encountered along a line intercept transect, the following parameters were recorded:

1. distance intercepted by the transect line (number of steps to the closest 0.25 fraction);
2. the patch-interpatch subclass ID; and
3. the number of perennial plant species present.

Transect step data were converted into metric measurements (average observer step = 0.93 m). A total distance of 31.7 km was covered by the transects and a total of 7,887 individual patches-interpatches were measured.

4.3.3 Statistical analysis

The data from the transects were compiled and basic descriptive statistics including one and two-way ANOVAs were conducted to identify any obvious differences and trends in the proportions of the patch-interpatch subclasses. On completion of this initial examination, general linear models, regressions and ANOVAs were used to determine the significance level of all the factors and variates (**Table 4-1**). The following is a list of the factors and variates included in the models that may have caused significant variation:

- the land-type (a total of 4);
- the distance of the transect starting point from permanent water (km);
- paddock stocking rate (the average percentage difference from the recommended carrying capacity from 1991 to 2007); and
- the grazing history (grazing history was differentiated by whether the paddock was continuously grazed or summer-rested during 2001 to 2007).

All factors, variates and their interactions were initially included in the general linear models (maximal model) and non-significant terms were eliminated from the fitted models after examination of the accumulated analyses of variances. The principle of marginality was adhered to (i.e. non-significant main effects of factors and variates were not removed if they were involved in a significant interaction).

Table 4-1: Summary table of statistical approach used to test the Chapter 4 hypotheses

Hypothesis	Approach used to test null hypothesis	Factors (F) and Variates (V)	Outcome of analysis
1. There was significant variation between the proportions of the different patch-interpatch subclasses at a paddock scale.	General linear model with step-wise forward and backward elimination. Use of the predictive function of the model. Diagnostic biplot. Principal component analysis.	Grazing history (F), Land-type (F) Distance-from-water (V) Stocking rate (V), Transect data (V)	Characterisation of patch heterogeneity of different land-types within the four case study paddocks.
2. There are significant spatial associations between certain patch-interpatch subclasses.	Pearson Chi-square test.	Expected and observed probabilities of spatial association of patch-interpatch subclasses	Differences between observed and expected probabilities of spatial associations that will indicate the degree of spatial organisation.
3. The proportion of functional patch-interpatch subclasses increased at greater distances from permanent water.	General linear regression with step-wise forward and backward elimination.	Grazing history (F), Land-type (F) Distance-from-water (V) Stocking rate (V), Transect data (V)	The fitted relationships between distance-from-water and the proportions of the different patch-interpatch subclasses grouped according to land-type.

4.3.3.1 Hypothesis 1 – Spatial self-organisation at a paddock scale?

The final general linear model used to test hypotheses 1 was (see footnote[6]):

Maximal model: land type * distance from water + stocking rate * distance from water + land type.stocking rate + grazing history * stocking rate + grazing history.land type + distance from water.grazing history

Fitted model: Constant + land type + distance from water + land type.distance from water

A diagnostic biplot was used to identify the variation in the proportions of the subclasses of each transect. The biplot also assisted in highlighting the relationships between the patch-subclasses themselves. A principal component analysis was used to identify how much of the total variation was accounted for by the first two components presented in the biplot.

4.3.3.2 Hypothesis 2 – Spatial association - patches-interpatches working together?

A Pearson Chi-square distribution was used to test hypothesis 2. If the null hypothesis was true (i.e. no spatial associations exist between the patch-interpatch subclasses), each subclass would have a chance of neighbouring each of the different subclasses in proportion to the frequency of their occurrence. The Pearson Chi-square test investigated whether certain patches-interpatch subclasses have a higher probability of occurring with other particular subclasses. The results would identify the specific associations between different patch-interpatch subclasses in terms of how they both fit and work together.

4.3.3.3 Hypothesis 3 – Effect of distance-from-water on how patches-interpatches fit and work together

A general linear regression was first used to determine whether distance-from-water had an effect on the proportions of the different subclasses. These results would identify how grazing pressure would impact on how the subclasses fit together. The final general linear model used to test hypothesis 2 was:

Fitted model: Constant + distance from water + land type + distance from water.land type

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[6] Within the models "*" signifies multiplication of both the main effects and the interaction of two components in the model and "." signifies only the interaction between two components of the model.

4.4 Results

4.4.1 Hypothesis 1 – spatial self-organisation at a paddock-scale?

There was significant variation in the proportions of the different patch-subclasses within the study paddocks ($P< 0.05$). Patch-interpatch subclasses P2, P5, P10 and P11 occurred most frequently and dominated the length of the transects (**Table 4-2**). The four study paddocks had relatively similar proportions occupied by patches (the sum of subclasses P1 to P8). Study paddock 1 had the highest proprtion (%) occupied by patches and study paddock 4 had the lowest (35.7% and 27.5% respectively).

The general linear model (as described in **Section 4.3.3.1**) indicated that the highly significant variation between the transects was primarily the result of land-type ($P<0.001$) and to a lesser extent distance-from-water ($P=0.165$) and the interaction between these two factors ($P=0.256$). Based on this result, hypothesis 1 was accepted as significant variation in the proportions of the patch-interpatch subclasses could be detected at a paddock-scale. The results clearly demonstrated that some patch-interpatch subclasses occurred more frequently than others.

Table 4-2: Proportions of the transects occupied by the different patch-interpatch subclasses

Patch-interpatch subclass	Proportional length of transects (% mean and ± standard error)			
	Paddock 1	**Paddock 2**	**Paddock 3**	**Paddock 4**
P1	0.64 ± 0.41	0.54 ± 0.36	1.70 ± 0.62	0.83 ± 0.45
P2	13.85 ± 1.82	11.95 ± 2.98	10.67 ± 3.52	6.80 ± 2.24
P3	0.60 ± 0.31	0.67 ± 0.37	2.36 ± 1.06	2.55 ± 0.77
P4	0.84 ± 0.67	0.03 ± 0.03	0.47 ± 0.17	0.34 ± 0.22
P5	18.25 ± 3.30	17.82 ± 2.09	16.05 ± 4.04	13.28 ± 3.44
P6	0.29 ± 0.15	1.51 ± 0.65	2.74 ± 0.77	3.62 ± 1.37
P7	0.008 ± 0.008	0.04 ± 0.04	0.12 ± 0.12	0 ± 0
P8	1.24 ± 1.004	0.33 ± 0.24	0.08 ± 0.04	0.05 ± 0.02
P9	10.96 ± 1.31	9.83 ± 1.41	5.65 ± 1.77	3.29 ± 1.15
P10	47.84 ± 2.47	48.34 ± 2.25	34.21 ± 4.89	38.17 ± 5.50
P11	5.44 ± 1.71	8.88 ± 1.72	25.90 ± 8.89	31.02 ± 8.53

The general linear model was also used to predict the composition of the patch-interpatch subclasses for the four major land-types (**Table 4-3**). Granitic shrublands had a much greater proportion of the high resource-shedding interpatch P11 subclass compared to the other land-types. In fact, over 85% of granitic shrublands comprised interpatch subclasses (P9, P10, and P11). This land-type had small proportions of the ecologically functional patches (namely P1, P4, P7 and P8), and had comparatively high proportions of P3 and P6 subclasses which have a limited capacity to capture and retain water and nutrients (**Chapter 3**). The granitic shrublands had very few perennial grass patches.

In contrast, *Acacia* sandplains had a higher proportion of functional patches (P5), highly dysfunctional interpatches (P10) and ecologically functional patches (P1 and P4) compared to granitic shrublands. Hardpan washplains were dominated (>70%) by interpatch subclasses P10 and P11. Furthermore, ecologically functional patches were poorly represented in hardpan washplains (≤ 0.2%) while low-order patches (P2, P3, P5 and P6) occupied over one quarter of the area. Alluvial plains had the largest proportion of ecologically functional patches compared to the other land-types. Subclasses P1, P2, P4, and P5 were all significant features of this land-type; perennial grass patches P7 and P8 also were comparatively well represented.

Table 4-3: Patch-interpatch subclass composition of different land-types

Patch-interpatch subclass	**Predicted proportions of patch-subclasses (% mean and ± standard error)**			
	Granitic shrubland	***Acacia* sandplains**	**Hardpan washplains**	**Alluvial plains**
P1	0.0 ± 1.50	0.9 ± 0.29	0.1 ± 0.56	2.4 ± 0.56
P2	1.9 ± 8.12	12.4 ± 1.55	5.0 ± 3.00	15.0 ± 3.01
P3	5.6 ± 1.81	0.6 ± 0.35	3.5 ± 0.67	1.9 ± 0.67
P4	0.0 ± 1.31	0.5 ± 0.25	0.2 ± 0.48	0.4 ± 0.48
P5	3.4 ± 8.90	18.8 ± 1.70	12.6 ± 3.29	16.5 ± 3.30
P6	3.1± 1.77	0.8 ± 0.34	4.1 ± 0.65	2.1 ± 0.66
P7	0.0 ± 0.22	0.0 ± 0.04	0.0 ± 0.08	0.2 ± 0.08
P8	0.0 ± 1.85	0.6 ± 0.35	0.1 ± 0.68	0.1 ± 0.68
P9	1.6 ± 5.12	9.3 ± 0.98	2.6 ± 1.89	6.8 ± 1.90
P10	8.9 ± 11.40	47.9 ± 2.17	37.7 ± 4.22	36.5 ± 4.23
P11	75.5 ± 14.34	8.2 ± 2.73	34.0 ± 5.3	18.1 ± 5.32

4.4.2 Hypothesis 2 – spatial associations – patches-interpatches working together?

A Pearson Chi-square distribution test investigated whether certain patches-interpatch subclasses have a higher probability of occurring with other particular subclasses. These results would identify the specific associations that may exist between different patch-interpatch subclasses and provide insight into how the subclasses both fit and work together.

Based on the second principle of landscape function theory concerning „spatial self-organisation", it was anticipated that some patch-interpatch subclasses would have a higher probability of being associated with other particular subclasses. Specifically, it was predicted that highly functional and functional patches (P1, P2 and P4 subclasses respectively) would occur with interpatches that have moderate to high amounts of surface litter and woody debris (P9 and P10 subclasses). In contrast, leaky, dysfunctional shrub patches (P3 and P6 subclasses) would occur with highly dysfunctional interpatch areas (P11 subclass).

The expected probabilities of occurrence were calculated for particular patch-interpatch subclasses based on the assumption that there was no spatial self-organisation. The probability of sampling particular subclasses if they were all randomly distributed was modeled (**Figure 4-4**). If there was no spatial self-organisation in the study paddocks (i.e. homogeneous landscape) then all of the patch-interpatch subclasses would occur in equal proportions. However, the results indicate the opposite; there was significant variation in the probability of occurrence of the different patch-interpatch subclasses (i.e. heterogeneous landscape). For example, there is a 27.3% probability that subclass P5 (woody patch < 3 metres in height) will occur in the landscape compared to only a 0.1% probability of subclass P7 (groups of perennial grasses) occurring.

The significantly higher proportions of P5, P9, and P10 subclasses reflect the general functionality of the study paddocks. The very low occurrence of perennial grass patches (P7 and P8 subclasses) was of notable concern, but may have partially reflected the below-average seasonal conditions in 2006 (this topic is explored in detail in **Chapter 5**). It was predicted that a functional ecosystem will have balanced proportions of P1, P2, P4, P5, P7 and P9 subclasses as these will be the most effective at capturing and retaining water and nutrients. In contrast, a degraded ecosystem will have higher proportions of the ecologically dysfunctional P3, P6, and P11 subclasses.

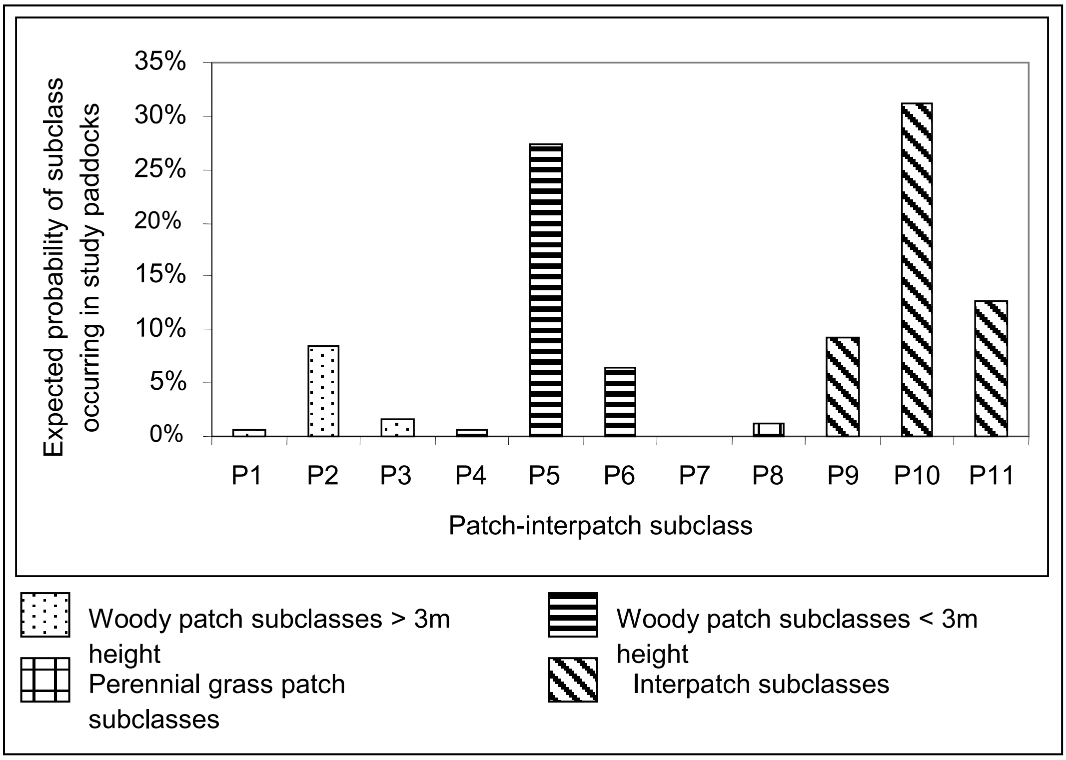


Figure 4-4: Expected probabilities of patch-interpatch subclasses occurring based on the calculated chi-square distribution

The expected probabilities were compared to the observed. The results from this analysis suggested that there were clear associations between particular patch-interpatch subclasses and that there was a defined level of spatial self-organisation. The differences between observed and expected probabilities of patch-interpatch subclasses occurring in association were analysed (**Table 4-4**). The greater the value in the body of **Table 4-4**, the stronger is the association between the two subclasses. If the difference is positive, it means that there is a higher than a random probability that those two subclasses will occur adjacent to each other. Conversely, a negative difference suggests that there is a lower than a random probability that the two subclasses will be „neighbours‟. For example, if there was no spatial organisation the expected probability of subclass P1 directly neighboring a P5 patch is 27.3%, the observed probability was 7.6% (therefore the difference was -19.7%, hence there is a strong disassociation between P1 and P5 patches, and they are unlikely to occur as neighbours.

Table 4-4: Difference between observed and expected probabilities (%) of patch-interpatch subclasses occurring in association with each other

***Expected probability %**	0.5	8.4	1.6	0.5	27.3	6.4	0.1	1.1	9.2	31.2	12.6
	P1	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**	**P11**
P1	2.3	-2.9	-1.6	1.6	-19.7	-6.5	-0.1	0.2	15.8	15.3	-3.6
P2	-0.2	6.6	-1.3	-0.5	-19.0	-6.2	0.0	-0.9	7.0	20.6	-5.8
P3	-0.5	-6.9	1.4	-0.5	-23.4	-3.4	-0.1	-0.7	-6.8	2.9	38.9
P4	1.5	-7.8	-1.6	0.8	-22.6	-5.1	-0.1	2.2	16.5	14.0	-0.5
P5	-0.4	-5.9	-1.4	-0.4	-12.5	-6.1	0.0	-0.8	1.3	24.2	2.4
P6	-0.5	-8.1	-0.9	-0.4	-25.5	-1.7	-0.1	-1.1	-7.8	7.8	38.8
P7	-0.5	0.6	-1.6	-0.5	-9.1	-6.5	-0.1	-1.2	-0.1	32.4	-12.6
P8	0.1	-6.3	-1.0	1.0	-18.4	-6.2	-0.1	-1.2	0.3	37.6	-5.2
P9	0.9	6.4	-1.2	0.9	3.9	-5.5	0.0	0.0	-8.8	11.6	-7.6
P10	0.2	5.6	0.2	0.2	21.1	1.6	0.1	1.4	3.4	-30.7	-2.9
P11	-0.1	-3.9	5.1	0.0	5.3	19.9	-0.1	-0.5	-5.6	-7.2	-12.6

***The expected probabilities on the first row indicate the occurrence of the different subclasses within a landscape if their patterning was completely random. The values in the body of the table are the differences between the observed and expected probabilities; the larger the value (whether positive or negative) the greater the degree of association (+) or disassociation (-).**

There were a number of consistent associations among the patch-interpatch subclasses. First, high-order patches (P1, P2, and P4) had a strong association with high-order interpatches (P9). For instance, there was a strong probability (difference 15.8%) that patch P1 would have interpatch P9 as a neighbour. The converse to this pattern also held true; the lowest-order shrub patches (P3 and P6) probably will occur next to ecologically dysfunctional interpatch areas (P11) rather than next to interpatches which are more functional (P9).

The second association was that high-order patches tend to occur with other high-order patches. Referring back to the field data, this appears to result from the existence of small groves (generally three to four adjoining patches) in which the individual woody patches form a dense canopy and understorey and creates a grove of trees/shrubs. The third association evident in the data is that groups of perennial grasses (P7 subclass) and isolated perennial tussocks (P8 subclass) tend to occur more regularly with ecologically functional interpatches than with larger, functional shrub or tree patches. For example, the observed probability of groups of perennial grasses (P7) occurring with highly dysfunctional interpatches (P10) was 32.4% more than the expected probability (i.e. a strong association). This is in contrast to the tendency of disassociation of perennial grass patches P7 and P8 from all the other patch subclasses.

4.4.3 Hypothesis 3 - the effect of distance-from-water on how patch-interpatches fit and work together

One would expect that at increasing distances from water the total area occupied by patches would increase and gradually plateau off and reflect the natural proportions of an undisturbed landscape. This is based on the premise that overgrazing can reduce the number of functional patches. Hence, at greater distance-from-water the level of impact from overgrazing may be reduced. However, the results suggest that distance-from-water had no significant effect (P=0.165) on the proportion of total patches (P1 to P8) and total interpatches (P9, P10, P11) recorded along the transects, even when analysed according to land-type (P=0.256). This indicates that the proportion of functional patches was not significantly influenced solely by distance-from-water.

When the subclasses were analysed individually (as opposed to subtotals of patches and interpatches), distance-from-water and its interactions still had no significant effect (P>0.05). In other words, not only did distance-from-water have no effect on total patch cover, it also did not affect the „quality" of the patches, irrespective of land-type.

There was a greater number of transects located in *Acacia* sandplains (n=18), hence the effect of distance-from-water on patch cover within this land-type is considered to be the most definitive. Distance-from-water had a negligible effect on total patch cover in this land-type. The majority of the transects within *Acacia* sandplains were in study paddocks 1 and 2 (n=14). Based on this result, it was inferred that previous grazing pressure might not significantly have altered the total patch cover. In summary, no clear relationships or trends were detected between distance-from-water and patch patterning in any of the study paddocks.

4.5 Discussion

4.5.1 Spatial self-organisation at a paddock-scale

Resources were not evenly distributed throughout the landscape and highly functional patches appear to be the product of a process of „self-enhancement‟ whereby they capture additional water and nutrients (Pickup, 1985). There were significant associations ($P<0.05$) between particular subclasses which concurred with other studies that identified similar high levels of self-organisation and spatial patterning (Aguiar and Sala, 1999; Holm *et al.* 2002a; Ludwig *et al*. 2005; Ludwig *et al*. 2002; Rietkerk *et al.* 2000; Schlesinger and Pilmanis, 1998; Tongway *et al*. 2003). This innate patterning can be altered when overgrazing occurs and initiates degradation processes that can be self-perpetuating (particularly in the form of subclass P11) even if grazing is subsequently eliminated (Pringle *et al.* 2006).

Functional patches (e.g. subclasses P1, P2, and P4) are likely to be more resistant to disturbance and they will benefit from the increased outflow of water from stripped dysfunctional patch-interpatches (Pickup, 1985). This process can further consolidate the ecological functionality and erosive resilience of functional patch-interpatches (Pickup, 1985). At a paddock scale, this may reduce the overall primary productivity, fragment habitat and compromise many ecosystem services (e.g. water recharge, biosequestration, and biodiversity). This is because the previously patterned distribution of nutrients and moisture becomes concentrated in a limited number of isolated patches.

The high level of spatial self-organisation of patch patterning can be progressively reduced by homogenisation of the ecosystem‟s resources. Noy-Meir‟s „ineffective precipitation‟ model (refer to **Figure 4-1**) highlights that homogenisation of the resources will have an adverse effect on the inherent productivity of the ecosystem and can significantly limit its capacity to respond to rainfall events. Therefore, management may need to respond to the early warning signs of change to the natural proportions of patches and interpatches and / or their relative patterning in order to prevent any systemic degradation impacts.

The prediction that functional ecosystems will have balanced proportions of ecologically functional patches and interpatches was supported by the results. Overall, the paddocks had moderate to low proportions of high-order patches; however, where they did occur, they were closely associated with each other. Results from **Chapter 3** indicate that the high-order functional patches were acting as a sink for the additional water and nutrients transported from the run-off areas in poorer condition, and were biologically rich. The run-off areas were composites of patches and interpatches (namely P3, P6, and P11) that had very few obstructions to restrict the movement of overland water-flow.

Pringle *et al*. (2006) discuss how the spatial linking of leaky patches (primarily woody shrub canopies over bare-ground and stripped soil interpatches) is a clear indicator that the ecosystem has undergone a fundamental shift in the ecohydrological conditions; the „plug has been pulled" at critical control points. When the ecosystem gets to this stage, restabilisation and restoration will not occur through above-average seasons and rest from grazing and may require some form of active intervention.

The second principle of the landscape function theory was demonstrated by the results. The four land-types within the study paddocks (i.e. granitic shrublands, hardpan washplains, *Acacia* sandplains and alluvial plains) each had a characteristic patch pattern indicating a strong spatial self-organisation. Sections **4.5.1.1** to **4.5.1.4** discuss the innate patch patterning of each individual land-type.

4.5.1.1 Granitic shrublands patch patterning

Over 86% of granitic shrublands was comprised of interpatch, much of which was of the highly dysfunctional subclass P11 that indicates that this land-type acts as an erosional surface within the study paddock. Shrub subclass P3 was the most common patch in granitic shrublands and was dominated by resilient shrub species that usually produce limited amounts of litter (namely *Acacia grasbyi, A. xiphophylla* and *Hakea preissii*). The paucity of surface litter and related poor soil conditions (i.e. low infiltration, lower microbial activity, higher soil bulk density, and variable soil temperature) within these patches provide few sites where less xerophytic sub-shrubs and grasses can establish (refer to **Chapter 3**). These patches were generally interspersed with moderately fertile P5 patches (dominated by *A. aneura*), and smaller P6 patches which were dominated by coloniser species (e.g. *Ptilotus obovatus*) (refer to **Appendix 2** for raw data).

The extended dry conditions prior to the field survey meant that although the *P. obovatus* P6 patches were mature, they were primarily just woody stems without much standing leaf and poor litter accretion around the patch. Despite this, the *P. obovatus* patches are valuable components because they will respond rapidly with the return of effective rainfall and produce substantial amounts of litter and seed. The collective patch pattern of granitic shrublands produces a comparatively „depressed" biotic feedback loop and causes the land-type to remain a resource-shedding, erosional surface (Payne *et al.* 1998).

This role is important because rainfall is relatively low and evapotranspiration is high in the region. Evapotranspiration of mulga communities has been recorded at 4.7 mm per day and soils can reach wilting point within 60 days after effective rainfall (Pressland, 1976b). Therefore, the depositional land-types often rely on additional inflow from run-off land-types to maintain their vegetation communities.

Maintaining the limited number of shrub patches within granitic shrublands (<15%) is crucial to its long-term functionality as recruitment can be low and episodic (Watson *et al.* 1996). If the dominant shrub of a patch dies and grazing inhibits a juvenile taking its place, then there is a higher risk in this land-type that the patch will be destroyed and the nutrients mobilized and dispersed. If this phenomenon becomes widespread it may have adverse consequences for patch patterning and associated ecological processes within the study paddocks. Therefore, it is suggested that grazing pressure and other disturbances be limited in this land-type during periods of plant recruitment and establishment.

4.5.1.2 Hardpan washplains patch patterning

Hardpan washplains also had a large area of run-off subclasses (71.7%) and had the highest proportion of dysfunctional P3 and P6 shrub patches compared to the other land-types. This indicates two things: 1) the land-type plays a role in carrying diffuse sheet-flow to communities down-slope; and 2) the land-type is easily disturbed. Dysfunctional P3 shrub patches in this land-type were dominated by *Acacia* spp. (namely *A. aneura* and *A. grasbyi*), indicating that any litter that accumulates under these shrubs had been mobilized. A redistribution of litter is a natural and necessary process; however, the high frequency of established *Acacia* shrubs with limited litter underneath indicated that this process had been accelerated. Patch subclass P5 dominated by *A. coolgardiensis* was a major feature (12.5%) of this land-type, and this shrub species is known to generate significant loads of litter which can enhance nutrient cycling.

To maintain hydrological function in hardpan washplains a close association between perennial grasses and the established shrub patches is necessary (Anderson and Hodgkinson, 1997; Greene *et al.* 1994). Dunkerley and Brown (1999) found that on a given gradient, flow speeds and soil shear stresses are inversely proportional to the surface roughness. The opportunity time for infiltration was promoted by the surface roughness acting to retard flow, and the lowered flow speeds restricted the degree of surface scour (Dunkerley and Brown, 1999). The negligible representations of perennial grass patches (<1%) in this land-type indicated a reduced surface roughness and associated increase of surface run-off. Consequently, the reduced surface roughness may require even bigger rainfall episodes in order to wet-up the profile and permit the reestablishment of perennial grasses (Chartier and Rostagno, 2006).

The functional patterning (i.e. a balanced assemblage of shrubs, grasses, woody debris and interpatches) of hardpan washplains may be reconstituted through a build-up of organic matter during effective seasons and management of total grazing pressure (Payne *et al*. 1994). Depending on the seasons, this may occur over an inter-decadal timescale; however, the process will be compromised if there are extensive, incised drainage tracts and / or an exposed, dispersive subsoil (Pringle, 2006).

4.5.1.3 Acacia sandplain patch patterning

Acacia sandplains were characterised by a high frequency (18.8%) of low *Acacia* shrubs (namely *A. coolgardiensis* and *A. linophylla*) with reasonable amounts of accumulated litter (P5 patches). The combination of the deep sand profile and the minimal distances between functional patches results in mostly diffuse, internal drainage. The species diversity of this land-type was unexpected; it had over 50 different shrub and grass species which is an indication of high ecological functionality. Indeed, sandplains had the lowest percentage of degraded interpatches (P11) and had balanced proportions of high-order patches, including perennial grass patches.

Despite this generally functional patch patterning, there were differences between the transects primarily in a shift from high proportions of functional P1, P2 and P9 patches towards increasing proportions of P5 and P10 patches. This indicated a decline in surface roughness. However, in this land-type the internal drainage assists in preventing major shifts to lower subclasses (e.g. P1 to P3 or P9 to P11) due to disturbance. Disturbance generally causes only a reorganization of the patch pattern through the local redistribution of resources without any major loss in overall functionality.

4.5.1.4 Alluvial plains patch patterning

Alluvial plains are often the preferred grazing lands for sheep because of the abundance of high quality and quantity forage (Burnside *et al.* 1995). The results from this study reflected this innate productivity; this land-type was characterised by the largest proportion of high-order patches (including perennial grass patches) and the smallest area occupied by interpatches (61.4%). Furthermore, the mature, functional patches in this land-type had the highest number of desirable perennial sub-shrubs and grasses within their patch areas (namely *Maireana tomentosa, M. thesioides, M. platycarpa, M. planifolia, Rhagodia eremaea* and *Monochather paradoxus*).

Alluvial plains receive broad run-on sheet-flow and therefore total available moisture can be substantially higher than the annual rainfall. Consequently, the level of biological feedback and functionality of the land-type relies heavily on the depositional processes that are initiated further upslope in the landscape. For example, Ludwig (1987) reported that the lower slopes of a Chihuahan desert basin had more than four times the annual (above-ground) net primary productivity (ANPP) compared to the basin upper slopes. The limited area occupied by interpatches provides alluvial plains with a degree of structural resilience to disturbance.

4.5.2 Spatial associations – patch-interpatches working together

The results clearly identified significant spatial associations between a number of the different patch-interpatch subclasses. This evidence substantiates the second principle of landscape function theory which states that: natural landscapes have a spatial self-organisation, often expressed as patchiness (Ludwig *et al*. 1997). The three major associations that were identified by the results were:

- highly functional patches (P1, P2 patch subclasses) have a strong association with highly functional interpatches (P9 subclass);
- highly functional patches tend to be associated with other highly functional patches. The converse of this also held true; and
- groups of perennial grasses (P7 subclass) and isolated perennial tussocks (P8 subclass) tend to occur more regularly with ecologically functional interpatches than with larger, functional shrub or tree patches.

Strong associations between highly functional patches demonstrate the „self-enhancement‟ concept that Pickup (1985) and others have reported in their studies. The results suggest that additional resources are deposited into highly functional patches which enhance the capacity of the patches to attract, retain and cycle water and nutrients. The additional resources also may increase its ecological resilience to degradation. As a functional patch grows to reach its „optimal‟ size (generally determined by the genetic potential of the dominant plant species) it will act as a substantial obstruction to surface runoff. Hence, the interpatch area directly upslope of the functional patch benefits from additional deposition of surface litter and increased moisture. This is likely to explain why a strong association between highly functional patches and interpatches was found within the study area.

The strong association between highly functional patches is likely to be caused by the same phenomenon except that the association is at a more advanced evolutionary state. A functional interpatch (P9 subclass) can eventually transition into a highly functional patch (P1 subclass) if a plant colonises the interpatch. It may take 15 to 20 years for an interpatch to transition into a functional patch (based on the growth rates of most woody shrub and tree species in the semi-arid shrublands) and during this period there would be a gradual accumulation of deposited surface litter. This process would result in two neighbouring highly functional patches which are likely to continue to expand in size as more plants germinate and establish on their outer limits. The ultimate constraint on the development of a sequence of neighbouring highly functional patches is the amount of water and nutrients that falls directly within the patches and the additional amount that is transported from upslope.

The converse of this association was also observed, whereby dysfunctional patches regularly occurred with other dysfunctional processes. This highlights that the same process that leads to the enrichment of functional patches can accelerate erosive forces and removes limited resources from existing dysfunctional patches. This results in a sequence of dysfunctional patches, which have limited capacity to impede surface flow.

The results indicated that perennial grasses were more likely to associate with functional interpatches than with functional patches. This suggests that the soil environment within interpatches may be more conducive to the germination and establishment of perennial grass plants than the environment within stable, mature shrub patches. A potential cause for this association is that the perennial grass species may not be able to compete with other shrub, annual species that occur within patches or the high amount of surface litter and/or shading effects of patches may impede germination and establishment. Although the latter is less probable because Pressland (1975) demonstrated the radiation reaching the ground even under very dense stands of mulga was adequate for photosynthetic activity of the ground storey plants. Determination of the causes of this specific association was beyond the scope of this thesis, suffice to say that a significant associations did occur which substantiates the second principle of landscape function theory.

Studies have found that the distribution and connectivity of interpatches can be more important than their absolute proportion in a landscape in determining potential run-off and soil erosion rates under a given rainfall event (Chartier and Rostagno, 2006). This is an important point, because even though there was little difference in the mean size of the subclasses between land-types (i.e. a P5 patch was relatively the same size in either *Acacia* sandplains or hardpan washplains), there was a substantial range in overall proportions. For instance, over 10% of the highly dysfunctional interpatches (P11) in the granitic shrublands were greater than 20 m in length. This was more than double the proportion of P11 interpatches of this size in the other land-types and indicates that there were a greater number of long run-off zones which could cause accelerated erosion. Highly dysfunctional interpatches (P11) in granitic shrublands were found to be closely associated with dysfunctional patches (P3 and P6). Therefore, the transport of water and nutrients could be distributed even further and the run-off rate increased beyond that promoted by P11 interpatches alone.

In summary, ecological and hydrological processes in semi-arid landscapes are intrinsically linked to the patterning of patches and the way they serve to capture and retain water and nutrients (Ludwig *et al.* 2005). It was clear that there were spatial associations and dependencies between a number of the subclasses and this may have a positive or negative impact on landscape processes, depending on the subclasses involved in the association. Where there is a high frequency of association of dysfunctional patches, the land-type will collectively act as a source site for areas down-slope. Conversely, land-types that have high proportions of associations among functional patches-interpatches (i.e. P1, P2, P4, P5, and P9 subclasses) will have negligible losses from the ecosystem and will be more resilient to abiotic and biotic disturbances.

4.5.3 The effect of distance-from-water on how patch-interpatches fit and work together

The general lack of significant effect due to distance-from-water in this study was consistent with findings from extensive land surveys in the region (Curry *et al.* 1994; Payne, *et al.* 1998). They reported that “key characteristics, such as perennial cover, species richness and diversity of all woody perennials, and of the palatable species showed no significant differences in relation to distance-from-water” (Curry *et al*. 1994, p. 304). They concluded that the “best indicators” of a grazing gradient were the density of woody perennials and palatable perennial species, as both parameters increased with distance-from-water (p. 304). In contrast, other researchers have found clear piosphere effects due to grazing (James *et al*. 1999; Lange, 1969; Squires, 1976).

A plausible explanation for the general lack of distance-from-water effect in this study is that any significant effects occurred within one kilometre of the watering point. The closest starting point of a transect from a watering point was 960 metres. Consequently, the study may have failed to detect significant impacts that occurred within the traditional „sacrifice zone" around the watering point. An alternative inference was that grazing had indeed substantially affected patch patterning, perhaps as a part of a historical legacy; however, the grazing impact was distributed evenly over the paddock (Barnes *et al.* 2008). In other words, the sheep and other grazers disturbed the paddock to a degree that patch cover was reduced or increased regardless of distance-from-water. Regardless of the specific cause, the results suggest that grazing has not had a significant effect on the relative proportions of the different patch-interpatch subclasses at a paddock scale. Improvements to the research design of future studies may produce a different outcome.

4.6 Conclusion

This chapter tested the second and third principles of landscape function theory at a large spatial scale within semi-arid shrublands. This was achieved by measuring the proportions of the eleven different patch-interpatch subclasses within four study paddocks. Empirical evidence was found to substantiate the second principle that vegetation and soil nutrients are patchily distributed and demonstrate a distinct level of spatial self-organisation. Patch-interpatch subclasses P2, P5, P10 and P11 occurred most frequently and dominated the proportions of the transects.

There was distinct patch patterning between the different land-types within the study area. The granitic shrubland land-type had a much greater proportion of the high resource-shedding interpatch P11 subclass (> 85% of the area) compared to the other land-types. In contrast, *Acacia* sandplains had a higher proportion of functional patch subclasses (P5) and ecologically functional patches (P1 and P4) compared to granitic shrublands. Hardpan washplains were dominated (>70%) by highly dysfunctional interpatch subclasses P10 and P11. Depending on the land-type, it was concluded that a functional ecosystem will generally have balanced proportions of P1, P2, P4, P5, P7 and P9 subclasses as these will be the most effective at capturing and retaining water and nutrients. In contrast, a degraded ecosystem will have higher proportions of the ecologically dysfunctional P3, P6, and P11 subclasses.

A number of significant spatial associations and repeating sequences of individual patch-interpatch subclasses were found to occur in the study area. Distance-from-water did not have any significant effect on the relative proportions of the different patch-interpatch subclasses at a paddock scale.

This chapter found that the second and third principles of landscape function theory have application at larger spatial scales. Patch heterogeneity maximises primary productivity by distributing and cycling scarce water and nutrients through specific sequences and associations of patch-interpatch subclasses. Negative changes to the innate patch patterning of a land-type may lead to suboptimal productivity, however at a paddock scale the specific effect of grazing pressure can be difficult to detect.

A fundamental assumption of landscape function theory is that seasonal conditions and grazing are the two key factors which can drive an ecosystem towards the dysfunctional end of the gradient. Therefore, **Chapters 5** and **6** examine the impact of seasonal conditions and grazing by conducting two short-term studies.

Chapter 5
The effect of sheep grazing on perennial grass plants

Plate 5-1: The break-down of a perennial grass patch (*Eragrostis eriopoda*)

Photo: Mark Alchin

5.1 Abstract

Native perennial grasses support perennial shrub patches in maintaining ecological stability and landscape processes in semi-arid shrublands. Perennial grasses can capture and retain water and nutrients, improve edaphic conditions due to a high turnover of fine roots and provide habitat for many soil micro-organisms. Perennial grasses can be preferentially grazed by sheep and other grazers in shrubland environments because they provide high energy, high organic matter digestibility and have a low salt content.

Perennial grasses were monitored over a 12 month period to determine whether summer rest from sheep grazing had an impact on the net change of the number of perennial grasses. The net change in the number of perennial grasses over the 12 month period was variable ranging from a 36.7% increase to a loss as high as 80.2%. There was evidence to suggest that the grasses in the exclosure treatments were conditioned by grazing in such a way that made them highly susceptible to extended periods of moisture stress. Protection from grazing (as provided by the exclosures), grazing history (summer rested vs no-summer rest) and stocking all had a significant impact on the change in the number of perennial grasses over the 12 month period (P<0.001, P<0.001, and P=0.011 respectively). Resting perennial grasses during the summer may be of benefit; however, given the high losses of grasses in most of the paddocks, it was clear that seasonal conditions had a substantial overriding influence on the outcome.

5.2 Introduction

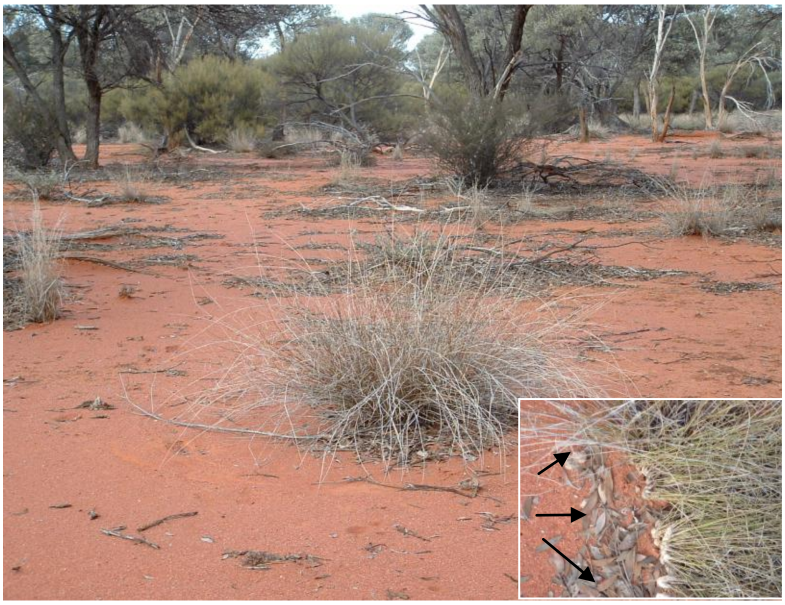
Perennial grasses are an important component of semi-arid shrublands as they play a number of inter-related roles in ecological processes (Anderson and Hodgkinson, 1997; Freudenberger *et al*. 1999; Hacker, 2006; Wilcox, 1973). **Chapter 4** found that perennial grasses occupy approximately 0.05 to 1.25% of the case study paddocks. Pressland and Lehane (1982) recommend that perennial grasses only need to comprise >2% of the landscape to decrease excessive runoff. Therefore, perennial grasses may not need to occupy a large proportion of the study paddocks in order to play a key role in ecological processes.

Woody shrubs are generally deeper rooted than perennial grasses; this gives them access to sub-surface water which is not available to the grasses (Walker *et al.* 1981). During periods of water stress, woody shrubs will have an advantage over perennial grasses since their growth processes will be able to proceed, while the grasses may be forced into a period of semi-dormancy.

Results from **Chapter 3** and **Chapter 4** demonstrated the capacity of functional shrub patches to concentrate nutrients, water, organic matter and microbiological activity. This increased supply of water and nutrients may increase the chances of survival of grasses if they are located near shrub „islands of fertility". Grasses reciprocate the benefit to shrubs by contributing to the longevity and stability of mature woody shrub patches with improve soil surface conditions (Anderson and Hodgkinson, 1997). In this sense, whilst competition for resources may occur, the increase in the availability of resources leads to net gain for both perennial shrubs and grasses that occur within the same patch area (Cipriotti and Aguiar, 2005). Although the findings from **Chapter 4** revealed that perennial grasses are likely to be located near, but not within woody shrub patches.

Other studies suggest an increase in tree density can lead to a decrease in herbage yield (Beale, 1973). Beale (1973) showed that herbage yield (comprising mainly of *Aristida* spp., *Neurachne mitchelliana* and *Danthonia bipartita*) decreased sharply when the tree basal area exceeded 1.5 m^2 per ha. Furthermore, increasing tree density can also increase evapotranspiration and lead to a more rapid depletion of the available soil moisture (Pressland, 1976b). This suggests that grass:shrub dynamics may not always be mutually beneficial.

By measuring xylem water potential, Anderson and Hodgkinson (1997) demonstrated the importance of perennial grasses (namely *Thyridolepis mitchelliana* and *Monachather paradoxus*) in capturing overland water flow and contributing to the total soil water balance necessary for the stability of mature *Acacia aneura* (mulga) communities (**Plate 5-2**). Grasses also appeared to assist in the recruitment of mulga seedlings by providing stable, moist micro-sites within the interception zone immediately upslope from the mature groves (Anderson and Hodgkinson, 1997). The removal of perennial grasses resulted in enhanced xeric conditions that caused increased mortality of mature mulga plants lower down the slope (Anderson and Hodgkinson, 1997). Pressland (1987) found that perennial grass species would have substantial difficulty in germinating if topsoil is eroded from mulga woodlands because of reduced soil fertility and an unsuitable pH level.



The base of a mature perennial grass tussock (*Eragrostis eriopoda*) accumulates material transported from neighbouring patches within the study paddock.

Plate 5-2: Perennial grass patches play a role in the capture of overland flow of water and nutrients (photo taken within study paddock 1, October 2006 by Mark Alchin)

Grasses protect the soil surface from raindrop splash and their extensive networks of fibrous roots can improve soil structure and water infiltration (Roux, 1981). In the Karoo (South Africa), Roux (1981) showed that over a 16-year period sheet erosion in grass-dominated communities averaged 4.4 mm of soil compared to 191 mm in a community dominated by shrubs. Another study reported similar interactions between cover and run-off (Eldridge and Koen, 1993). Reduced densities of small-scale grass „filters" will result in substantial outflow of valuable water and nutrients and limit stored moisture capacities and related plant production pulses.

The role of perennial grasses in enhancing soil structure, particularly macroporosity, has been substantiated by Eldridge and Koen (1993). In their study of three rangeland condition classes in western NSW, they attributed the differences in macroporosity to the variation in the cover and composition of perennial grasses, and to the activity of macro-invertebrates. Perennial grasses such as *Stipa* spp. enhanced infiltration by maintaining active flow paths for water along root canals (Eldridge and Koen, 1993). *Stipa* spp. grasses were also present in the study area. The increase in fibrous grass root mass adds substantial amounts of organic matter to the soil that in turn provides food for micro-organisms. The aboveground detached litter provides habitat for micro-organisms as well as creating a more stable soil temperature.

Studies have shown that at a landscape scale, perennial grasses can play a key role in the capture of overland water flow. Freudenberger *et al*. (1999) reported from their long-term study at Lake Mere that a loss of perennial grasses equated to a loss of effective rainfall. Grasses provide a high degree of surface roughness that effectively obstructs the movement of water and enhances water infiltration. A reduction in water infiltration will result in a proportional increase in the erosive capacity of overland flow. The herbaceous litter and fine roots that perennial grasses produce are readily assimilated by micro-organisms and they in turn enhance soil structure and fertility. The benefit of increased fertility has been demonstrated by Silcock *et al*. (1976). Silcock *et al.* (1976) found that phosphorus produced a marked growth response of two native grasses (*Monachather paradoxa*, *Digitaria ammophila*) and reduced the time between emergence and tillering.

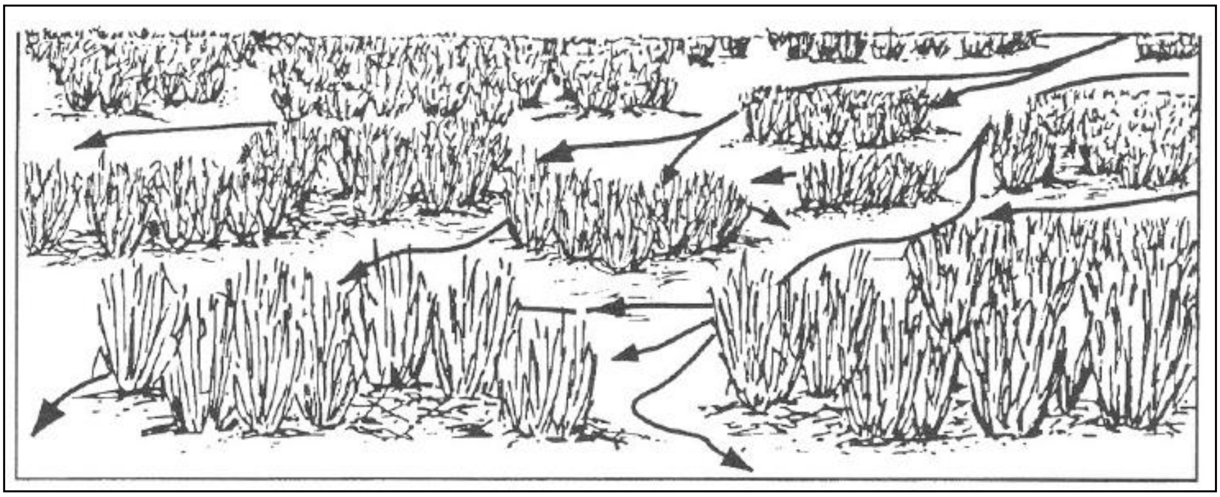


Figure 5-1: Capturing of overland water flow by perennial grasses (reproduced from Ludwig *et al.* 1994)

The reported impacts of grazing on perennial grasses are varied and are often the result of the frequency, intensity and duration of the grazing and resting periods. The known adverse impacts of overgrazing on perennial grasses include:

- reduction in root mass by excessive and repeated removal of the photosynthetically active leaf matter;
- acute damage to meristems (growing points);
- spatial redistribution of preferred grasses into the physical protection of woody shrub canopies or debris and under the canopy umbrella of less-preferred plants;
- indirect increase in interspecific plant competition arising from changes in species distribution and local species composition;
- changes to sward composition from palatable, perennial and productive species to less desirable, prostrate or annual species;
- reduction in tussock density due to decreased seed production, destruction of germination and establishment micro-sites and/or overgrazing of new recruits; and
- altered soil surface conditions towards more exposed bare ground;

(Cipriotti and Aguiar, 2005; Friedel, 2005; Hacker *et al.* 2006; Hardy *et al*. 1999; Huang, *et al*. 2007; Hodgkinson, 1995; Kinloch and Freudenberger *et al.* 1999; Pazos *et al*. 2007; Rodriguez *et al*. 2007; Wolfson and Tainton, 1999).

In South African semi-arid shrublands that have evolved with large herbivore grazing, the mortality of perennial grasses in is considered to be largely driven by rainfall and grazing is thought to only have a minimal impact (Hardy *et al*. 1999). However, small positive or negative responses to grazing can accumulate over time and can determine the trajectory of the change following a major climatic episode (Hardy *et al.* 1999). In Australia, the perennial grass „death trap" model which originally suggested that drought was the main factor resulting in grass mortality, has been reconsidered (Hodgkinson, 1995).

Hacker *et al*. (2006) reported in their study of *Thyridolepis mitchelliana* (Mulga Mitchell grass) that grazing can effectively „condition" mature tussocks in a way that may determine their survival during and after extended dry periods. The conditioning of tussocks generally relates to the amount of aboveground biomass removed. Mortality rates of mulga mitchell grass tended to increase when utilisation exceeded 30% (Hacker *et al.* 2006). The season of grazing was highly significant in determining the mortality of tussocks. During dry times mulga can comprise at least 35% of the diet of sheep (McMeniman *et al*. 1986). Due to the high nitrogen content of mulga this could increase the demand for grass material that provides a higher source of digestible dry matter (Daly, 2010). Hence, the season of grazing and the magnitude of grazing are interrelated in their effects on survival of perennial grasses.

Brown (1986) also demonstrated that rainfall has a major impact on perennial grass populations. Brown (1986) studied the effects of rainfall, burning, fertilizing and defoliation of a *Aristida armata*, *Thyridolepis mitchelliana* and *Monachather paradoxa* community in Western Queensland. Low rainfall reduced the grass populations, whilst protection from grazing increased the populations over the four year trial period. Based on these results, Brown (1986) considered that protection from grazing offered the best prospect of increasing the populations of desirable perennial grass species.

The nutrient status of the soil environment can also influence perennial grass populations (Friedel *et al*. 1980). A study of three central Australian plant communities (Mitchell grassland, open woodland and mulga shrubland) found that most soils are deficient in macronutrients and the addition of nitrogen of phosphorus will result in improved plant growth (albeit the growth response of the different plant species was not equal). An important finding was that rangeland condition of mulga shrublands was not associated with nutrient status. Friedel *et al*. (1980) suggested that mulga shrublands can be in „poor condition" and still have adequate macronutrients to support plant growth. This means that whilst the nutrient status can have a „background effect", ultimately seasonal conditions and grazing are likely to have the overriding effect on perennial grass populations.

In summary, the literature suggests that perennial grasses support perennial shrub patches in maintaining ecological functionality in semi-arid shrublands. They do not need to comprise a large proportion of the total area to perform this role (Pressland and Lehane, 1987). Perennial grass demography is largely driven by seasonal conditions. Grasses are likely to be more susceptible to overgrazing compared to shrubs. This is primarily due to the fact that they are preferentially selected by sheep and kangaroos (Wilson, 1991) and they have fewer adaptations to increased xerophytic conditions which result from degradation processes, particularly erosion and a reduced water retention. A decrease in perennial grass cover may provide an early indicator of a trend for mid to long-term ecosystem dysfunction (Chartier and Rostagno, 2006). Based on this assertion and results from **Chapter 4**, it is possible that areas within the study paddocks may be dysfunctional.

A fundamental assumption of landscape function theory is that seasonal conditions and grazing are the two key factors which can drive an ecosystem towards the dysfunctional end of the gradient. Therefore, the aim of this chapter was to investigate the impact of Merino sheep grazing on the populations of perennial grasses. Perennial grass plants were selected due to the short timeframe available and their increased sensitivity to grazing compared to perennial shrub patches. Specifically, this chapter answers three questions: (1) does summer rest from Merino sheep grazing during the 12-month period reduce the loss of perennial grass plants?; (2) do higher stocking rates result in increased losses of perennial grass plants?; and (3) is the number of perennial grass plants at a site affected by distance-from-water? This chapter concludes by discussing the impacts of grazing pressure on perennial grass populations in the context of the four principles of landscape function theory.

5.3 Methods

To investigate the impact of grazing and seasonal conditions on perennial grass plants, exclosures were installed around groups of individual tussocks throughout the study paddocks. These exclosure sites were used as benchmarks from which companion sites were used to assess the level of grazing utilisation and assess the change in perennial grass populations (mortality and recruitment). Individual perennial grass tussocks within exclosures were affected by seasonal conditions only, whilst perennial grasses next to the exclosures were affected by both seasonal conditions and grazing. A total of 246 individual grass tussocks were monitored over a 12 month period (September 2006 to September 2007). The site installation method and parameters recorded at these sites are described in the following section.

The monthly rainfall for the lead-up period and actual trial period is provided in **Figure 5-2**.

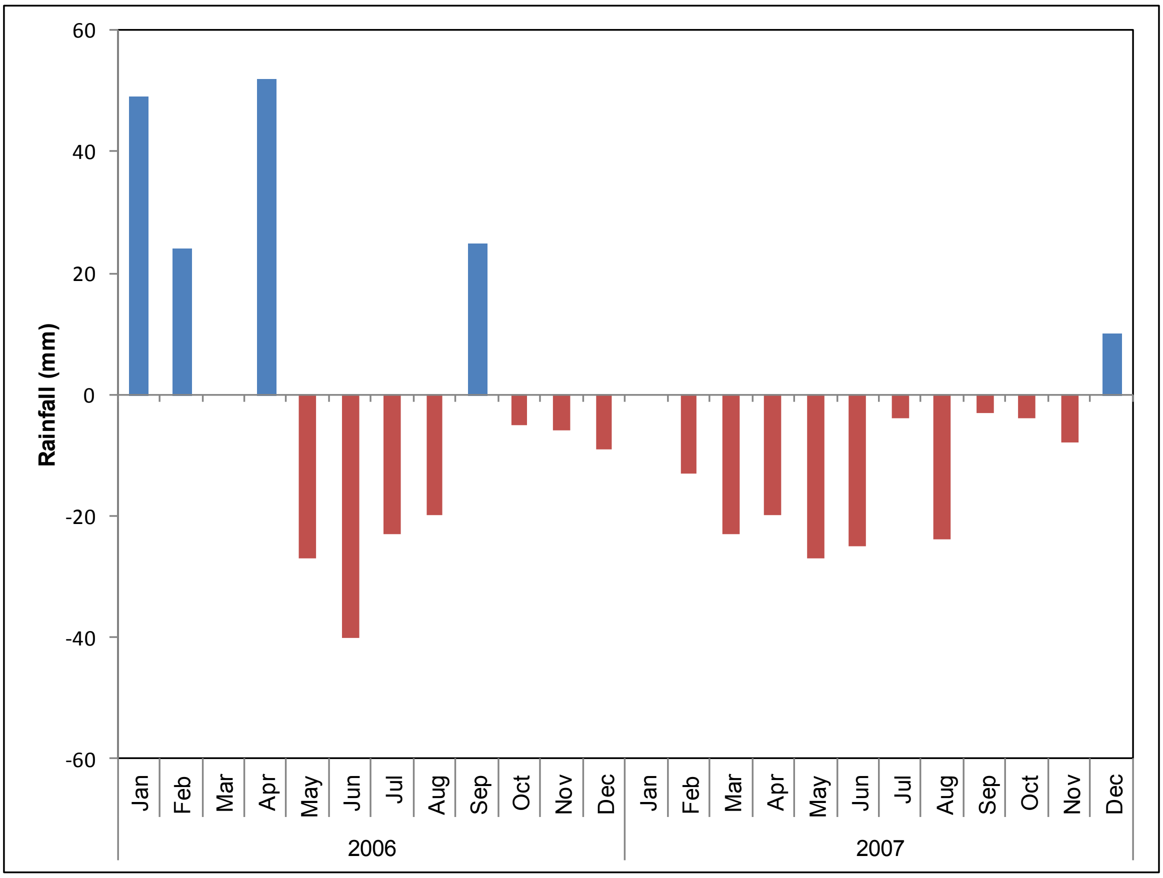


Figure 5-2: Monthly rainfall relative to the mean (+/-) at study area (Yalgoo Post Office) during the experimental period (2006 to 2007) (Clewett *et al*. 2003)

5.3.1 Exclosure site selection

The factors determining the location of the exclosure sites were: land-type; distance from permanent watering point, and existing vehicle access tracks. Nine exclosures were placed in each paddock involved in the study (a total of 36 exclosures) (**Figure 5-3**). For a description of the study paddocks refer to **Chapter 2**. The first exclosure was installed one kilometre from the main permanent watering point that the Merino sheep frequented (as determined by the pastoralist and personal observations). The first exclosure was located at this distance because there were few grasses closer to the watering point at the time of inspection. Exclosures were then installed at every successive kilometre (up to a maximum distance of five kilometres from permanent water), and the distribution of the exclosures was designed to achieve adequate representation of the study paddocks.

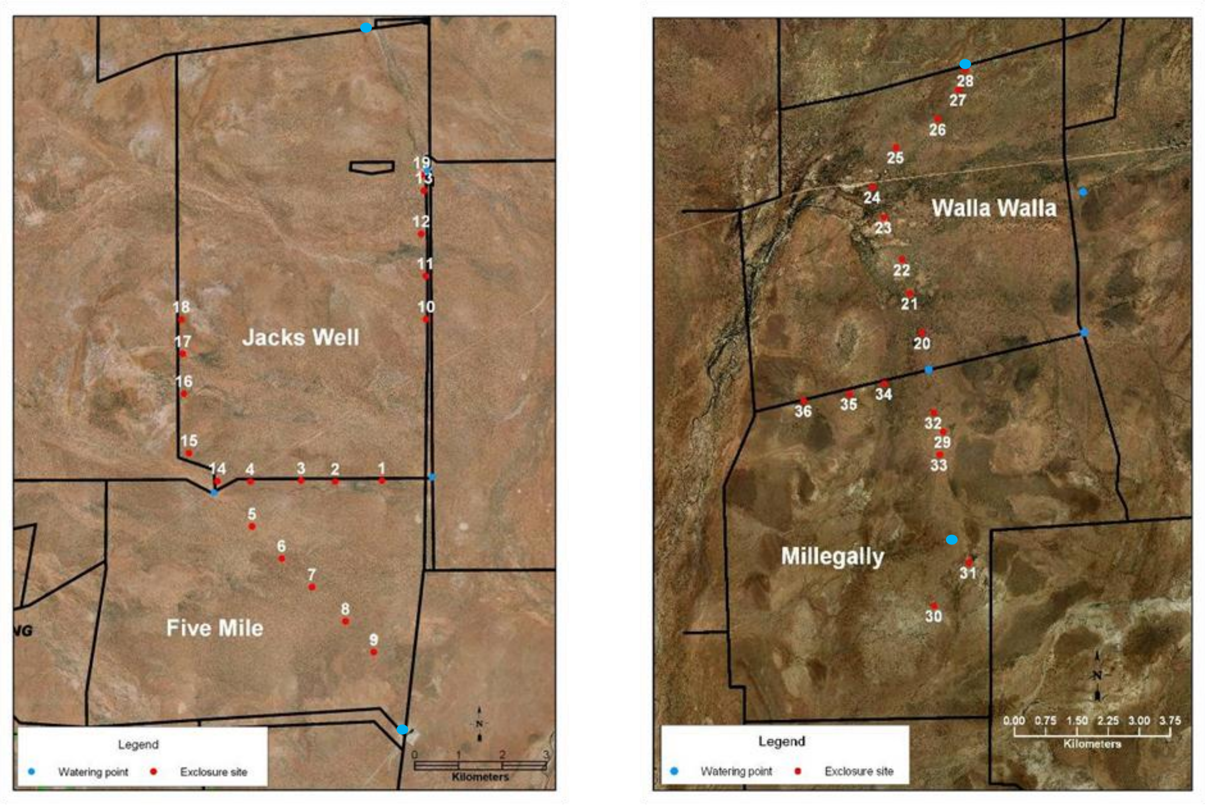


Figure 5-3: Landsat image showing the locations of perennial grass exclosure sites in study paddocks 1 (top left), 2 (bottom left), 3 (top right) and 4 (bottom right)

The exact location of an exclosure was determined by making a brief visual reconnaissance around the area at each one kilometre interval. Groups of perennial grass tussocks which were not protected from grazing by woody shrubs were randomly selected. Exclosures were at least 100 metres from the vehicle track. A minimum of three mature perennial tussocks were required to qualify as an exclosure and companion site (refer to **Plate 5-3** for example of a site). Individual perennial tussocks did not qualify for monitoring if they had a basal diameter of less than 10 mm.

The intention was that only *Monachather paradoxus* would be used for this study to limit the „variation between species‟ factor. However, there was a general scarcity of perennial grasses across all four paddocks. Therefore, although *Monochather paradoxus* was the predominant species monitored (62% of sites), a number of other perennial grass species had to be included in order to have an adequate sample size. These were: *Stipa scabra* (18% of sites), *Stipa elegantissima* (8% of sites), *Eragrostis dielsii* (3% of sites), *Eragrostis eripoda* (3%) and *Eragrostis setifolia* (3%). It is possible that the minor to moderate differences in palatability, growth form and susceptibility to grazing of the grass species could influence the result, however this level of error was unavoidable. The variation that may be caused by this variable was tested in the statistical models.

5.3.2 Exclosure materials and installation

The exclosure and companion sites were established during two individual field trips in September and October 2006. The height of the mesh used for the exclosures was 900 mm and the mesh squares were 75 mm x 50 mm. The total soil surface area that an individual exclosure protected was 0.49 m^2. The exclosure was fixed to the ground with tie wire to four 500 mm galvanised steel fence droppers in the corners. The size of the quadrat used to measure the companion site was 0.7 m x 0.7 m (0.49 m^2). The companion sites were permanently marked with a wooden or steel picket driven into the centre of the quadrat.

Plate 5-3: Example of companion site with measuring quadrat (left) and exclosure (right)

5.3.3 Parameters measured at each exclosure and companion site

After installation of a site, a GPS waypoint and digital photo were taken and flagging tape was fixed to the mesh to assist in the relocation of sites. Additional photos from an overhead view were taken of the exclosure and companion sites. The parameters recorded for each site were recorded twice (September 2006 and September 2007), these were:

1. number of living, perennial grass tussocks present (basal width > 10 mm)[7];
2. the grass species name;
3. list of other plant species that were present; and
4. the percentage of total bare-ground within the exclosure or quadrat (< 50% or > 50%)[8].

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[7] The overhead photos at the two recording periods (i.e. September 2006 and 2007) were used to identify the individual grass species and validate the assessment of whether the grass species had died or lived. The photos were also used to validate the recruitment of individuals.

[8] The < and > 50% categories were used in favour of smaller interval categories (i.e. 25, 50, 75, 100%) to avoid the subjectivity in the assessment that can arise when smaller intervals are used and because the samples would have been lumped into large interval categories in the final analysis due to the limited sample size.

After being installed and initially monitored in October 2006, the sites were reassessed in March and October 2007. This allowed the potential impacts of seasonal conditions and grazing pressure to be assessed over a 12 month period. Merino sheep grazed the paddocks at the typical stocking rates and grazing regimes as discussed earlier in **Sections 2.5** and **2.6**. Grazing from non-domestic grazers (i.e. kangaroos and unmanaged goats) is likely to have occurred on the unprotected grass tussocks. There was no evidence of kangaroo or goat grazing on the perennial grasses within the exclosures.

5.3.4 Statistical analysis

The aim of this chapter was to investigate the impact of Merino sheep grazing on both the net change in the number of perennial grasses. A summary of the three specific hypotheses and the analyses that were used to test them is provided (**Table 5-1**). The data was compiled and basic descriptive statistics were conducted to identify any apparent differences and trends in the data.

General linear models were used to test for significance levels. The factors and variates involved in the analysis included:

- fully protected or unprotected from grazing pressure (exclosure *cf* no exclosure);
- the grazing history (summer rested *cf* no-summer rest);
- the relevant land-type of the exclosure and companion sites (a total of four);
- the percentage bare ground of the exclosure and companion sites (< 50% or > 50% bare ground)
- the perennial grass species monitored at each site;
- the distance of the exclosure and companion sites from permanent water (km);
- the change in the number of perennial grass plants over the 12-month monitoring period; and
- the paddock stocking rate between 1991 and 2007 (see footnote[9]).

The paddock stocking rates were as follows:

- study paddock 1 (59% above RCC);
- study paddock 2 (100% above RCC);
- study paddock 3 (28% below RCC); and
- study paddock 4 (58% above RCC).

On completion of this initial examination, general linear models were developed to determine the significance levels of all the factors and variates. Perennial grass mortality and recruitment were analysed individually at first and then integrated into one measure (net change in perennial grasses). The overall low level of recruitment meant that analysis of it independently was not useful because of the large number of zero values. The analysis of the mortality results by themselves yielded similar results when compared to the analysis that combined both mortality and recruitment into a single

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[9] The stocking rates used in this analysis was based on records from 1991 to 2007. A separate analysis was conducted using records for a much shorter time period (2005 to 2007) and the trends were relatively similar so the longer period of stocking rate data was used.

measure. Therefore, the analysis was based on the variable of net change in perennial grasses in the study paddocks.

The factors, variables and interactions which were not significant were sequentially dropped from the fitted models. Protection from grazing pressure, grazing history, stocking rate and land type were the terms that were significant and these were used to formulate the final model. The model used to test hypotheses 1 to 3 (see footnote[10]) was as follows:

Maximal model (initial): protection from grazing * distance from water + grazing history * stocking rate + land type * grass species + bare ground + grazing history.protection from grazing + grazing history.distance from water + land type.distance from water + stocking rate.distance from water + grass species.protection from grazing + stocking rate.grazing history + stocking rate.land type + grass species.grazing history + protection from grazing.stocking rate + protection from grazing.grazing history + protection from grazing.land type + distance from water.grazing history + grazing history.land type

Fitted model (final): constant + protection from grazing + grazing history + stocking rate + land type + protection from grazing.land type

The veracity of the inferences that can be made from this study is moderated by the depth of the data and the relatively brief data collection period.

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[10] Within the model "*" denotes multiplication of both the main effects and the interaction of two components in the model and "." denotes only the interaction between two components of the model.

Table 5-1: Summary table of statistical approach used to test the Chapter 5 hypotheses

Hypothesis	Approach used to test hypothesis	Factors (F) and Variates (V) (see footnote[11])	Outcome from the analysis
1. Summer rest from Merino sheep grazing will result in a net increase in the number of perennial grass plants.	General linear model with step-wise forward and backward elimination	Protection from grazing (F), Grazing history (F), Land-type (F), Ground-cover (F), Grass species (F), Distance-from-water (V), Stocking rate (V), Change in number grasses (V)	The net change in the number of perennial grasses in response to summer rest from grazing compared to no-summer rest from grazing.
2. High stocking rates will result in a net loss of perennial grass plants.	General linear model with step-wise forward and backward elimination	Protection from grazing (F), Grazing history (F), Land-type (F), Ground-cover (F), Grass species (F), Distance-from-water (V), Stocking rate (V), Change in number grasses (V)	The impact of stocking rate on the number of perennial grass plants.
3. The number of perennial grass plants will increase at increasing distance-from-water.	General linear model with step-wise forward and backward elimination	Protection from grazing (F), Grazing history (F), Land-type (F), Ground-cover (F), Grass species (F), Distance-from-water (V), Stocking rate (V), Change in number grasses (V)	The relationship between distance-from-water and the number of perennial grass plants.

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[11] Rainfall was not included in the model because only rainfall records were available for one measurement point, so it would be the same for all samples. Utilisation rate was initially assessed and it was decided not to include it in the model due to limited variation between samples and the confounding effect it would have on the analysis (i.e. too many zero values).

5.4 Results

5.4.1 Hypothesis 1 and 2 – impact of summer rest from grazing and stocking rates

There were clear differences in the mortality, recruitment and the net change (see footnote[12]) in the number of perennial grass plants between sites over the 12-month monitoring period (October 2006 to October 2007) (**Table 5-2**) (refer to **Appendix 3** for results of each individual site). Sites that were unprotected from grazing had greater losses of perennial grass plants compared to the protected exclosure sites. Furthermore, higher stocking rates appeared to result in greater losses of mature plants and reduced recruitment.

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[12] Net change is based on: number of grasses at start experimental period + new grass recruits minus any grass mortalities.

Table 5-2: Mean mortality, recruitment and the net change in the number of perennial grass plants during the 12-month period

Case study paddock	Actual stocking rate between 1991 to 2007 (% difference to the RCC)	Mean mortality rate (%) ± standard error		Mean recruitment rate (%) ± standard error		Mean change in the number of perennial grass plants (%) ± standard error	
		Protection (total exclosure)	Unprotected (no exclosure)	Protection (total exclosure)	Unprotected (no exclosure)	Protection (total exclosure)	Unprotected (no exclosure)
Paddock 1	**59 (high)**	0 ± 0	-8.3 ± 8.3	36.7 ± 12.0	16.25 ± 8.75	36.7 ± 12.0	7.9 ± 13.3
Paddock 2	**100 (very high)**	-2.7 ± 2.7	-33.7 ± 13.8	17.5 ± 11.1	0 ± 0	14.8 ± 12.0	-33.7 ± 13.8
Paddock 3	**28 (moderate)**	-39.3 ± 15.0	-53.7± 15.4	0 ± 0	0 ± 0	-39.3 ± 15.0	-53.7 ± 15.4
Paddock 4	**58 (high)**	-48.1 ± 16.7	-80.2 ± 12.7	0 ± 0	0 ± 0	-48.1 ± 16.7	-80.2 ± 12.7

***Standard error was derived by taking the standard deviation of means and dividing by square root of the number of exclosures within each treatment.**

The fitted general linear model (described in **Section 5.3.4**) found that three factors and one interaction made significant contributions to the deviation in the net change in perennial grasses between sites, these included:

- protection from grazing (P<0.001);
- grazing history (P<0.001);
- stocking rate (P=0.011); and
- the interaction between protection from grazing and land type (P=0.007).

Therefore, hypotheses 1 and 2 were accepted. Complete protection from grazing, summer rest over the 2006 to 2007 summer period and the relatively lower stocking rate appeared to increase the number of perennial grass plants in the paddocks.

The fitted model accounted for 52% of the variation within the data. I expected that more fertile land-types (e.g. alluvial plains) to have reduced losses of perennial grass plants than less fertile land-types (e.g. granitic shrublands) because the former provides soil conditions more conducive to plant growth. Consequently, it was unexpected to find that land-type had an insignificant effect (P=0.659) on the variation between sites. The fact that the species of grass species monitored did not have a significant effect (P=0.292) on the net change of grass species was expected because they all had relatively similar tolerance levels to grazing and dry conditions. The effect of the surrounding bare-ground of the tussock (whether it was less than or greater than 50%) was not significant.

While all paddocks were moderately to very overstocked, paddocks which had been summer rested (paddocks 1 and 2) had reduced losses of perennial grass plants compared to no-summer rest paddocks (paddocks 3 and 4) (**Figure 5-4**). Complete exclusion from grazing in the no-summer rest paddocks still resulted in a reduction of 39.3 to 48.1% in perennial grasses over the 12-month monitoring period. This suggested that either the below-average rainfall during the study period and / or the grazing history prior to the installation of the exclosure had an influence on the outcome (refer to **Figure 5-2** for monthly rainfall data over the study period). No-summer rest and no protection during the below-average rainfall period clearly had a negative impact on the perennial grasses.

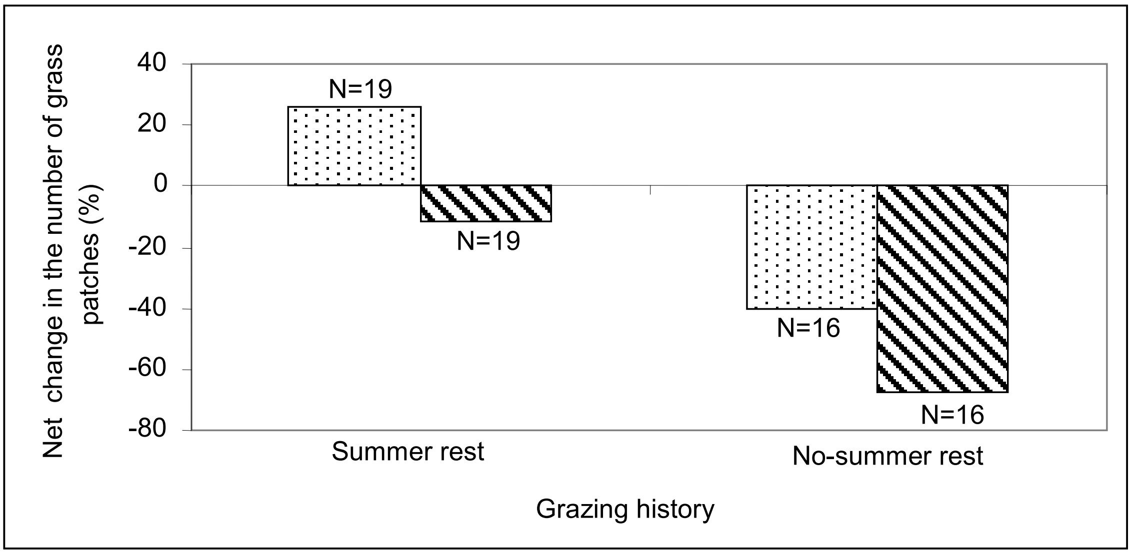

Figure 5-4: Effect of protection from grazing and grazing history on the mean change in the number of grass plants ░ **protected (inside exclosure) and ▧ unprotected (outside exclosure). NB: The differences between the protected and unprotected sites and between the grazing history were highly significant at the P<0.001 level. N = number of sites.**

The fitted model was used to predict the impact of grazing on the number of perennial grasses over a 12-month period at a range of stocking rates (**Figure 5-5**). The predicted values were interpolated based on marginal weightings of the actual stocking rate values. The robustness of this linear trend is limited by the lack of replication. Nonetheless, the results reflect the expected relationship between stocking rates and the net change in the number of perennial grasses.

The results suggest that stocking rates during below-average seasons may reduce the number of perennial grasses. The model suggested that stocking rates may have to be reduced by as much as 40% below the RCC if grazing is to have a benign impact on perennial grass populations. Non-linear effects were unable to be included in the model because there were only four original data points (four paddocks with different stocking rates).

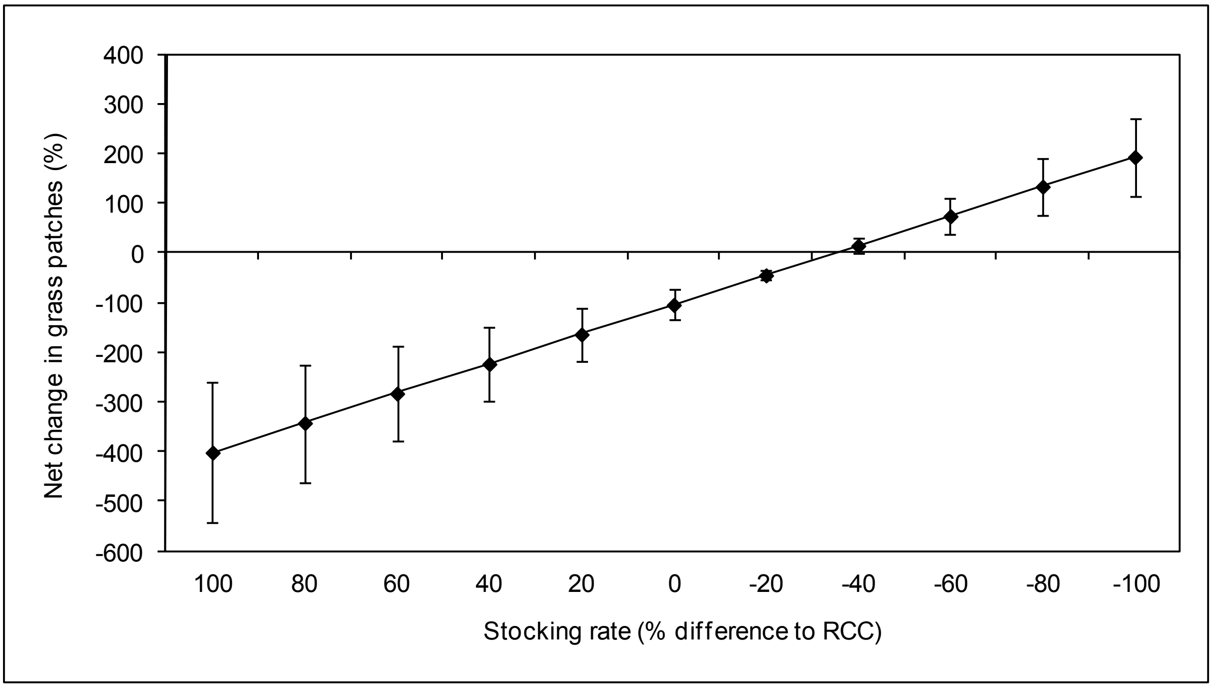

Figure 5-5: **Predicted impact of stocking rate on the change in the number of perennial grasses in the study paddocks over the 12 months. Standard error bars are shown (fitted response significance level P=0.011)**

5.4.2 Hypothesis 3 – impact of distance-from-water

Distance-from-water is a surrogate often used for grazing pressure and this study found that it had no significant effect on the net change of the number of perennial grasses (P=0.130) (**Figure 5-6**). One would expect a positive linear response at increasing distances-from-water (i.e. reduced losses and increased recruitment at greater distance-from-water). This was not demonstrated by these data and therefore, hypothesis 3 was rejected.

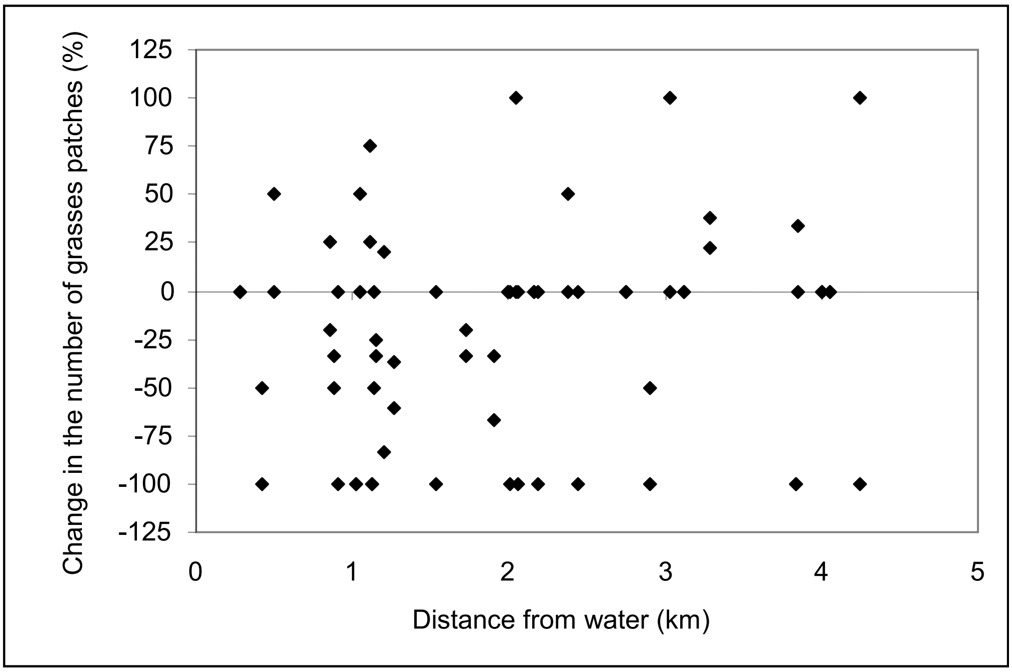

Figure 5-6: Non-significant effect of distance-from-water on the net change in the number of perennial grasses (%) over the 12-month study period.

5.5 Discussion

A fundamental assumption of landscape function theory is that seasonal conditions and grazing are the two key factors which determine the position of an ecosystem along a continuum of functionality and dysfunctionality. This chapter found evidence in these case study paddocks to substantiate this assumption. The difference in the change in number of perennial grasses between grazing and no grazing was as high as 117%. This is based on the difference between unprotected and no-summer rest grass plants (-80.2% decrease in grass population) and protected and summer rested grass plants (36.7% increase in grass population). This highlights that grazing had a significant influence on the number of perennial grasses at a site over and above that imposed by seasonal conditions.

There was a general decline in perennial grasses at the majority of exclosure and companion sites. Perennial grasses increased in the exclosures within the summer rested paddocks and they decreased in the exclosures in the no-summer rest paddocks. Why would this difference have occurred? With no grazing pressure inside the exclosure over the 12 month study period, any differences are likely to be the result of either highly localized rainfall events or the residual effects of the preceding grazing history.

The rainfall between September 2006 and September 2007 was 59% below the long-term annual average (**Figure 5-2**). The highest rainfall month in the region over that period was July when 31 mm fell. Very small rainfall events (~10 mm) were distributed throughout the remainder of the year. Prior to 2007, the rainfall was still below-average; however it was increased by isolated good summer and winter seasons.

The 2006 summer season was particularly good as the region received monthly falls of 64, 49, 24 and 72 mm from January to April. However, there was little rainfall during the subsequent 2006 winter season, and high evaporation over the 2006/07 summer would have depleted the soil moisture profile. Burrows (1973) has shown how high soil temperatures and moisture deficits are a major limiting factor for germination in an *Acacia aneura* community in southwest Queensland. Therefore, the perennial grasses would have had to persist during a full, hot summer with limited moisture. In the absence of rain gauges at each of the perennial grass sites, it is difficult to definitively disregard localised rainfall events as a factor. However, visual observations of the paddocks during the transect data collection phase suggested that certain areas had not received disproportionate amounts of rain (evidenced by general lack of annual growth throughout all the paddocks).

Hacker *et al.* (2006) in their 4-year study of grazing-induced mortality on *Thyridolepis mitchelliana* found that grazing history, in relation to drought conditions, clearly influenced the death rate of the grass plants they studied. This work followed on from earlier work by Hodgkinson (1995) who explained that grazing during a dry period could set up the initial step of a perennial grass „death trap". The trap can be „sprung" by a dry period after excessive grazing or the converse of these events. In this model, death is seen as episodic, rather than continuous. The below-average seasons in the study paddocks may have resulted in increased grazing pressure on grasses and palatable shrubs because of a scarcity in ephemeral herbage.

Grazing may have affected the vigour of the perennial grasses by limiting the growth rates of the roots and thereby restricting their size, depth, penetration and capacity to source scarce water and nutrients (Wolfson, 1999). The grasses would have a correspondingly low amount of leaves which would be photosynthesising and replenishing root reserves. In the context of the death trap model, the repetitive, excessive grazing pressure may have conditioned the perennial grasses into a very susceptible state and they subsequently died in 2007 even when they were fully protected from grazing. Hodgkinson (1995) recorded similar high mortalities of *Monochather paradoxus* (up to 70%) as a function of drought and heavy grazing. Similarly, *Thyridolepis mitchelliana* can have mortality rates as high as 80% during droughts (Brown, 1981).

Photosynthesis is the process by which solar radiation, intercepted by green leaves, provides energy to convert carbon dioxide and water into simple carbohydrates which are either used as energy to drive metabolic processes or stored as reserves (Wolfson and Tainton, 1999). The leaf system will only begin to translocate carbohydrates to storage organs (stem base, roots) once its own demands are fulfilled (Wolfson and Tainton, 1999). Consequently, limited carbohydrates are diverted as reserves during the early growth phase or recovery phase post-grazing. The low level of perennial grass mortality at sites that had summer rest from grazing preceding the study period, may have provided an opportunity for the grasses to maintain photosynthesis, replenish the root reserves and thereby enhance their resilience throughout the 12-month dry period. In contrast, preferential grazing in the no-summer rest paddocks may have inhibited the accumulation of stored reserves and hence they were unable to survive the 12-month dry period even when they were fully protected (by the exclosure).

The ability of grasses to extract moisture from drying soil is a primary factor leading to their survival (Hodgkinson and Becking, 1977). Grasses have to remain ahead of the drying front through continued root extension (Taiz and Zeiger, 1998). It has been shown that if grasses are completely defoliated, root development almost stops within 1 to 2 days (Crider, 1955). During the period prior to the installation of the exclosures, preferential grazing pressure in the no-summer rest paddocks may have reduced the photosynthetic and shoot growth rate and thus inhibited root extension of the grasses. Shallower, less extensive root systems would have stifled the capacity of the grasses to source adequate moisture even in the absence of grazing.

Another contributing factor to the increased mortality of grasses in the exclosures in the no-summer rest paddocks may have been that the exclosures were too small. The size of the exclosures may not have provided an adequate buffer from the effects of outside disturbance (Tongway, *pers comm*. 2008). Grazing pressure outside the no-summer rest exclosures may have impacted the local soil environment by removing herbaceous material or breaking down cyanobacterial crusts, thereby increasing soil temperatures, evaporation and wind erosion. This change in edaphic conditions may have reduced the drought resilience of the grasses inside the exclosures.

The physiological conditioning of the grasses under different grazing regimes during the 12 to 24-month period prior to the installation of the exclosure probably predisposed them to either tolerate the moisture deficit or perish. The impact of defoliation by grazing was considered to be the overriding causal factor. The direct impacts on edaphic conditions (e.g. trampling, compaction, excrement enrichment) on perennial grass mortality were considered to be unimportant. The veracity of these inferences is moderated by the depth of the data and the relatively brief data collection period.

Monochather paradoxus is known to exhibit a peak of growth and regrowth following summer and winter rains but it only germinates in the summer (Mitchell and Wilcox, 1994; Wilcox, 1973). The other grasses studied also generally have a summer growing season. Therefore, sheep grazing only during the winter-spring period would allow for substantial accumulation of grass biomass, perhaps far in excess of that which can be produced in no-rest grazing systems. It is known that arid zone grasses can compensate for moderate defoliation if it occurs during the vegetative growth phase (Brown, 1987; Chaieb *et al.* 1996; McNaughton, 1983). However, in the no-summer rest paddocks the grasses were probably utilised opportunistically, thus limiting the amount of dry matter production over an annual cycle. Without an adjustment of stocking rate, less available dry matter intensifies the grazing pressure on the existing plants. The finding in this study that higher stocking rates resulted in a change in the population of perennial grasses is one which is supported by other studies (Anderson *et al.* 1996; Ash and Stafford Smith, 1996; Briske *et al.* 2008; Fletcher, 1995; Tainton, 1999; Taylor *et al*. 1993).

The distance-from-water effect is often used as a surrogate for grazing pressure (Pringle and Landsberg, 2004). This is because sheep drink at least every day and in the absence of incidental surface water, the permanent stock watering point is the only source of supply. Accordingly, sheep spend a disproportionate amount of their grazing time at close proximity to water. This can result in greater physiological stress on plants close to watering points. In the study paddocks, there were very few areas where natural surface water could be obtained for any extended length of time. It was therefore surprisingly that increasing distance-from-water did not reduce perennial grass mortality. Instead, there was no clear trend. A total of 246 grass tussocks were assessed within this study. This sample size should have been adequate to detect any significant trends. This result suggests that there may have been other factors which influence the patterning of perennial grasses in the paddocks, these may include: the prevailing wind direction, the paddock configuration, landscape heterogeneity, topography, grazing history and competition from other grazers (particularly kangaroos and feral goats).

Based on previous study, it was probable that the preceding dry period enhanced the demand by the sheep for high energy, highly digestible organic matter (McMeniman *et al*. 1986b). McMeniman *et al.* (1986b) found from a study of sheep nutrition in mulga shrublands that the apparent digestion of dietary N within the rumen ranged from 70 to 90% when there was green forage in the diets, but fell to 37.6% when the pastures were drought affected. Hence, the general lack of feed of sufficient quality would also have caused them to graze out further from water troughs, particularly during the winter months when temporary surface water is available, and utilise a much greater proportion of the paddock. Consequently, this may have „blurred‟ or weakened any distinct distance-from-water effect.

Kangaroo and goat numbers were not included in the paddock stocking rate calculations, and they may have contributed to the distortion of any significant grazing gradient. Kangaroos are known to have a strong dietary preference for grasses (Wilson, 1991; Dawson *et al*. 2009). In particular, it has been shown that kangaroos can directly compete with sheep for key grass species including *Monachather paradoxa* and *Thyridolepis mitchelliana* (Wilson, 1991).

The removal of perennial grass plants by grazing and below-average seasonal conditions are likely to have an impact on the functionality of the landscape. A reduction in grass patches may lead to an increase in overland flow (Anderson and Hodgkinson, 1997) which could result in a net loss of water and nutrients and reduce productivity of the landscape. Raindrop splash and associated erosion may increase in the intervening areas between mature shrub patches which could ultimately undermine the stability of these patches if incised erosion channels develop.

In the extreme, the removal of all perennial grass plants could result in homogenisation of many of the resources into large functional patches and reduce the natural spatial self-organisation or patchiness of the landscape (landscape function principle three). In contrast, an increase in the number of perennial grass plants, as occurred in the summer rested paddocks, may play a role in restoring or replacing ineffective processes in the landscape which may improve soil surface condition and stabilise the ecosystem (landscape function principle four).

5.6 Conclusion

A fundamental assumption of landscape function theory is that seasonal conditions and grazing are the two key factors which can drive an ecosystem to the dysfunctional end of the continuum. The results of this chapter support this assumption, grazing caused a reduction in the number of functional perennial grass plants with the study paddocks. Hacker *et al.* (2006) consider that semi-arid environments are stable when death of individual tussocks is determined by drought alone. Based on this principle, it could be concluded that the landscape of this study is not „stable" and parts of it may indeed be dysfunctional.

This chapter found that in these case study paddocks summer rest from grazing may reduce the loss of perennial grasses particularly during periods of below-average rainfall. Furthermore, high stocking rates can cause an increase in the loss of perennial grass plants. Losses of perennial grass plants outside exclosures were relatively high in all paddocks which highlighted the impact that prolonged below-average rainfall periods can have on perennial grass populations. The consequences of losing perennial grasses in this landscape due to grazing and drought should not be overstated given that **Chapter 4** found that they only occupy less than 1.25% of the case study paddocks.

There may be implications for ecological processes because of the high mortality rates of perennial grasses. Reduced perennial grass density limits the capacity of the landscape to obstruct overland flow and retain the moisture necessary to drive fundamental biogeochemical processes. Developing management systems that encourage recruitment and establishment of perennial grasses should be part of a strategy to promote functional ecological processes. **Chapter 6** will investigate how knowledge of grazing behavior can assist in the development of these management systems.

Chapter 6

The effect of sheep grazing behaviour on patch patterning and ecological processes

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Plate 6-1: Merino sheep grazing within study area, April 2006

Photo: Mark Alchin

6.1 Abstract

Effective management of grazing pressure in large, heterogeneous paddocks that actively restores and / or replaces missing or ineffective processes in the landscape requires a high level of planning and skill. The aim of this chapter was to improve the present understanding of sheep grazing behaviour so land managers can harness the natural instincts of a flock to align grazing pressure with the natural patch patterning of the landscape. Eight adult sheep were fitted with GPS-tracking collars for a period of 20 days and their grazing habits in a paddock in the semi-arid shrublands were digitally recorded. The results indicate that there were five major factors that influenced sheep grazing behaviour in the study paddock; these include: land-type, green cover, time of day, air temperature and distance-from-water.

The GPS-collared sheep demonstrated a clear grazing preference for the higher value land-types that were the alluvial plains and hardpan washplains. The results also indicated that the sheep were selectively grazing areas with high greenness cover (as indicated by Normalised Difference Vegetation Index [NDVI]). It is vital that managers understand the selective grazing characteristics of sheep when designing paddock layouts and developing management plans. This is because repetitive, selective grazing of high-value land-types has the potential to modify their geomorphological functions in the landscape. This research into the drivers of Merino sheep grazing behaviour is the first of its kind in the Gascoyne-Murchison. Further research in this field would enhance our understanding of specific behavioural cues and patterns that could be creatively manipulated to enhance livestock productivity and potentially restore ecological process and landscape functionality in the region or simply mitigate its adverse impacts.

6.2 Introduction

A fundamental assumption of landscape function theory is that seasonal conditions and grazing are the two key factors which can drive an ecosystem to the dysfunctional end of the continuum. **Chapter 5** presented evidence of the impact of seasonal conditions and grazing on perennial grass populations in the study paddocks. Whilst seasonal conditions are beyond human control, land managers can manipulate grazing pressure to capitalise on the natural patch patterning and ecological processes at a paddock scale. However, grazing pressure is not exerted in a homogeneous, mechanistic manner across semi-arid landscapes. Rather, it is influenced by an array of inter-related stimuli and factors that cause the impact of livestock grazing to be varied in time and in space (Hunt *et al*. 2007; Tomkins and O‟Reagain, 2007). Due to this complexity, there have been few studies that have quantified spatial heterogeneity in relation to grazing distribution (Adler *et al*. 2001).

Grazed vegetation communities are heterogeneous in space and time (Chapman *et al.* 2007). Grazing behaviour and forage intake interact strongly with the feed supply-demand balance, pasture composition and grazing management. These interactions are not completely understood, even for relatively simple pasture communities (Chapman *et al.* 2007). **Chapters 3** to **4** demonstrated that resource heterogeneity in the study paddocks is significant at multiple scales. Therefore, sheep must be adept at making decisions as their environment changes in order to optimise their diet for growth and reproduction (Hinch, 1999).

The three major factors that may determine grazing behaviour are: the land-type and its associated biogeochemical characteristics; the climatic or seasonal conditions; and the distance-from-water. Limited information is available regarding the grazing behaviour of Merino sheep in semi-arid shrublands. Recognising the patterns of grazing behaviour will enable land managers to harness the natural instincts of their herd-flock to optimise production and align grazing pressure with the natural patch patterning of the landscape. This may lead to the successful application of principle four of landscape function theory (i.e. restoration or replacement of missing or ineffective processes in the landscape will improve soil surface conditions and soil habitat quality).

This chapter investigates the grazing behaviour of Merino sheep, specifically, addressing three main questions:
(1) which areas receive increased grazing activity and why?;
(2) does the time of day influence Merino sheep grazing activity?; and
(3) does distance-from-water determine the amount of grazing activity that different areas receive? (Question 3 is an extension of Question 1).

6.3 Methods

In collaboration with researchers from the CSIRO (Thomas *et al.* 2008), an investigation was conducted from September to October 2007 in study paddock 3 (refer to **Chapter 2** for a description of the study paddock). The September to October period represents the end of the growing season and the availability of surface water at this time was strictly limited to the permanent watering point. The hotter weather during September to October would cause any distance-from-water effects to be accentuated compared to if the study was conducted during the winter period.

Animal ethics approval for the study was obtained from the relevant Department of Agriculture and Food WA and the CSIRO sub-committees. At the time of this study the paddock was stocked with 394 adult Merino ewes and 130 lambs. The paddock contained four watering points and was well-fenced. All sheep were removed from the paddock immediately after this study because feed supply was low due to significantly below-average seasonal rain. The average rainfall for 2007 was 120 mm (less than 50% of the average). The average daily temperature for October at the site was 20.2 °C, with less than 10% of days above 25 °C (www.nrw.qld.gov.au/silo). Refer to **Figure 2-5** in **Chapter 2** for the monthly rainfall leading up to and after the September to October trial period.

Experimental animals were selected from a group of approximately 150 sheep that were captured in a self-mustering yard (see footnote[13]) around the central water point on the southern boundary (known as the Division well watering point). Eight Merino ewes (not lactating), three years of age and weighing 62.5 ± 1.9 kg, were selected and fitted with WildTrax GPS collars (Bluesky Telemetry Ltd, Scotland) (**Plate 6-2**).

GPS tracking data was recorded at the site for 20 days, from 28th September to 17th October 2007. The length of the GPS tracking period was determined both by the battery life of the collars and the financial costs of mobilisation of the study. The study was conducted in September 2007 to assist in the trapping of the sheep on the watering point. The collars remained on the sheep for the full study period. Data collected from all eight collars were suitable to include in all analyses. The collars recorded the location of the individual and the altitude every five minutes. A total of 40,504 individual waypoints were logged (an average of 5,328 recordings per GPS-collared sheep).

Activity sensors installed in collars recorded left-right and up-down collar rotation. Periods of grazing activity were identified from changes in left-right and up-down collar rotation arcs in the sheep. Left-right rotation arcs and up-down rotation arcs were calculated as the difference between the maximum and minimum tilt angles recorded per five minute interval; these are referred to as roll range and pitch range respectively. Horizontal velocity (or walking speed) was calculated as the sum of straight line distances between successive points over time (kilometres per hour). Energy use for horizontal travel in sheep was assumed to be 28 kilojoules per kilometre (Standing Committee on Agriculture, 1990). Estimates of maximum and minimum daily temperature, relative humidity, radiation and rainfall were obtained for the study paddock from the SILO climate data drill system (www.nrw.qld.gov.au/silo).

Plate 6-2: Example of GPS-collar fitted to adult Merino ewe involved in the study

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[13] A self-mustering yard is a fenced holding compound which encloses the watering point and is fitted with a one-way gate which is set by a manager when the livestock need to be handled for sale or husbandry practices.

Each GPS waypoint of sheep locations was uploaded into a geo-referenced image of the study paddock in GIS software (Geomedia^{TM}). The spatial query function was used to determine the land-type that each GPS waypoint was recorded in and the distance from the nearest watering point. A MODIS image (resolution 250 x 250 m) of the paddock from September 2007 was uploaded into Geomedia^{TM}. The MODIS image was used to derive the greenness index value for each waypoint (normalized difference vegetation index or NDVI). This value was used as a coarse indicator of the relative distribution of the available forage within the paddock at the time of the study.

The GPS waypoints of sheep locations were initially visually assessed for any obvious trends and patterns. The data was assessed on an individual sheep basis and then lumped together for analysis. General linear models were then used to investigate the source and significance level of the variation. The factors and variates included in the models were:

- recording time of each waypoint (24 hour clock);
- daily maximum and minimum air temperature;
- daily maximum and minimum relative humidity;
- daily radiation;
- rainfall (total millimetres per day);
- altitude (metres above sea level of each waypoint);
- the land-type that each waypoint was recorded in (a total of three)[14];
- distance from the nearest watering point of each waypoint (km);
- an index of grazing activity expressed as a percentage for each waypoint and calculated as follows: ((log(roll range + 20) + log(pitch range + 20))÷2); and
- NDVI value (greenness index at 250 x 250 m resolution).

Normalised Difference Vegetation Index (NDVI) values provide an estimate of green cover, however it can be used as a broad indication of the seasonal trend and spatial variation of green cover within a paddock. The NDVI values ranged from 113 to 128 across the study paddock. The higher the NDVI value implies a greater amount of green cover. NDVI values usually range from -1 to +1. However, to facilitate statistical analysis the NDVI values were converted using the following formula: (NDVI value * 100) + 100. Shrublands tend to have values of 120 to 130 and usually decline to approximately 110 during the summer months (December to February).

NDVI can be limited in its use to infer green cover if projected foliar cover (PFC) is high. This is because if a dense woody overstorey exists (that is either not available or represents no pastoral value to sheep) then the NDVI may simply be reporting that the overstorey is „green". The PFC of the study paddock is estimated to be less than 20% in most areas. The PFC is higher towards the southern end of the paddock in the areas dominated by hardpan washplains (estimated 30% PFC).

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[14] Land-type was chosen instead of land-system in order to increase the sample size for analysis. Some land-systems had very few grazing activity recordings.

A summary of the three hypotheses and the statistical approach used to test them in this study is provided (**Table 6-1**). A linear mixed model was fitted to the grazing activity index. The model included fixed effects for: time of waypoint recording, distance-from-water, land-type, NDVI value, air temperature, relative humidity, radiation, rain and altitude. There were strong correlations between individual waypoints because they were adjacent to each other (five minute intervals) and therefore they were modeled using an autoregressive (order 2) process (R software).

There were highly significant effects of recording time, distance-from-water, land-type and NDVI ($P<0.001$) and no effects of air temperature, relative humidity, radiation, rainfall and altitude. A model including only the significant fixed effects was fitted for each variable and the coefficients were estimated. Due to the size of the dataset and the complexity of the correlation model, the linear mixed model could not be fitted using Genstat^{TM} and was fitted using a REML in the statistical program R^{TM}.

Table 6-1: **Summary table of statistical approach used to test the Chapter 6 hypotheses**

Hypothesis	**Approach used to test hypothesis**	**Factors (F) and Variates (V)**	**Outcome from the analysis**
1. GPS-collared sheep will demonstrate clear preferences areas of the paddock.	Linear mixed model (REML in R software) fitted to the grazing activity index	Land-type (F) Time of recording (F) Air temperature (V) Relative humidity (V) Radiation (V) Rainfall (V) Altitude (V) Distance-from-water (V) MODIS NDVI (V) Grazing index (V)	Total amount of time spent by sheep in specific land-types and identification of any clear spatial patterning. The relationship between grazing activity and NDVI (or greenness index).
2. GPS-collared sheep will graze at generally the same time each day.			The relationship between the time of day and the time spent grazing.
3. The amount of grazing activity by GPS-collared sheep will be less at increasing distance-from-water			The relationship between the distance-from-water and the time spent grazing.

6.4 Results

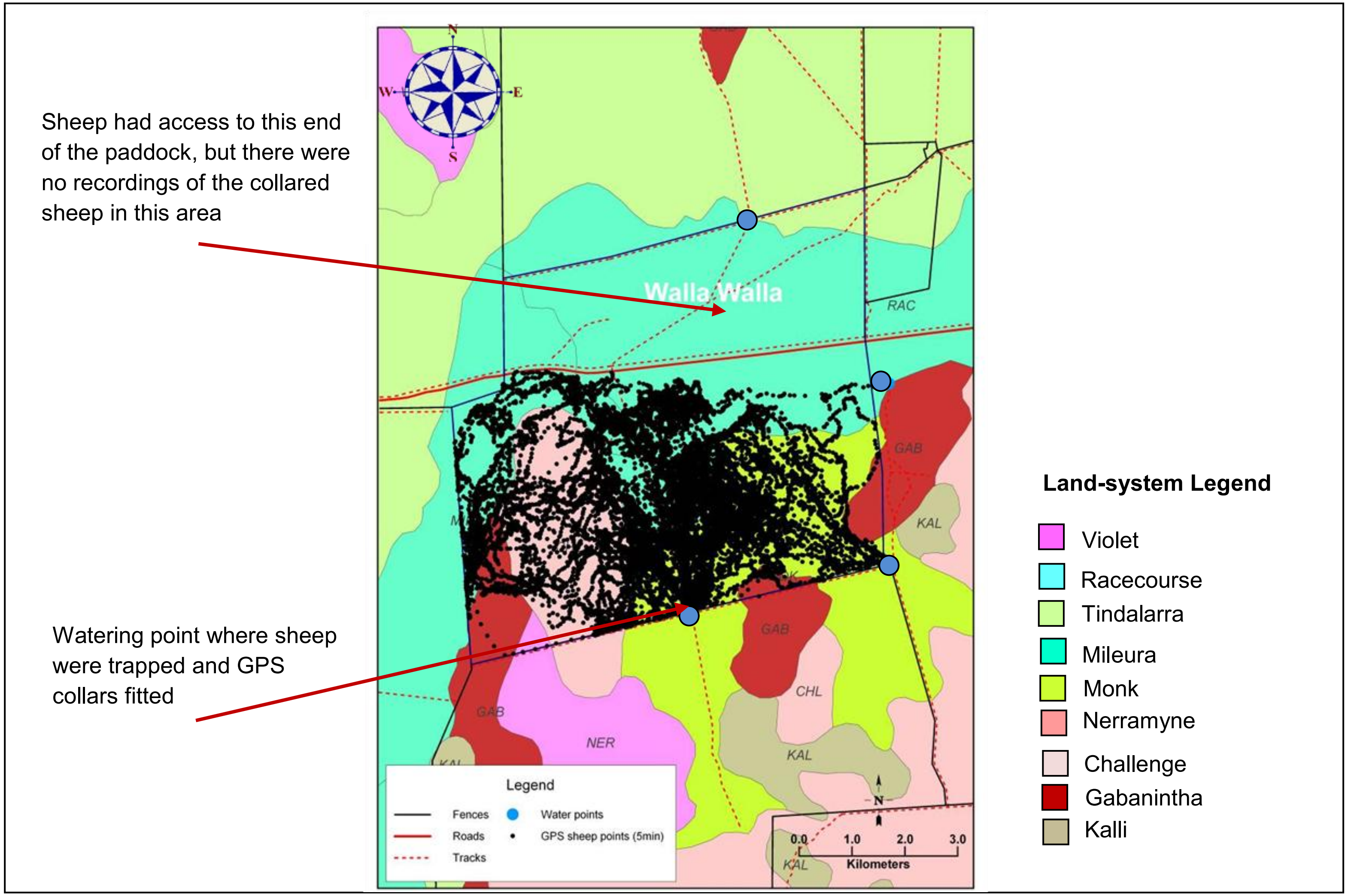
6.4.1 Hypothesis 1 – grazing preferences in the paddock

There were clear spatial movement patterns of the GPS-collared sheep within the paddock during the study period (**Figure 6-1**). The area of the paddock directly north of the central watering point on the southern boundary was highly represented in the distribution of the sheep. The GPS-collared sheep did not cross the highway, which runs east-west approximately two-thirds toward the northern end of the paddock, although other sheep in the paddock were observed north of the highway. Sheep spent little time in the north-eastern area directly below the highway.

Hypothesis one was accepted as there was a highly significant difference (P<0.001) in the level of grazing activity of the GPS-collared sheep between the three different land-types of the study paddock (**Figure 6-3**). Hardpan washplains comprised less than 20% of the total area of the study paddock; however, the GPS-collared sheep spent the majority of the grazing time in this area. Distance to water was likely to have influenced this result as the majority of the hardpan land-type was within three kilometres of a watering point. Therefore, the sheep would have had an increased propensity to graze this area compared to the other land-types.

The NDVI values provide an estimate of green cover and can be used as a broad indication of the seasonal trend and spatial variation of green cover within a paddock. The limitations of applying NDVI in this experiment were discussed in **Section 6.3**. The alluvial plains land-type consistently had higher NDVI values with a mean of 122 compared to granitic shrublands and hardpan washplains that had mean values of 119 and 118, respectively. The NDVI values of the alluvial plains land-type were also more variable (standard deviation: 1.9) compared to the other two land-types.

The NDVI values were highly significant (P<0.001) in determining the amount of time that the GPS-collared sheep spent grazing in an area (**Figure 6-4** and **Figure 6-6**). This indicates that the sheep were selecting areas with higher green cover. It is acknowledged that this result is also partially an artifact of the proportion of the area covered by each individual NDVI value (i.e. the relative area [ha] of individual NDVI values was higher than others) (**Figure 6-5**). For example, 27.5% of the study paddock had an NDVI value of 119 (the single largest proportional area), therefore one would expect that a high proportion of the grazing activity would occur in this area. The GPS-collared sheep walked through the different land-types at a similar speed (the variation in ground speed was less than one metre per second).



Sheep had access to this end of the paddock, but there were no recordings of the collared sheep in this area

Watering point where sheep were trapped and GPS collars fitted

Land-system Legend

Figure 6-1: Grazing movement patterns of the GPS-collared sheep in the paddock over the study period (land systems included in paddock were: Racecourse [RAC]; Gabanintha [GAB]; Monk [Mok]; Challenge [CHL]; and Mileura [MIL]).

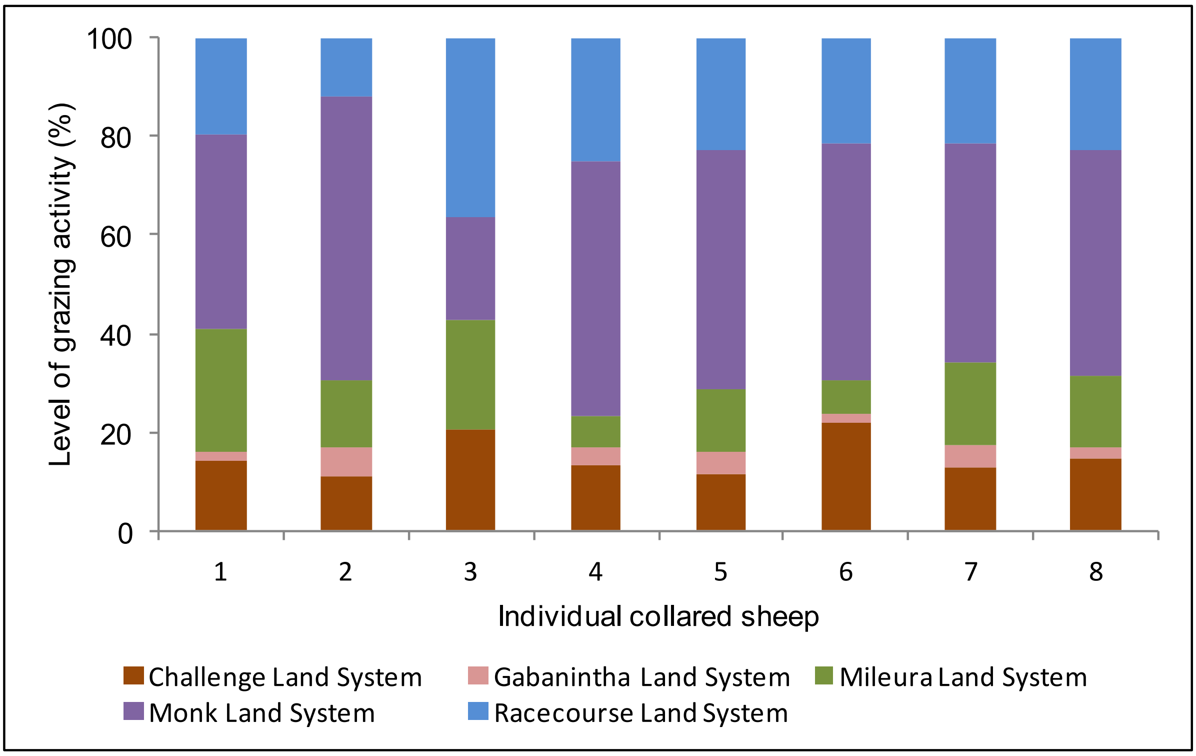


Figure 6-2: Comparison of the level of grazing activity of the eight collared sheep based on land system.

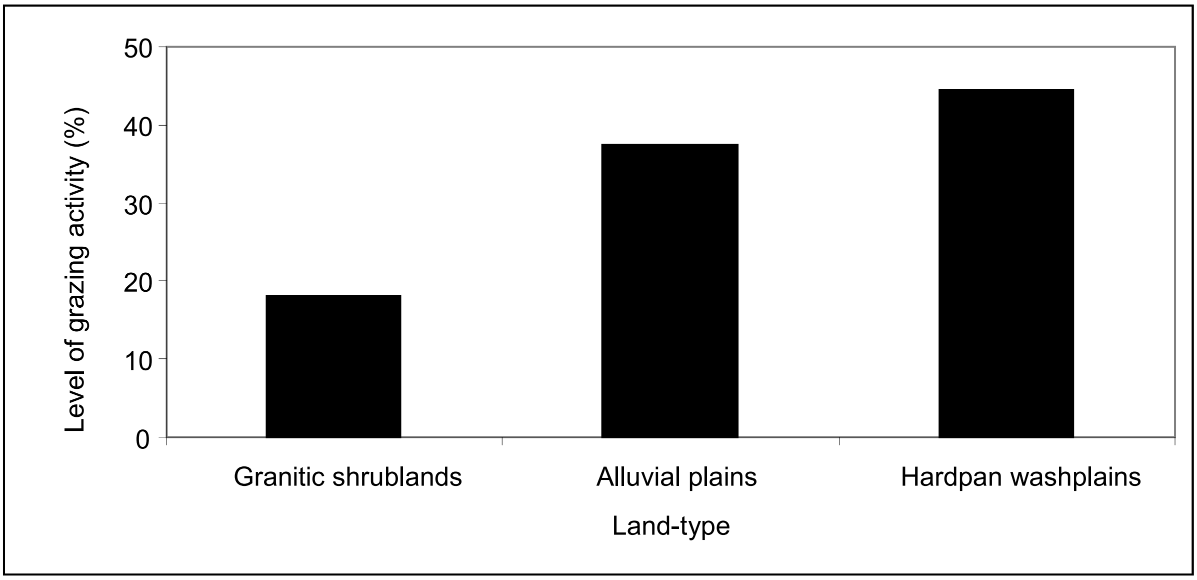


Figure 6-3: Comparison of the level of grazing activity of the three different land-types in the study paddock (P<0.001) (standard error bars are not shown because they represented < 1% of the mean values). Data is weighted averages to account for the differences in the areas of the land types.

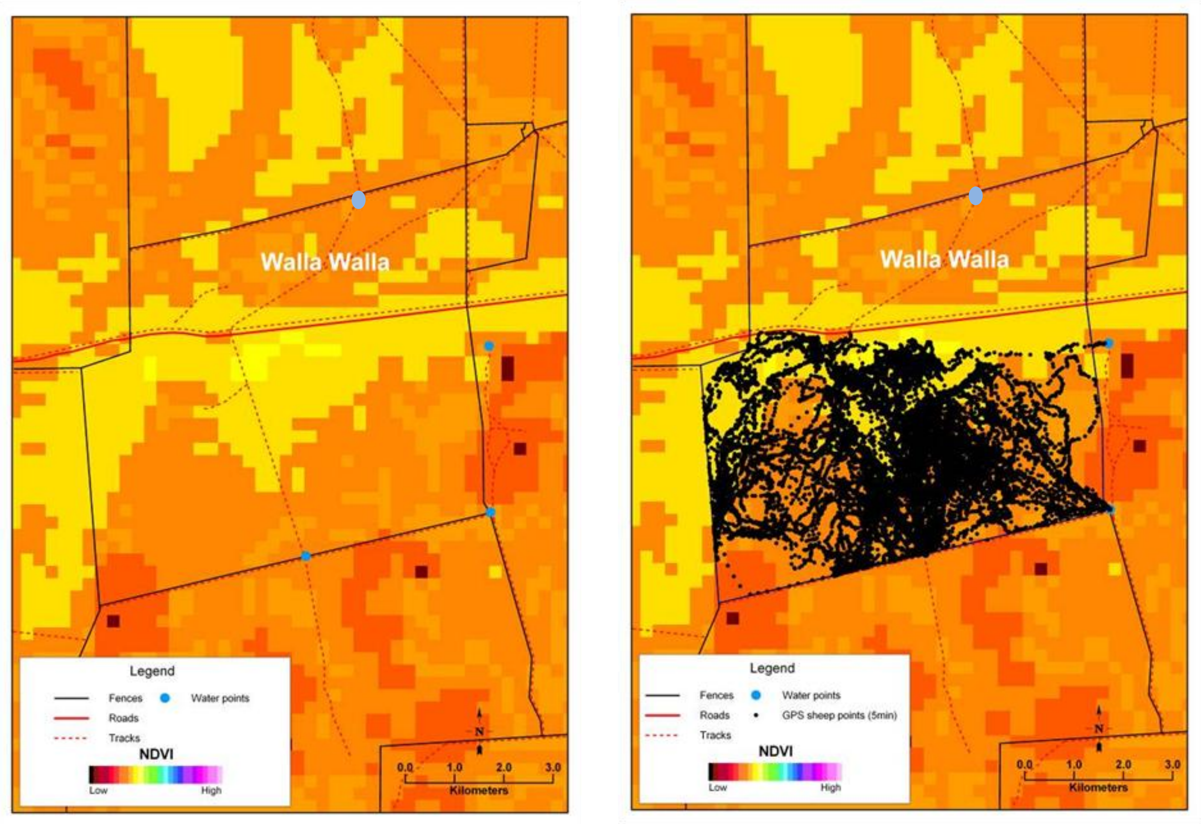


Figure 6-4: MODIS NDVI image (index of estimated green cover) of the study paddock in September 2007 (left) with grazing movement patterns illustrated (right) NB: Each dot represents a GPS recording and sheep may not necessarily be grazing at each displayed recording.

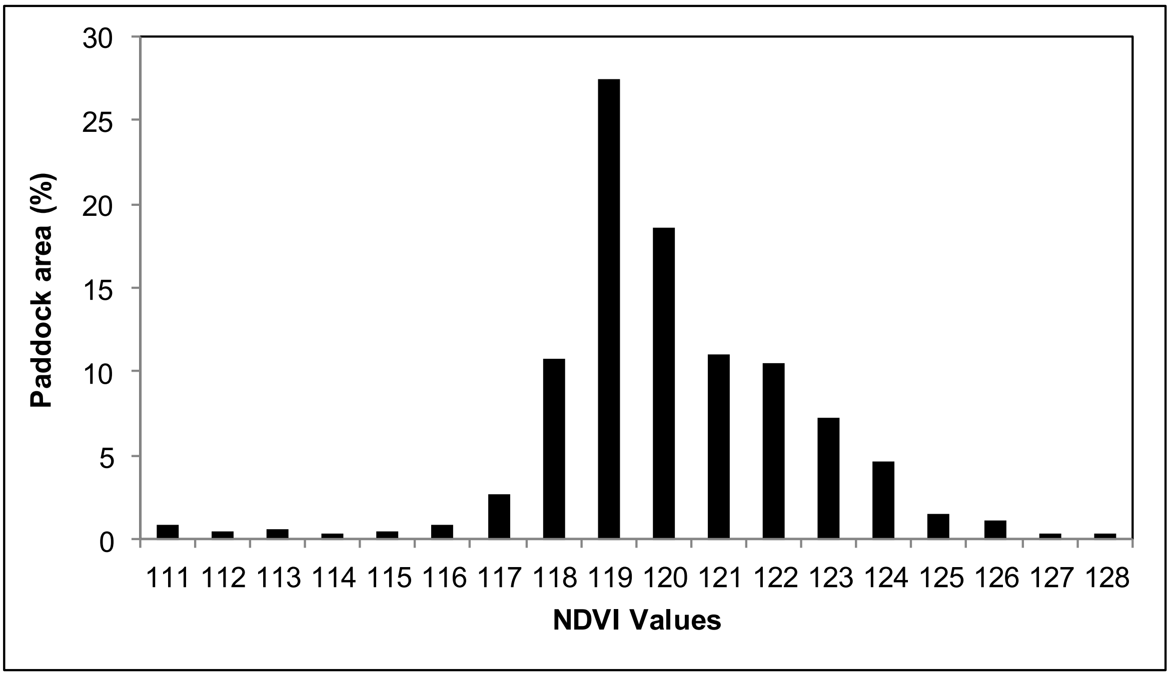


Figure 6-5: Proportional area of study paddock (%) occupied by different NDVI values

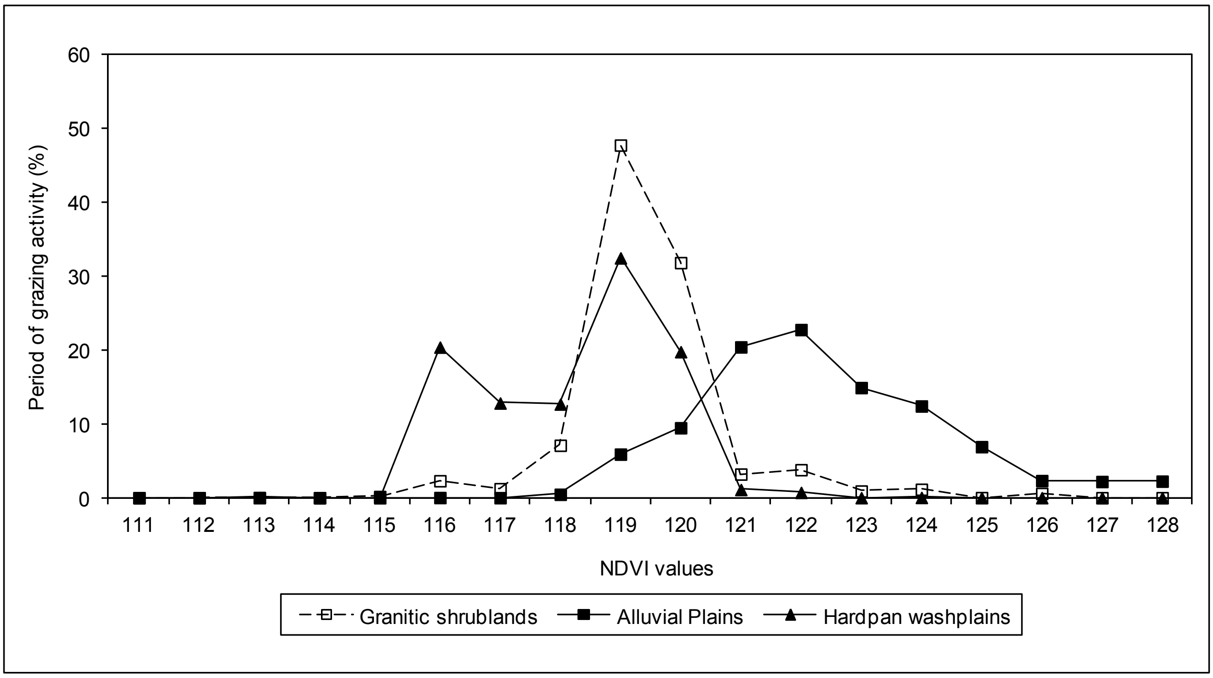


Figure 6-6: Comparison of the level of grazing activity of areas based on NDVI (index of estimated greenness cover) (P<0.001)

6.4.2 Hypothesis 2 – time of grazing activity

Hypothesis 2 was accepted as there was a highly significant relationship (P<0.001) between the time of day and the level of grazing activity of the GPS-collared sheep. Grazing activity was highest during the morning and afternoon periods (0400 to 900 hours and 15:00 to 18:00) and the lowest during the night period (2000 to 0400 hours) (**Figure 6-7**). There was very limited grazing activity during the afternoon period (1200 to 1800 hours). An interaction between time of grazing and land-type was tested using the model in order to determine if the sheep were grazing different land-types at certain times of the day. No significant interactions (P>0.05) were detected. During periods of grazing activity, sheep travelled further from the watering points on cool days compared to hot days (3.74 *cf* 2.73 km; P<0.001). Linear regression analysis indicated that 29% of the variation in distance travelled was accounted for by mean daily temperature (P<0.05).

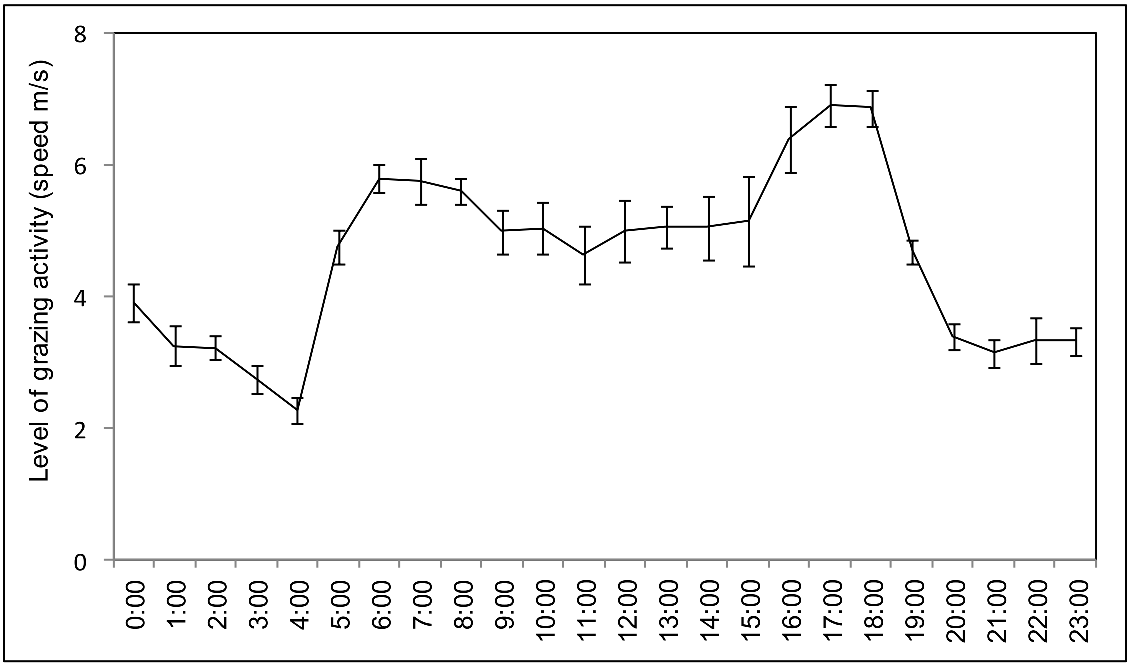


Figure 6-7: Comparison of the level of grazing activity of areas based on time of day (standard error bars are shown)

6.4.3 Hypothesis 3 – Effect of distance-from-water

Hypothesis 3 was accepted as there was a highly significant relationship (P<0.001) between distance-from-water and the level of grazing activity of the GPS-collared sheep (**Figure 6-8**). There was a clear preference of the sheep to graze within the zones of 0.0 to 0.5 km and 2 to 4 km distance-from-water. The high level of grazing activity within 0.0 to 0.5 km of water is likely to be explained by the fact that the sheep camped within this area, hence the sheep would have spent a large proportion of their time in this area (albeit the time they spent grazing would have contributed little to their overall dietary intake due to the low supply of available feed in this area).

It was unexpected to find that nearly 40% of the grazing activity occurred beyond three kilometres from the closest watering point (this was calculated by dividing the number of grazing activity recordings that occurred beyond 4 km by the total of the grazing recordings). The interaction between distance-from-water and land-type was tested; however, no significant effects were detected. However, NDVI values generally increased at increasing distance from water (**Figure 6-9**).

The mean period of time between visits by the sheep to a watering point was once every 37.5 hours. The variation in time between visits corresponded with differences in temperature, i.e. decreased time with higher temperatures. The central watering point on the southern boundary fence was used most frequently, with 83% of visits to water at this point. The mid-east watering point was visited by only one of the GPS-collared sheep in this study, and appears to be highly under-represented compared to the other watering points. Sheep returned to watering points between 0600 and 1000 hours on 58% of occasions, and infrequently in the afternoon or evening.

During the three weeks of this study, the GPS-collared sheep lost 34 ± 53 grams per day live weight. Energy used for travel during periods of activity was calculated to be 0.89 ± 0.03 megajoules per sheep per day. Using the GrazFeed™ model (Freer *et al*. 2009) it was predicted that the sheep would have maintained live-weight if they did not expend a high proportion of their energy intake on walking extended distances for forage.

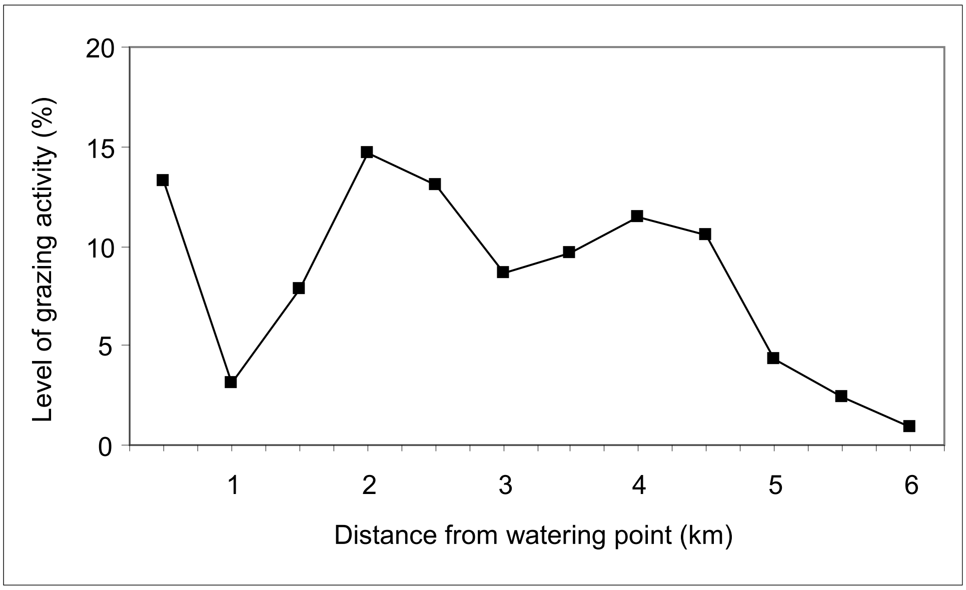


Figure 6-8: Effect of distance-from-water on the level of grazing activity in the study paddock (variation is highly significant at the P<0.001 level)

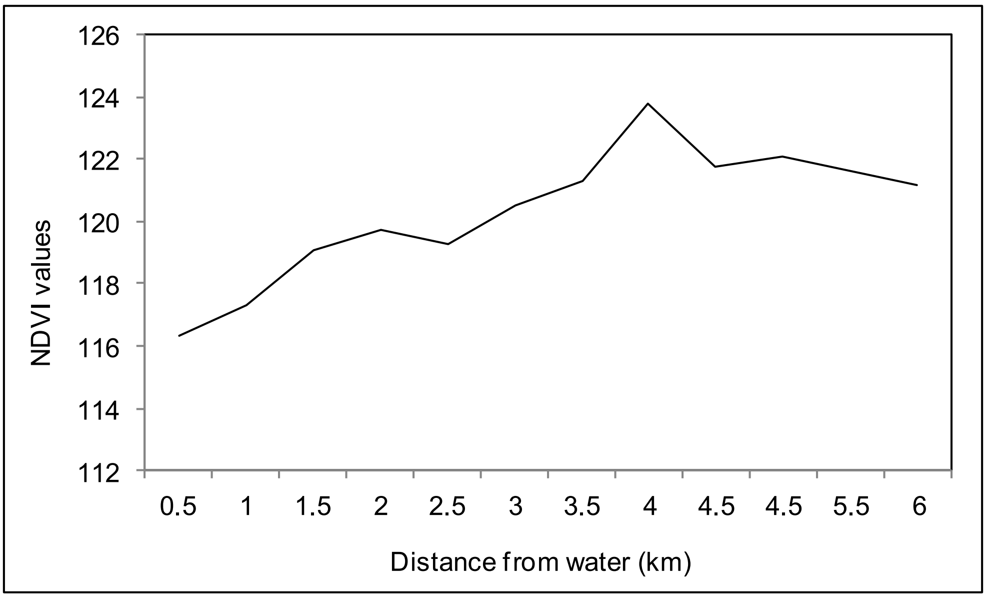


Figure 6-9: Effect of distance-from-water on NDVI values in the study paddock (variation is significant at the P<0.05 level)

6.5 Discussion

The results demonstrated that grazing behaviour of the eight GPS-collared sheep was driven by: land-type, green cover (as interpreted by NDVI), time of day, air temperature and distance-from-water. The sheep expressed clear behavioural patterns, these were:

- a preference to graze land-types with a high pastoral potential, i.e. hardpan washplains and alluvial plains (as defined by Curry *et al*. 1998);
- a propensity to graze areas which have moderate to high green cover (as indicated by the NDVI data);
- a routine pattern of grazing in the morning periods (0600 to 1200 hours);
- a tendency to travel further out from a watering point on cooler days compared to hot days; and
- a tendency to graze 0 to 0.5 km and 2 to 4 km from permanent water.

It is acknowledged that any interpretation and extrapolation of the results is limited by the fact that only eight sheep were studied during the trial over a period of only 20 days. The GPS-collared sheep in the study paddock preferred to graze the land-types with high pastoral potentials (hardpan washplains and alluvial plains) (as defined by Curry *et al*. 1998). If this behavioural characteristic is not taken into consideration when managing grazing pressure, there is the potential for initiation / exacerbation of degradation processes at a landscape scale. The hardpan washplains and alluvial floodplains land-types in the study paddock play an important role in paddock-scale ecological processes. The hardpan washplains largely govern the rapidity at which water and nutrients are transported down from the breakaway escarpment onto the alluvial floodplain (refer to **Chapter 4**, namely **Section 4.5**).

When the natural patch patterning is undisturbed by overgrazing, water will flow in a diffuse manner through the hardpan washplains and gradually supply the alluvial plains with additional resources. Pringle and Tinley (2003) outlined examples in the Gascoyne-Murchison region where this geomorphological process has been severely disturbed. They consider the primary cause of the landscape dysfunction to be excessive grazing pressure over an extended period in combination with below-average rainfall periods. Therefore, the increased grazing activity in hardpan washplains could cause a deviation of the „natural" patchiness towards a more dysfunctional end of the continuum (third principle of landscape function theory).

Pringle and Tinley (2003) outline the process and symptoms of landscape dysfunction of hardpan washplains and alluvial plains. Excessive grazing pressure over an extended period may gradually reduce the number of resource-capturing patches in the hardpan washplains which can lead to incised drainage tracts that enlarge and eventually coalesce. This can have a major effect on the alluvial plains further down the slope, particularly if they are also subjected to excessive grazing pressure. During the earlier stages of desiccation, the alluvial plains in the study paddock may benefit because they could receive additional water from further upslope. However, unless remedial action is undertaken, incised channels cutting headward through the alluvial plain are likely to form and these can breach the outlets of drainage foci and pans (Pringle and Tinley, 2003). Consequently, the density and distribution of the dominant chenopod shrubs (namely *Maireana pyramidata*, *Atriplex bunburyana*, *Cratystylis subspinescens*) can be reduced because the water-logging events of the alluvial plains become less frequent and last for shorter periods of time.

The frequency and amount of rainfall becomes increasingly important because the soil / water balance is affected. Reduced soil water retention capacity causes alluvial plains to dry out more rapidly, which can harm the stability of plant communities. There are localised examples in the study paddock where it appears that valuable pasture species (e.g. *Maireana* spp.) have been replaced by plants more adapted to shorter periods of positive soil moisture balance (*Acacia tetragonaphylla*, *Acacia victoriae*) (**Chapter 4**).

The high propensity of the GPS-collared sheep to graze the alluvial plains and hardpan washplains results in a degree of rest from grazing of the granitic shrublands. Therefore, the granitic shrublands may provide plants refuge from overgrazing and act as a default conservation area. Milchunas and Noy-Meir (2002) highlight the value of geologic refuges for maintaining plant diversity. They report positive effects on plant diversity as a result of areas being less frequented by grazing animals due to avoidance behaviour. However, the capacity of the granitic shrublands to effectively act as a conservation refuge will be limited by its relative size and its proximity to grazing disturbance (Brandis, 2008).

During the study period, the average daily temperature at the site was 20°C which was well below the long-term monthly average temperature of 28°C. The study paddock is located in a region that is characterized by a hot, dry climate. Between November and March the average monthly temperature is >30°C which peaks in January with a monthly average of 38°C (Clewett *et al*. 2003). The influence of high temperatures on grazing patterns is accentuated by the presence of palatable plant species which have high salt contents (Daly, 2010; see footnote[15]) and a drinking water supply that is moderately brackish (270 to 900mS/m). These factors may cause the sheep to drink more regularly and could restrict the spatial area that the sheep can graze (Squires, 1981). Hence, this study could be replicated in the summer period (November to February) for comparison of results.

It was concluded that temperature-dependent grazing patterns (sheep travelled more than one kilometre further from watering points on cooler days) would not have a significant impact on patch patterning and ecological processes. This is based on the fact that this study was unable to detect a significant effect due to distance-from-water on patch patterning and perennial grass mortality (refer to **Chapters 4** and **5** respectively). In addition, the mean period of time between visits by the sheep to a watering point was once every 37.5 hours. The extended period between drinking episodes suggests

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[15] Fiona Daly collected plant samples from Carlaminda pastoral lease and conducted comprehensive nutritional analyses as a part of her PhD study (Daly, 2010). She found a number of species had high salt contents, these included: *Atriplex bunburyana*. (7.20 ± 1.3%), *Enchylaena tomentosa* (6.22 ± 1.8), *Maireana convexa* (7.63 ± 4.0), *Maireana pyramidata (*9.17 ± 1.8) and *Maireana thesioides* (11.16±1.1).

that the sheep were not regularly thirsting for water and had the opportunity to utilise the full extent of the paddock.

Extremes in air temperature can also cause higher energy demands as the sheep seek to regulate their body temperatures. Upper critical air temperatures for a number of livestock production traits range from 24 to 27°C (Fuquay, 1981). The study paddock regularly exceeds these critical temperatures and as a consequence the sheep will have to increase their dietary intakes if they are to maintain productivity. Reid *et al.* (1958) found that maintenance requirements for grazing cattle were 40 to 50% higher than of those cows which were confined to and fed in a well-ventilated barn. The variation was largely accounted for by the difference in air temperatures and associated demands of foraging to achieve hunger satiety. The necessary increase in dietary intake due to high temperatures may deplete forage reserves more rapidly and have consequences for the stability of individual plant patches.

The significant distance-from-water effect identified in this chapter concurs with evidence by other researchers (Cowley *et al*. 2002; Foran, 1980; Hunt, 2001; Pringle and Landsberg, 2004). The addition of watering points in the study paddock may substantially alter the behaviour of the sheep within the paddock. The sheep would be able to access effectively a much larger proportion of the paddock (namely the northern end of the paddock), particularly during the hot summer period. It may also provide them with the flexibility of establishing a foraging circuit between watering points (at present the distance from the north to the south watering point is greater than six kilometres). Greater access to a larger proportion of the paddock may alter the impact on patch patterning, the magnitude of which would be determined by the relative grazing pressure and seasonal conditions.

In summary, there is evidence to suggest that grazing pressure in the case study paddock was not exerted in a homogeneous, mechanistic manner within the case across semi-arid shrublands. The findings of this chapter substantiate anecdotal evidence from pastoralists who generally extol the capacity of Merino sheep to forage in marginal, extensive semi-arid shrublands. To maintain body weight and rear healthy lambs in the study paddock, the sheep must have a well developed spatial memory of forage reserves (Laca, 1998). However, the propensity of Merino sheep to selectively graze areas with high green cover could adversely impact the natural patchiness of the ecosystem and lead to dysfunctional ecological processes (third principle of landscape function). Repetitive, overgrazing may decouple complex patch associations and assemblages (as were identified in **Chapter 4**). Conversely, the innate grazing behaviour of sheep could be harnessed to restore and / or replace missing or ineffective processes in the landscape in order to improve soil surface conditions and soil habitat quality (fourth principle of landscape function).

6.6 Conclusion

A comprehensive understanding of grazing behaviour is critical for the development of paddock infrastructure designs and management systems that capitalize on the inherent behavioural traits and instincts of sheep. Effective manipulation of sheep grazing behaviour may result in reduced cost of production, increased productivity and enhanced ecological functionality of the landscape.

The results indicate that there were five major factors that influenced sheep grazing behaviour in the study paddock; these include: land-type, greenness cover, time of day, air temperature and distance-from-water. The GPS-collared sheep in the study paddock demonstrated a clear grazing preference for the higher value land-types that were the alluvial plains and hardpan washplains. The results also indicated that the sheep were selectively grazing areas with high green cover. It is vital that managers understand the selective grazing characteristics of livestock when designing paddock layouts and developing management plans. This is because repetitive, selective grazing of high-value land-types has the potential to modify their geomorphological functions in the landscape (Curry *et al*. 1994; Pringle *et al*. 2006; Pickup, 1985).

This research into the factors that influence Merino sheep grazing behaviour is the first of its kind in the Gascoyne-Murchison. Further research in this field would enhance our understanding of specific behavioural cues and patterns that could be creatively manipulated to enhance livestock productivity and restore ecological process and landscape functionality in the region.

Chapter 7
Conclusions and management implications

Plate 7-1: Patch-scale regeneration, a colonising *Maireana convexa* plant recruit emerges from surface litter, study area. Photo: Mark Alchin

7.1 Introduction

Australia‟s rangelands encompass approximately 80% of the continent and generate significant wealth through a range of industries. The rangelands comprise four major ecosystem types, these are: grasslands, shrublands, woodlands and savanna. The ecological legacy of early pastoral development in most of Australia‟s semi-arid shrublands is largely one of degradation and desertification (Curry *et al.* 1994; Mabbutt *et al.* 1963; McKeon *et al*. 2004; Wilcox and McKinnon, 1974). The scale of degradation is exemplified by the fact that approximately 30% of the Western Australian semi-arid shrublands are in poor to very poor condition (Curry *et al*. 1994; Payne *et al*. 1998). This ecological degradation poses a number of challenges for the sustainability of the region, regardless of its land-use (e.g. pastoralism, carbon sequestration, tourism, mining, Indigenous heritage, nature conservation).

Many pastoralists within the WA semi-arid shrublands have responded to the challenge of addressing the ecological degradation by adopting new management systems. Since the 1980s, there has been a slow and general shift by industry towards grazing systems that better align stocking rates carrying capacity (Watson *et al.* 2007; Pringle and Tinley, 2001). To implement sustainable stocking rates with a high level of precision in the semi-arid shrublands, pastoralists require a much more advanced understanding of patch patterning and ecological processes at a paddock scale. This understanding or theory could improve the management decisions made by pastoralists and other land managers (e.g. conservation park rangers, carbon offset developers, Indigenous communities, mining company environmental officers) and assist them in addressing the ecological degradation. Landscape function theory was developed partly for this purpose (Ludwig *et al*. 1994).

Landscape function theory was developed as a way to assess and interpret patch patterns and ecological processes that occur at a range of spatial scales (Ludwig *et al*. 1997). Landscape function theory is also used to explain the concept of „functional heterogeneity‟, namely that landscape heterogeneity is not random variation that simply confounds robust statistical analyses. Instead, functional heterogeneity is an information-rich phenomenon that has enabled the development of cross-scale metrics. These cross-scale metrics recognize the role of surface and near surface processes in the allocation and re-allocation of resources in space and time (Tongway *et al*. 2003). Undisturbed areas can act as „analogue‟ sites and provide insight into the natural patch patterning of different land-types. Analogue sites are benchmarks of the natural patchiness that can be used to compare the progress of rehabilitation and restoration activities in degraded / disturbed areas.

Landscape function theory is based on four primary principles, these are:

1. Patchiness can be characterized by the patch size, orientation, spacing and soil surface condition.
2. Natural landscapes have a characteristic spatial self-organisation, often expressed as patchiness.
3. Deviations from the „characteristics" or „natural" patchiness are seen as degrees of dysfunctionality, and there is a long continuum from highly functional to highly dysfunctional patches.
4. Restoration or replacement of missing or ineffective processes in the landscape will improve soil surface conditions and soil habitat quality.

The landscape function theory and the associated LFA methodology have largely become an accepted standard for the ecological assessment of rangeland environments. However, there have been a limited number of studies in Australia that have thoroughly examined the four principles that underpin the landscape function theory. Further interrogation of the principles that underpin the theory in the field has the potential to enhance its utility and the robustness of its assumptions. This information would strengthen the empirical basis of the theory and potentially lead to improved management recommendations and decisions for rangeland landscapes. Therefore, the aim of this thesis was to test the four principles of landscape function theory in a semi-arid shrubland environment. The overarching hypothesis of this thesis was that clear spatial patch patterns occur at a range of scales within the case study paddocks and these patterns determine the ecological functionality and resilience of the area. The hypothesis was tested by taking a similar „three-stage" approach to the LFA methodology, whereby the study:

1. identified the patch-interpatch components;
2. evaluated how the patch-interpatch components „fit and work together"; and
3. investigated how disturbance impacts on the different patch-interpatch components.

Specifically, this study sought to find evidence of distinct patch-interpatch patterns and associations at a range of scales in the lower Murchison region of WA and it examined the impact that grazing and seasonal conditions can have on this natural patchiness.

7.2 Summary of key findings

This study started with the recognition that a significant proportion of the WA semi-arid shrublands is in poor condition and a substantial effort is required to restore the natural patchiness and ecological processes in these areas. To optimise the investment in any restoration effort, whether for pastoral production, nature conservation or mine rehabilitation, it is critical that land managers / administrators are equipped with a detailed understanding of the inherent patch patterning and key drivers of ecological processes. Landscape function theory has provided the conceptual framework and monitoring methodology for this to occur.

This thesis found empirical evidence that substantiates the principles and assumptions of landscape function theory. The thesis also provides detailed information about the unique patch-interpatch patterning and associations of some of the major land-types in the lower Murchison region of WA (namely *Acacia* sandplains, hardpan washplains, granitic shrublands and alluvial plains). This chapter synthesises the main findings from the original questions that were investigated in **Chapters 3** to **6**, and discusses the implications of the findings for monitoring techniques and sustainable management of the semi-arid shrublands in Australia (**Figure 7-1**).

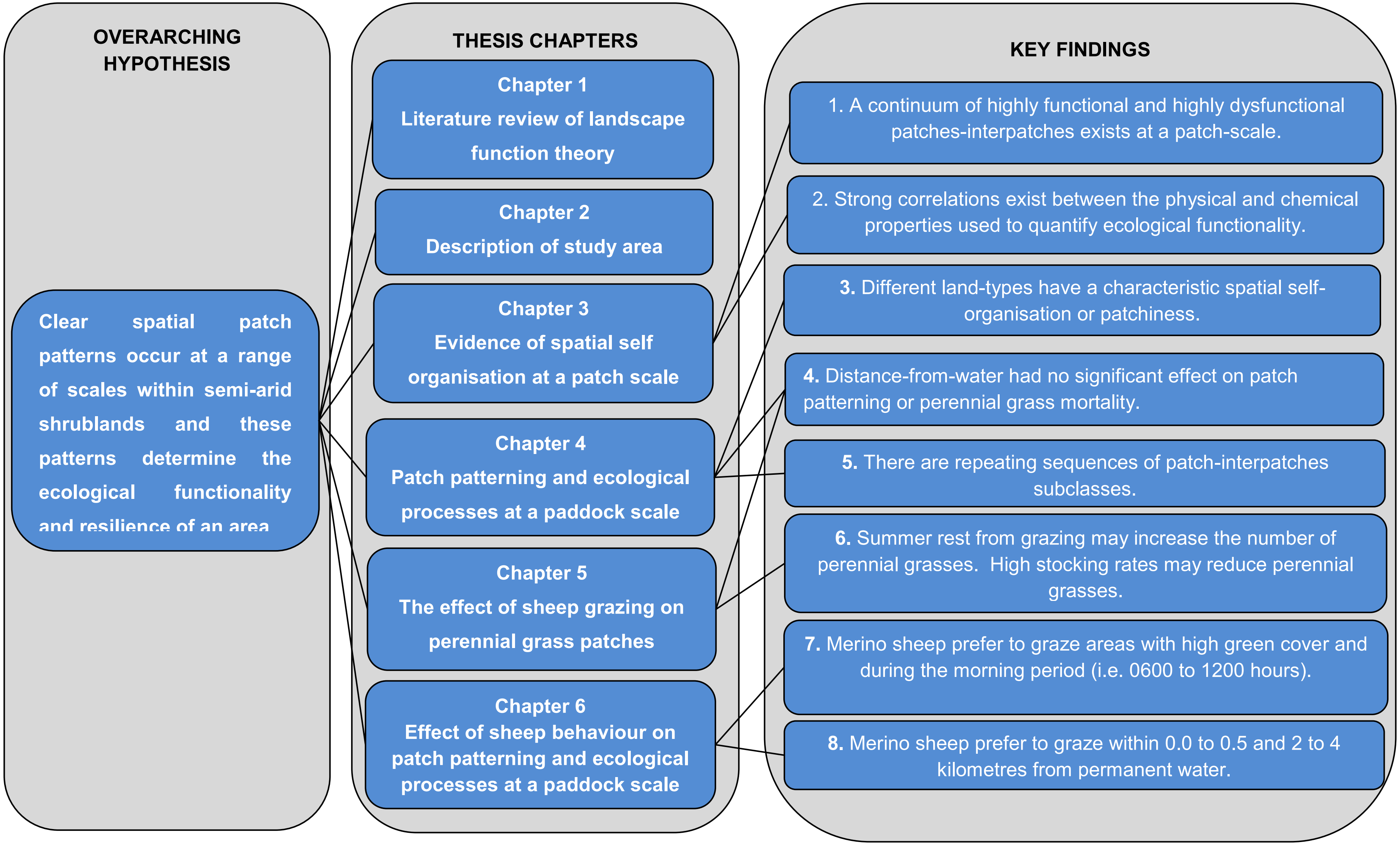

Figure 7-1: Structural outline of thesis and key findings

7.2.1 A gradient of highly functional and highly dysfunctional patches-interpatches exists at a patch-scale

In **Chapter 3**, the following question was investigated: **is there empirical evidence to support the concept that vegetation and soil nutrients are patchily distributed?** A total of six physical and chemical properties were measured on 11 different patch-interpatch subclasses to empirically quantify the level of patchiness at a patch scale. This information was then used to determine if a gradient exists between highly functional patches at one end to highly dysfunctional interpatches at the other end (as suggested by the third principle of landscape function theory).

The results of **Chapter 3** demonstrated that there was significant patchiness at a patch-scale in the study paddocks. Highly functional patch subclasses were more biologically active, had more than twice the number of perennial species, soil infiltration rates were 50% higher, and they had up to five times more carbon and nitrogen than low-order highly dysfunctional interpatches. A principle component analysis biplot clearly illustrated the gradient of ecological functionality that exists between the 11 different patch-interpatch subclasses and validated the intuitive classification that was made of the landscape components (**Figure 3-15**). In this semi-arid shrubland environment, the properties that characterise highly functional patches are:

- approximately < 25% bare-ground and a substantial amount of surface litter that is at varying stages of decomposition;
- elevated soil respiration rates (> 200 milligrams $CO_2/m^2/hr$);
- moderate to high amounts of soil carbon and nitrogen (soil carbon > 1.5%; C:N ratio > 10:1)
- moderate to high water infiltration rates (> 10 mm/hr);
- moderate plant species richness (> three plant species within the patch area); and
- moderate patch size (> four metres width).

Patchiness (as indicated by soil bulk density) was found to occur at a finer scale as there was significant intra-variation within the inner, middle and outer zones of individual patches and interpatches. The water and nutrients within more stable, fertile patches (e.g. P1 subclass) are likely to be more heterogeneously distributed compared to low-order patches (e.g. P3, P6, P11 subclasses). The results suggested that as individual patches are disturbed over extended periods, this process might homogenise soil surface conditions and lead to a loss of ecological functionality. The role of the patchiness at fine scales has been investigated in other studies that have shown that fine-scale heterogeneity is critical to the ecological functioning of semi-arid landscapes (Ludwig *et al*. 2005).

The results of **Chapter 3** quantified the level of patchiness at a patch scale and thereby provided empirical evidence that substantiates the first and third principles of landscape function theory. The occurrence of significant patchiness at a patch scale suggests that similar heterogeneity may occur at larger spatial scales and this was investigated in **Chapter 4**.

7.2.2 Strong correlations exist between the physical and chemical properties used to quantify ecological functionality

In **Chapter 3**, the following question was examined: **are there significant correlations between the measured physical and chemical properties?** The purpose of this question was to determine if a smaller number of physical and chemical properties could be measured in subsequent research studies and / or monitoring programs without compromising the integrity of the data. In addition, the answer to the question provides insight into the primary drivers of ecological processes at a patch-scale.

Results from **Chapter 3** found that there were significant correlations (R^2 >0.60) between a number of the measured physical and chemical properties. Soil respiration and soil infiltration were highly correlated. Macropores (>0.75 mm in size) are created by invertebrates, microbial activity and both living and decaying roots (Eldridge and Freudenberger, 2005; Greenwood and McKenzie, 2001). Soil infiltration rates will generally increase when there are a large number of macropores and when the amount of ground cover is adequate. Increased soil moisture can support a higher plant density that in turn produces additional organic matter for soil microbial decomposition that generates greater amounts of soil respiration. This cyclical process explains why soil respiration and soil infiltration were strongly correlated. Correlations between other physical and chemical properties demonstrates the interrelated, dynamic nature of ecological processes in semi-arid shrublands and their capacity to efficiently attract, retain and cycle limited water and nutrients.

Soil bulk density was correlated with every other physical and chemical property that was measured in this study with the exception of „patch size". A decrease in soil bulk density had the most consistent relationship to an improvement in ecological functionality. Therefore, given that soil bulk density is relatively simple to measure and it is correlated with the majority of the other properties, it is suggested that it could be used as a reliable indicator to quantify the ecological functionality of patch-interpatch subclasses. This finding could substantially reduce the costs of future research studies and / or monitoring programs in semi-arid shrublands. This would need to be quantified for different soil types (e.g. clays) before it was applied more generally.

7.2.3 Different land-types have a characteristic spatial self-organisation or patchiness

Chapter 4 explored the potential application of the four principles of landscape function theory at a large spatial scale within semi-arid shrublands. The empirical information about the characteristics of the patch-interpatch subclasses that was developed in **Chapter 3** was used to examine patch patterning and ecological processes at a large spatial scale. Specifically, one of the questions examined in **Chapter 4** was: **is there empirical evidence to support the concept that vegetation and soil nutrients are patchily distributed at a large spatial scale?** This was achieved by conducting over 30 kilometres of line intercept transects whereby the size and spacing of patch-interpatch subclasses was measured within four study paddocks. These study paddocks comprised of four major land-types: granitic shrublands, hardpan washplains, *Acacia* sandplains and alluvial plains.

The results of **Chapter 4** demonstrated that distinct spatial self-organisation occurred within each of the study paddocks. Functional patches (P2, P5) and highly dysfunctional interpatches (P10 and P11) occurred most frequently and dominated the length of the transects. The four study paddocks had relatively similar proportions occupied by patches (the sum of subclasses P1 to P8). The total proportion occupied by patches within the study paddocks ranged 27.5 to 35.7% that is indicative of semi-arid shrubland landscapes (Payne *et al*. 1994).

The granitic shrubland land-type had a much greater proportion of the highly dysfunctional P11 subclass (> 85% of the area) compared to the other land-types. In contrast, *Acacia* sandplains had a higher proportion of patch-interpatch subclasses (P5 and P10) and ecologically functional patches (P1 and P4) compared to granitic shrublands. Depending on the land-type, it was concluded that a functional ecosystem will generally have balanced proportions of P1, P2, P4, P5, P7 and P9 patch-interpatch subclasses as these will be the most effective at capturing, retaining and cycling water and nutrients. In contrast, a degraded ecosystem will have higher proportions of the ecologically dysfunctional P3, P6 and P11 subclasses. These results substantiated the third principle of landscape function theory relating to a gradient of dysfunctionality.

Knowledge of the characteristic patchiness of the different land-types can be used to assist in the management planning of various land-uses. For example, the limited number of highly functional patch-interpatches in the granitic shrublands land-type implies that these areas are likely to have a low availability of livestock forage. Therefore, a paddock should not comprise solely of the granitic shrublands land-type, unless it was only going to be periodically grazed during periods of above-average rainfall. Alternatively, the low number of functional patches suggests that these areas may provide limited habitat for short-range endemics and other fauna species. Therefore, livestock production efforts may be better focused on other land-types such as *Acacia* sandplains or alluvial plains that have much higher proportions of functional patches and may support increased livestock productivity.

7.2.4 There are repeating sequences of patch-interpatches subclasses

The second question examined in **Chapter 4** was: **are there significant spatial associations and repeating sequences of individual patch-interpatch subclasses?** This was based on the recognition that previous studies had found strong associations between certain types of patches and the sequencing of patches and interpatches can inform the manner in which they „fit and work‟ together (Chartier and Rostagno, 2006; Pickup, 1985). The results of **Chapter 4** clearly identified a number of repeating sequences and associations between the different patch-interpatch subclasses. The three major sequences that were identified by the results were:

- highly functional and functional patches (P1, P2 and P4 patch subclasses respectively) often occur with functional interpatches (P9 subclass);
- highly functional patches typically occur together. The converse of this also held true; and

- groups of perennial grasses (P7 subclass) and isolated perennial tussocks (P8 subclass) tend to occur more regularly with ecologically functional interpatches than with larger, functional shrub or tree patches.

Ecological and hydrological processes in semi-arid landscapes are intrinsically linked to the patterning of patches and the way they serve to capture, retain and cycle water and nutrients (Ludwig *et al.* 2005). It was clear that there were spatial associations and dependencies between a number of the subclasses and this may have a positive or negative impact on landscape processes, depending on the subclasses involved in the association. Where there is a regular sequence of dysfunctional patch-interpatches, the land-type will most likely act as a source site for areas down-slope. Conversely, land-types that have a regular sequence of functional patches (i.e. P1, P2, P4, P5 and P9 subclasses) will have negligible losses from the ecosystem and may be more resilient to abiotic and biotic disturbances.

Clearly, promoting or maintaining sequences that involve a higher proportion of functional patch-interpatches should be the goal of land managers. Failure to recognize dysfunctional patch-interpatch sequences in the early stages of their development may lead to accelerated fragmentation of the natural patchiness and associated loss of productivity and resilience.

7.2.5 Distance-from-water had no significant effect on patch patterning or perennial grass mortality

Chapter 1 reported that grazing and seasonal conditions are the two major factors that determine the trajectory of patch patterning and landscape function in the rangelands (Ludwig *et al*. 1997). Seasonal conditions are generally beyond human control, therefore grazing management is the primary mechanism through which pastoralists can potentially maintain or restore the natural patchiness and ecological processes. **Chapter 4** discussed how distance from permanent water is often used as a surrogate for grazing pressure and was supported by results in **Chapter 6**. To test the assumption that grazing is a major source of disturbance (usually negative), the effect of distance-from-water on patch patterning and perennial grass mortality was assessed in **Chapters 4** and **5** respectively.

To test the effect of distance-from-water on patch patterning in **Chapter 4**, the proportion (%) of the 11 different patch-interpatch subclasses were analysed at varying distances from water in the study paddocks (up to a distance of approximately five kilometres). The results from **Chapter 4** indicated that grazing did not have a significant effect (P>0.05) on the proportions of the different patch-interpatch subclasses. The general lack of significant effect due to distance-from-water is not unexpected as the extensive land surveys of the region were also unable to detect clear relationships for the majority of land-types (Curry *et al.* 1994; Payne, *et al.* 1998). They reported that "key characteristics, such as perennial cover, species richness and diversity of all woody perennials, and of the palatable species showed no significant differences in relation to distance-from-water" (Curry *et al*. 1994, p. 304).

The lack of a distance-from-water effect in **Chapter 4** was explained by the fact that any significant impacts by grazing may have occurred within one kilometre of the watering point (the traditional „sacrifice zone" of a paddock). The closest starting point of a transect from a watering point was approximately 960 metres. Consequently, the study may have failed to detect significant impacts that occurred within the „sacrifice zone" around the watering point. Nonetheless, it was suggested that the impact on ecological process is likely to be relatively inconsequential if the major grazing disturbance only occurs within an area less than one kilometre. The relatively high proportions of functional patches within the study paddocks (**Chapter 4**) provided evidence to support this notion.

To test the effect of distance-from-water on the change in the number of perennial grasses in **Chapter 5**, a total of 246 individual grass tussocks in four study paddocks were monitored over a 12 month period. Half of the grass tussocks were protected by exclosures and the remainder could be grazed by the sheep in the paddocks. The finding of **Chapter 5** was similar to **Chapter 4**; distance-from-water did not have any significant effect on the mortality of perennial grasses. Instead, perennial grass mortality was largely determined by the below-average rainfall conditions that prevailed in the years leading up to and during the study period. Grazing is likely to have „conditioned" the grasses to be more susceptible to the impact of moisture-constrained conditions.

The findings of **Chapter 4** and **5** appear to conflict with other studies in semi-arid shrublands which found clear distance-from-water effects as a result of overgrazing (Hunt, 2001; Pringle and Landsberg, 2007). This finding suggests that there may have been other factors which influence patch patterning and perennial grass mortality in the paddocks, these may include: the prevailing wind direction, the paddock configuration, landscape heterogeneity, topography, grazing history and competition from other grazers (particularly kangaroos and feral goats). For example, Wilson (1991) concluded that the movement of kangaroos to rested paddocks can negate any benefit from periodic resting of pastures from sheep grazing. These factors interrelate and cause sheep to utilise landscape disproportionately (as reported in **Chapter 6**) and this can create ecological signals of disturbance that can be very difficult to discern.

This finding has implications for the design of long-term monitoring programs in semi-arid shrublands. It is recommended that the location of monitoring sites should not be based simply on the distance-from-water. Consideration of the other factors listed should be made to ensure that no inaccurate conclusions are derived from monitoring data. For example, an assumption that a site five kilometres from water represents the natural patchiness of an area (analogue site) may be incorrect if it is a preferred land-type and receives higher grazing pressure (as occurred in the hardpan washplains in **Chapter 6**).

7.2.6 Summer rest from grazing may reduce perennial grass populations while high stocking rates may increase perennial grass populations

Whilst distance-from-water did not have a significant effect on patch patterning and the perennial grass populations (**Chapter 4** and **5**), summer rest from grazing and higher stocking rates was found to have had an impact on the latter. The effect of summer rest from grazing and stocking rates on the perennial grass populations was investigated in **Chapter 5**. The results in **Chapter 5** indicated that there were significant differences in the change in the number of perennial grass plants over the 12-month monitoring period.

Complete protection from grazing (by an exclosure), rest in the preceding summer period and relatively lower stocking rates resulted in a general increase in the number of perennial grass plants in the paddocks. In contrast, higher stocking rates combined with no rest resulted in a reduction in the number of perennial grass plants at the study sites. Complete exclusion from grazing in the no-rest paddocks still resulted in a 40.6% reduction in perennial grasses over the 12-month monitoring period. This suggested that either the below-average rainfall during the monitoring period and / or the grazing history prior to the installation of the exclosure had an influence on the outcome. No-summer rest and no protection from grazing during the below-average rainfall period clearly had a negative impact on the perennial grasses. These results are consistent with the findings of Brown (1986) who also reported reductions in grass populations due to drought conditions and defoliation.

The results of **Chapter 5** found that below-average seasons might exacerbate the adverse impact of both higher stocking rates and no rest from grazing, on the resilience of perennial grasses. The results suggested that stocking rates might have to be reduced by as much as 40% if grazing is to have a benign impact on perennial grass populations during below-average rainfall periods. A fundamental assumption of landscape function theory is that seasonal conditions and grazing are the two key factors which determine the position of an ecosystem along the gradient of functionality and dysfunctionality (Ludwig *et al*. 1995). **Chapter 5** found evidence within the semi-arid shrublands to substantiate this assumption. This highlights that grazing had a significant influence on perennial grass mortality over and above that imposed by seasonal conditions.

The management implication of this finding is that grazing management must be applied in a judicious manner and pastoralists must seek to align stocking rates with the seasonal carrying capacity. Perennial grasses comprise a relatively small proportion of semi-arid shrublands (**Chapter 4**), however they contribute to the natural patchiness and associated ecological processes. They are also a valuable source of digestible energy for sheep. Accurate predictions of impending below-average rainfall periods remains somewhat elusive in semi-arid shrublands, and therefore pastoralists must develop the skills of assessing the amount of available forage. This should be performed on a regular basis to guide timely adjustments of livestock grazing pressure in order to maintain or promote healthy populations of perennial grass plants in the landscape. This may shift the landscape towards a higher level of ecological functionality of the gradient (**Chapter 3**).

7.2.7 Merino sheep prefer to graze areas with high green cover and during the morning period (i.e. 0600 to 1200 hours)

Chapter 6 investigated the grazing preferences of Merino sheep to enhance the understanding of how grazing can impact natural patchiness and ecological processes. Two questions investigated in the chapter were: (1) which areas receive increased grazing activity and why? and (2) does the time of day influence Merino sheep grazing activity? To test these questions eight adult Merino sheep were fitted with GPS-collars and their grazing behaviour was monitored over a 20 day period in one of the study paddocks. The results of **Chapter 6** showed that grazing pressure is not exerted in a homogeneous, mechanistic manner across semi-arid shrublands.

The GPS-collared sheep preferred to graze the land-types with high pastoral potentials (hardpan washplains and alluvial plains). The propensity of Merino sheep to selectively graze certain areas could adversely impact the natural patchiness of the ecosystem and lead to dysfunctional ecological processes (third principle of landscape function theory). Repetitive, overgrazing may decouple complex patch associations and assemblages (as were identified in **Chapter 4**). Conversely, the innate grazing behaviour of sheep could be harnessed to restore and / or replace missing or ineffective processes in the landscape in order to improve soil surface conditions and soil habitat quality (application of the fourth principle of landscape function theory). The findings of **Chapter 6** substantiate anecdotal evidence from pastoralists who generally extol the capacity of Merino sheep to forage in marginal, extensive semi-arid shrublands. To maintain body weight and rear healthy lambs in semi-arid shrublands, sheep must have a well developed spatial memory of forage reserves (Lace, 1998).

The results of **Chapter 6** also found that grazing activity was the highest during the morning period (0600 to 1200 hours) and the lowest during the night period (0100 to 0600 hours). There was also very limited grazing activity during the afternoon period (1200 to 1800 hours).

The implication of selective grazing to pastoralists relates to their ability to adapt their management strategies to harness the behavioural characteristics so they are expressed in a positive way. Practically, this may require fencing areas based on land-system so the patch patterning of preferred areas is not adversely impacted. Alternatively, installation of additional watering points in a paddock may distribute grazing pressure across a broader area (given that the results in **Chapter 6** found that distance-from-water influences grazing activity). Introducing periods of rest from grazing may also allow for the recovery of vegetation patches that have been temporarily impacted by defoliation / trampling. If grazing pressure is not actively managed then the natural patchiness of the landscape may transition towards the dysfunctional end of the continuum (principle 3 of landscape function theory).

7.2.8 Merino sheep preferred to graze 0.0 to 0.5 km and 2 to 4 km from permanent water

Chapter 6 investigated the effect of distance-from-water on the amount of grazing activity. The results indicated a clear preference of the sheep to graze within the zones of 0.0 to 0.5 km and 2 to 4 km distance-from-water. The GPS-collared sheep visited a watering point once every 37.5 hours. The variation in time between visits corresponded with differences in temperature, i.e. high temperatures decreased the time between visits. The preference to graze within the 2 to 4 km band of the study paddock was primarily caused by increased green cover. A broad drainage plain (part of the alluvial plains land-type) occurs between 1.5 and 3 km and this had higher amount of green cover and it was clearly attractive to the sheep (**Figure 6-5**). The area between 0.5 to 1.5 km had less green cover because it would have been repetitively grazed as the sheep „commuted" through the area to the drainage plain each day.

The preference of sheep to graze within a band of 2 to 4 km may have implications for patch patterning and ecological processes within semi-arid shrublands. If the grazing pressure is excessive, then it is possible that this area may lose functional plant patches and soil erosion may accelerate. The absence of a significant distance-from-water effect in the study paddock (results from **Chapter 4** and **5**) suggested that this critical threshold may not have been reached. However, there is conclusive evidence from other studies which demonstrates that repetitive, overgrazing will lead to a net loss in the ecological functionality of semi-arid shrublands (Ash and Stafford Smith, 1996; Graetz, 1986; Hunt, 2000; Watson *et al.* 1997). Therefore, pastoralists need to be cognizant of the potential effect of distance-from-water on patch patterning when they are designing the layout of new or existing infrastructure.

A paddock should have a sufficient number of watering points to ensure sheep are not required to walk distances greater than three kilometres. Any area beyond three kilometres from permanent water should be excluded from the calculation of paddock stocking rates, otherwise the grazing pressure may exceed the available forage supply and/or livestock productivity (i.e. weight gains, lambing and weaning rates) may be compromised.

7.3 Future directions

This thesis has provided empirical evidence which substantiates landscape function theory and concludes that it has significant application at a range of spatial scales in the semi-arid shrublands. The results from this thesis explain why the theory is the current basis for the assessment and interpretation of rangeland environments in Australia.

Landscape function theory is largely the result of an evolutionary synthesis of earlier work by Clements (1916), Charley (1961), Noy-Meir (1981), Pickup (1985), Westoby *et al*. (1989) and Ludwig *et al*. 1997. The theory continues to be progressively refined as our knowledge of the complex patterns and ecological processes of the rangelands is improved. In this context, I consider that there are three key areas of inquiry which could further assist land managers to practically apply landscape function theory and restore the ecological functionality of degraded Australian rangelands.

The first area of inquiry is: what is the „functional" composition of patch-interpatches subclasses for a range of land-types in the Australian rangelands? This thesis has demonstrated that different land-types have a natural patchiness or patch patterning. What remains unclear is whether the patch-interpatch subclass composition of the different land-types is at the highest level of functionality. Management plans require specific goals to be made in terms of the desired condition of an area. Therefore, the first area of inquiry could relate to defining the most functional patch-interpatch compositions of the major land-types in the Australian rangelands. These would effectively act as benchmarks that could be used by pastoralists, mining company environmental officers and others to gauge the relative progress of their rehabilitation efforts.

The second area of inquiry is: what level of management intervention is required to reconstruct dysfunctional patch patterns? I consider that we need further empirical quantification of ecological processes at a range of spatial and temporal scales across the major land-types of Australia"s rangelands. We now have a strong conceptual understanding of how water, nutrients and energy are exchanged and cycled in semi-arid shrublands; however, there are few datasets that actually quantify the inputs / outputs of different land-types. These datasets could be used to populate existing simulation models that are used to predict the relative cost / benefit of various restoration and rehabilitation projects. The datasets should be similar to the one presented in this thesis, except they would be for other land-types across various climatic zones. Robust datasets will enable the simulation models to accurately predict the „production pulses" that can be generated if the patch-interpatch patterning is reconstructed (i.e. prediction of the amount of biomass production per millimetre of precipitation). This information would assist in the planning of cost-effective rehabilitation programs by pastoralists, conservation park rangers, carbon offset developers and mining environmental officers alike.

The third and final area of inquiry is: can grazing be used to restore dysfunctional patch-interpatch patterns and ecological processes in the semi-arid shrublands? The impact of grazing on the soil and the vegetation in Australia"s rangelands has been under investigation since the early 1950s (Ash and Stafford Smith, 1996). Some consider that as a result of the substantial institutional effort and investment that has been made over the years, "the ecological relationships of grazing systems have been reasonably well resolved" (Briske *et al.* 2008, p.3). However, others consider that, while extensive information has been collected and it has enhanced our level of understanding of soil, plant and grazing animal processes at small scales, there has been difficulty in translating this understanding in a way that assists management at commercial scales (Ash and Stafford Smith, 2002; Ash and Stafford Smith 1996; Norton, 1998; Scott, 2003).

A general conflict remains regarding the potential role that grazing may have as a tool of disturbance to stimulate ecological processes (namely defoliation promotes healthy root systems and biomass production of some plant species; local concentration of animal faeces and urine to increase fertility; hoof action to break sealed soil surfaces to increase infiltration and porosity; transportation of seeds). I consider that further research is warranted into quantifying the effects grazing on semi-arid shrublands. The objective of this research should be to articulate the key principles that will restore dysfunctional patch-interpatch patterns and ecological processes. This area of inquiry could involve: identifying paddock designs that will capitalise on livestock"s natural grazing behaviour; identify the optimum time for grazing perennial grasses and the tolerance thresholds of grasses to disturbance; and determine the patch patterns that are the most vulnerable to disturbance / most likely to respond favourably to disturbance.

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APPENDICES

Appendix 1: Description of the static alkali absorption method for measuring soil respiration

Respiration ring materials and construction

A total of 50 respiration rings were fabricated based on the blueprint design supplied by David Tongway (Tongway, unpublished). Sheets of galvanised steel (1800 x 1200 x 0.60 mm) were cut to size and riveted to form rings with the dimensions: 100 mm height x 200 mm diameter (NB: retrospectively, an easier approach would have been to use air-conditioning ducting and cut rings to size). A clear-sealant was generously coated on the inside join of the ring and rivet plugs to create a gas-tight seal. High density rubber lining was affixed to the top edge of the respiration ring using a clear-sealant.

Sheets of clear perspex (1200 x 1200 x 3 mm) were cut into squares (250 x 250 mm) and covered with aluminium foil and clear adhesive contact to maintain the ambient temperature inside the ring. High density rubber was used to create gasket seals for the under-side of the perspex lids. Four brackets were riveted to the respiration ring and holes were drilled into the perspex lid. On the inside of the ring the bracket rivets were generously coated with sealant. The lid was fastened to the top of the ring using 1/4" cup-head bolts and nuts.

Respiration ring installation

A respiration ring was hammered 70 mm into the soil using a circular striking plate, leaving about 30 mm protruding (Figure 61). Rocks and roots interfered with this process, but were endured. Green vegetation was removed at ground level. The soil was tamped firmly around the perimeter of the ring inside and out to prevent carbon dioxide from escaping from the ring. Installation of the rings was done at 1600 to 1700 hours and required approximately 2 to 5 minutes per ring.

To reduce the potential influence that existing soil moisture would have on soil respiration values, the equivalent of 20 mm of rainwater was added (approximately 600 ml for the 20 cm diameter ring) and this was allowed to drain overnight (approx. 16 hrs). A plastic measuring container was used to dispense the water into the ring. This „primed" the soil biota to begin respiring. The overnight delay permitted the „drain-down" of water and the return of the soil to aerobic conditions and allowed carbon dioxide released as a consequence of soil disturbance to disperse. The ring was covered overnight with the perspex top screwed onto the top of the ring; this reduced drying to a minimum and discouraged fauna from interfering with the ring.

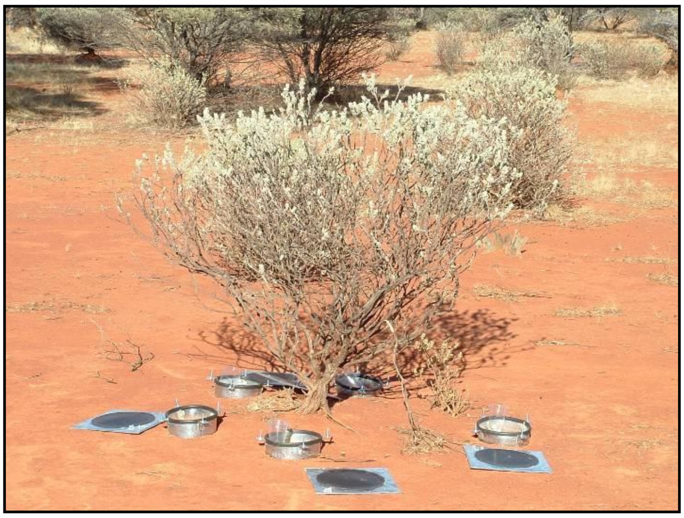

Plate A-1: Five respiration rings partly installed at a P6 shrub patch

Running the respiration equipment

At approximately 0700 hours on the day after installation, a Petri dish was numbered and placed inside the ring. Stones and debris were used to ensure the petri dish was level. One ampoule of 1.0 M potassium hydroxide (KOH) was rinsed into a 2 L glass volumetric flask which was filled to exactly 2 L with deionised water to make a solution of 0.5 M KOH. The volumetric flask was thoroughly agitated. 20 ml of 0.50 M KOH was dispensed into the Petri dish using a 20 ml volumetric „A" grade pipette. The pipette was washed thoroughly after use. The lid of the respiration ring was then rapidly set in place and screwed down against the rubber gasket.

The time of day to the nearest minute was recorded. Potassium hydroxide prepared from ampoules of concentrated volumetric solution has no carbonate contamination and facilitates the collection of very reliable data. The Titrisol® brand of 1.0 ML KOH ampoules was diluted in 2 L of deionised water in order to achieve the required 0.5 M concentration.

The plastic ampoules were very easy to use and posed few hazards for the operator. A fresh KOH solution was made up if the solution was not used within 48 hours. Tongway (unpublished) recommended that if the EC fell below 40 mS, then the entire respiration with twice the amount of KOH solution was to be repeated.

Measurement of CO_2

Approximately 24 hrs later, (again the time to the nearest minute was recorded), the perspex lid was removed and the KOH solution was poured into a measuring container through a wide-mouthed funnel, ensuring that it was well mixed. Using a Hanna® Multi-range Conductivity meter (0-199.9mS cm^{-1}) the electrical conductivity (EC) was measured immediately. The conductivity meter had an automatic temperature compensation feature.

It was essential to know with precision the EC values of both freshly prepared KOH solution and completely saturated solution. The former was done by taking a measurement of the solution every time a new batch was prepared. The latter was done on a green kikuyu lawn in Meekatharra (26°35"S, 118°51"E) and the respiration measurements were run over several days under good conditions to obtain a reliable value. This was done to ensure the accuracy of every respiration ring.

Soil respiration calculations

There is a straight-line relationship between EC and the amount of CO_2 absorbed by the KOH solution. It was recommended that 24 hrs is an appropriate period to collect CO_2. Previous studies have shown that shorter periods have produced unreliable data, due to disturbance effects.

An Excel^{TM} template (Tongway, unpublished) that does all the necessary conversion calculations was used to calculate the soil respiration values for each sample. The units of respiration are milligrams of CO_2 per m^2 per hour. There were cells on the spreadsheet where the specific volume of KOH used needed to be inserted as well as its fresh and saturated values (Table 26 provides an example of the spreadsheet table that was used for data entry and calculations). The conversion equation for 20 ml 0.5M KOH was:

$$\text{Respiration} = \frac{220(C - A)}{* 2 - B} * \frac{10000}{314} * \frac{1}{t}$$

where A is sample EC mS cm^{-1}

B saturated KOH EC = 24.32 mS cm^{-1}

C fresh KOH EC approx. 123.86 mS cm^{-1}

t time of respiration measured in hours

Table: Example of soil respiration data entry and conversion calculator sheet

		Date:	**26-28/09/06**		**Site:**	**Barnong pastoral lease - 5 Mile Paddock**				
Sample ID	**GPS Waypoint**	**Plate No.**	**Date on**	**Time on**	**Date off**	**Time off**	**Days**	**Hours**	**Respiration**	**EC**
P1	50J0440483 UTM6836552	1	27-Sep	6:24	28-Sep	6:40	1.01	24.27	272	30.1
		2	27-Sep	6:25	28-Sep	6:35	1.01	24.17	272	30.6
		3	27-Sep	6:26	28-Sep	6:36	1.01	24.17	260	34.5
		4	27-Sep	6:28	28-Sep	6:39	1.01	24.18	258	35.3

The mean and the variance were reported and analysed for each subclass.

Additional guidelines and recommendations for the soil respiration method

Respiration rates can be expected to be in the range of 100 to 1000 mg $CO_2/m^2/hr$. There is no theoretical limit to the volume of KOH that could be used, just the volumetric limit of what fits inside the ring/lid combination. It is important not to vary the concentration of the KOH as this may disturb the diffusion rate of CO_2 to the KOH. A criticism of this method is that it provides too effective a gradient for CO_2 and that it „drags" more CO_2 out of the soil than would normally diffuse out.

If possible, returning the KOH sample to the laboratory for measurement is an acceptable and preferable option to measuring EC in the field. Pre-labelled plastic bottles could be used to transport the samples and carried in a tray in the field. Leak-proof screw closures would be essential. The bottles should be approximately 100 ml capacity. This was not a practical alternative for this study.

Roots and rocks will always cause difficulties in the installation of the ring into the ground. It is important to remove litter inside the ring to the top of the mineral soil, after installation, but avoid disturbing the surface. This way, respiration within the soil itself is measured, rather than the soil plus varying amounts of litter in various states of decomposition. If the effect of litter is required, do two rings, one with retained litter, the other with litter removed.

Temperature variation changes the amount of respiration measured. This is one reason to take a full 24 hours on a morning-to-morning basis. The soil is somewhat buffered against violent fluctuations in temperature when respiration is carried out *in situ.*

Appendix 2: List plant species that occurred within each of the woody patches

Plant functional group	Plant Species	Patch-interpatch subclass							
		P1	P2	P3	P4	P5	P6	P7	P8
Trees	*Eucalyptus spp.*	6.0	1.6	0.0	0.8	0.1	0.0	0.0	0.0
	Callitris glaucophylla	4.6	6.8	0.8	0.0	0.9	0.0	0.0	0.0
	Melaleuca spp.	1.6	1.1	2.3	1.7	3.4	1.0	0.0	0.0
Palatable tall shrubs	*Acacia aneura*	2.5	7.4	9.0	0.0	2.3	2.1	0.0	0.0
	Eremophila compacta	3.3	0.6	0.0	0.8	1.3	0.2	0.0	0.0
	Eremophila forrestii	0.0	1.7	1.9	0.0	2.0	2.9	0.0	0.0
	Eremophila longifolia	1.6	0.3	0.0	1.7	0.2	0.0	0.0	0.6
	Eremophila latrobei	0.3	0.8	0.4	0.0	0.1	0.0	0.0	0.0
	Eremophila maitlandii	0.5	0.1	0.0	0.0	0.3	0.0	0.0	0.0
Unpalatable tall shrubs	*Acacia acuminata*	1.1	2.1	4.5	0.0	0.6	3.3	0.0	0.0
	Acacia coolgardiensis	6.3	11.5	2.8	9.1	17.1	3.1	0.0	0.0
	Acacia grasbyi	0.5	2.7	9.0	0.8	1.2	4.6	0.0	0.0
	Acacia linophylla	1.1	2.5	0.4	4.5	2.5	0.2	0.0	0.0
	Acacia sclerosperma	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Acacia sp. unidentified 1	4.9	1.8	9.0	8.3	3.7	8.6	0.0	0.0
	Acacia sp. unidentified 2	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Acacia tetragonaphylla	1.6	3.0	3.2	1.2	2.9	6.8	0.0	0.0
	Acacia victoriae	0.0	0.1	0.0	0.8	0.0	0.2	0.0	0.0
	Acacia xiphophylla	0.0	0.2	2.6	0.0	0.2	3.6	0.0	0.0
	Canthium latifolium	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
	Cassia nemophila	0.0	0.3	0.0	0.0	0.6	0.2	0.0	0.0
	Cassia sp. unidentified 1	2.7	1.3	0.0	1.7	0.2	0.0	0.0	0.0
	Dodonaea viscosa	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Eremophila clarkeii	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0
	Eremophila sp. unidentified 1	0.0	0.2	0.4	0.0	1.0	0.2	0.0	0.0
	Eremophila fraserii	0.0	0.0	0.4	0.0	0.1	0.7	0.0	0.0
	Eremophila sp. unidentified 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Eremophila nemophila	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Eremophila sp. unidentified 3	2.2	4.0	1.3	2.1	5.8	2.8	0.0	0.0
	Eremophila sp. unidentified 4	0.0	0.2	0.0	0.0	0.3	0.0	0.0	0.0
	Exocarpos aphyllus	1.6	0.6	0.0	2.5	0.7	0.2	0.0	0.0
	Hakea preissii	0.0	1.6	5.3	0.0	1.8	6.8	0.0	0.0
	Hakea sp. unidentified 1	0.0	0.4	1.5	1.7	1.1	4.0	0.0	0.0
	Hakea suberea	0.0	0.2	1.1	0.0	0.1	0.0	0.0	0.0
palatable mid-sized shrubs	*Atriplex bunburyana*	1.6	0.5	0.4	5.8	2.0	1.2	0.0	0.0
	Atriplex vesicaria	0.0	0.1	0.4	0.0	0.3	0.2	0.0	0.0
	Cratystylis subspinescens	0.0	0.2	0.8	5.8	8.0	6.9	0.0	0.0
	Maireana pyramidata	0.0	0.1	0.0	1.7	2.0	0.3	0.0	0.0
	Rhagodia drummondii	2.2	1.0	0.0	5.8	1.4	0.2	0.0	0.0
	Rhagodia eremaea	4.6	3.3	5.1	0.0	1.4	3.0	0.0	0.0
	Scaevola spinescens	5.5	1.1	0.8	1.7	1.5	1.2	0.0	0.0
	Sida calyxhymenia	0.0	0.2	0.0	0.0	0.2	0.3	0.0	0.0
	Solannum orbiculatum	0.0	1.7	0.4	0.0	0.3	0.4	0.0	0.0
	Spartothamnella teucriiflora	1.4	1.2	0.2	0.8	0.6	0.2	0.0	0.0
	Scaevola subspinescens	2.2	1.1	0.4	1.2	0.9	0.2	0.0	0.0
unpalatable	*Dianella sp. unidentified 1*	0.5	0.3	0.0	0.0	0.1	0.0	0.0	0.0

Plant functional group	**Plant Species**	**Patch-interpatch subclass**							
		P1	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**
mid-sized shrubs	*Roly poly unidentified 1*	1.6	1.3	0.0	1.7	0.1	0.0	0.0	0.0
palatable small shrubs	*Atriplex semilunaris*	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
	Chenopodium gaudichaudianum	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
	Enchylaena tomentosa	3.8	1.0	0.0	2.5	1.1	0.0	0.0	0.0
	Maireana convexa	0.8	1.5	4.9	0.0	0.6	1.2	0.0	0.0
	Maireana georgei	0.0	0.0	0.0	0.8	1.2	0.0	0.0	0.0
	Maireana melanocoma	0.0	0.2	0.0	0.0	0.1	0.0	0.0	0.0
	Maireana sp. unidentified 1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
	Maireana thesioides	2.5	0.6	0.0	1.7	0.8	0.3	0.0	0.0
	Maireana tomentosa	0.5	0.4	0.8	2.5	1.0	0.2	0.0	0.0
	Ptilotus divaricatus	1.1	0.6	0.4	1.7	0.6	0.0	0.0	0.0
	Ptilotus exaltatus	0.0	0.0	0.4	0.8	0.0	0.0	0.0	0.0
	Ptilotus obovatus	4.9	8.1	22.6	2.9	5.1	26.9	0.0	0.0
	Ptilotus schwarzii	0.3	0.4	0.6	0.4	0.4	1.4	0.0	0.0
	Solannum lasiophyllum	0.5	1.3	1.1	0.4	0.3	1.4	0.0	0.0
unpalatable small shrubs	*Frankenii sp. unidentified 1*	0.8	0.3	0.0	0.0	1.5	0.2	0.0	0.0
	Halosarcia doleiformis	1.1	0.4	0.4	0.0	0.5	0.0	0.0	0.0
	Maireana triptera	0.0	0.0	0.0	0.8	0.1	0.0	0.0	0.0
grasses	*Aristida contorta*	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
	Cymbopogon ambigutus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.1
	Eragrostis dielsii	0.0	0.0	0.0	0.4	0.0	0.0	18.2	0.6
	Eragrostis eriopoda	0.0	0.1	0.0	0.0	0.1	0.0	0.0	12.8
	Eragrostis setifolia	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Monocather paradoxa	11.7	14.9	2.1	12.8	12.5	0.9	81.8	74.4
	Stipa elegantissma	7.9	4.2	2.1	9.5	3.7	2.2	0.0	3.8
	Stipa scabra	0.0	0.6	0.0	0.8	0.1	0.0	0.0	2.6

Appendix 3: Plant mortality and recruitment rates of perennial grasses during the 12-month period

Case study paddock	Site ID number	Protected (exclosure site)		Unprotected site	
		Mortality rate (%)	Recruitment rate (%)	Mortality rate (%)	Recruitment rate (%)
Paddock 1	10	0	50	0	0
	11	0	100	0	0
	12	0	100	0	0
	13	0	20	-83	0
	14	0	0	0	0
	15	0	25	0	75
	16	0	50	0	0
	17	0	22	0	38
	18	0	0	0	0
	19	0	0	0	50
Paddock 2	1	0	0	-50	0
	2	0	0	-100	0
	3	0	0	0	0
	4	0	25	-20	0
	5	-25	0	-33	0
	6	0	0	0	0
	7	0	0	0	0
	8	0	33	0	0
	9	0	100	-100	0
Paddock 3	20	0	0	-100	0
	21	-33	0	-67	0
	22	0	0	0	0
	23	-100	0	-100	0
	24	0	0	0	0
	25	-50	0	-100	0
	26	-20	0	-33	0
	27	-50	0	-33	0
	28	-100	0	-50	0
Paddock 4	29	0	0	-100	0
	30	-37	0	-61	0
	31	-100	0	0	0
	32	-100	0	-100	0
	33	0	0	-100	0
	34	-100	0	-100	0
	35	0	0	-100	0
	36	0	0	-100	0