

Characteristics and dynamics of the
mulga-spinifex boundaries at
Mt Denison Station in Central Australia

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March 2007

**This thesis is presented as part of the requirements for the
award of Master of Science by Research through the
Institute of Advance Studies,
at the Charles Darwin University.**

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I hereby declare that the work herein, now submitted as a thesis for the degree of Master by research at the Charles Darwin University, is the result of my own investigations, and all references to ideas and work of other researchers have been specifically acknowledged. I hereby certify that the work embodied in this thesis has not already been accepted in substance for any degree, and is not being currently submitted in candidature for any other degree.

Signed:

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Acknowledgements

I would like to thank my supervisor Don Franklin for his patience, guidance and encouragement throughout the two years of this project. My co-supervisors David Bowman, Guy Boggs and Grant Allan are also thanked.

Much appreciation goes to Peter Latz, Kasia Gabrys and Warren McCaskill for help with field work. This project was made possible through the generosity of the owners of Mt Denison Station who welcomed us on their property, and the expert knowledge of Grant Allan who provided crucial resources and support from the Bushfires Council in Alice Springs. Many thanks are given to persons at Centralian College, Alice Springs who assisted with laboratory facilities and equipment, and the NT Geological Survey unit at the Arid Zone Research Institute. Special thanks to Hannah Hueneke and my family for supporting my education.

Gratitude goes to the Desert Knowledge Cooperative Research Centre (DK CRC) who funded the project as part of the 'Desert Fire' research program.

ABSTRACT

Mulga (*Acacia aneura*) and spinifex (*Triodia* spp.) are common throughout arid Australia, often dominating the landscape as discrete, abruptly alternating dominants of vegetation. The floristic, soil and fire frequency characteristics of the Mulga and spinifex dominated vegetation in the flat sandplain country at the southern limit of the Tanami Desert were explored to identify factors that are contributing to the distribution and possible dynamics of these vegetation types.

A floristic survey revealed that most woody species occurred on both sides of the Mulga-spinifex boundaries. The mulga to spinifex transition sat sharply across a diffuse soil surface textural gradient from loams through to sands. The woody species in both mulga and spinifex vegetation types shared functional life history and regeneration traits. Spinifex vegetation burnt on average three times more than Mulga vegetation. A positive correlation was found between Mulga structural diversity and time since fire. Summer fires are associated with stands dominated by younger Mulga trees. The species richness of woody plants was higher in spinifex than mulga vegetation at the local scale, but similar at the landscape scale.

The landscape was overwhelmingly characterized by the dominant mulga and spinifex. I argue that the boundary between mulga and spinifex vegetation types is created and maintained by fire, with possible dynamics associated with a fire-driven soil gradient. The fire effect was deemed most important because of the high degree of shared soil and other floristic features across the Mulga-spinifex boundary. The soil features argued to be reinforced by fire across the Mulga-spinifex boundaries may be contributing to conditions that heighten Mulga's capacity to regenerate after fire.

The reduction of structural complexity in frequently or intensely burnt Mulga stands is of concern for the current mulga-spinifex vegetation matrix in the southern Tanami Desert. It is conceivable that it could indicate a reduced structural state that has future consequences for the current mechanisms that mostly allow Mulga to maintain its boundary position under present conditions.

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CHAPTER 1: INTRODUCTION



...a spinifex stand

...recently burnt spinifex



A mulga stand



mulga meets spinifex

Mulga dominated communities together with hummock grasslands wooded with Mulga occupy about 1,500,000 km² or 20% of the total area of Australia (Figure 1.1). The total length of the boundaries created between mulga woodlands and spinifex sandplains has been described as longer than any other plant community boundary (in Australia?) (Griffin and Hodgkinson 1986). Concern has been raised about the impact that fire is having on the dynamics of these two communities. More specifically, the widely observed burning of Mulga stands from spinifex hummock grassland fires has generated speculation that mulga populations are declining. It is critical to know what defines these two populations to gain a better perspective on the way these two populations are interacting.

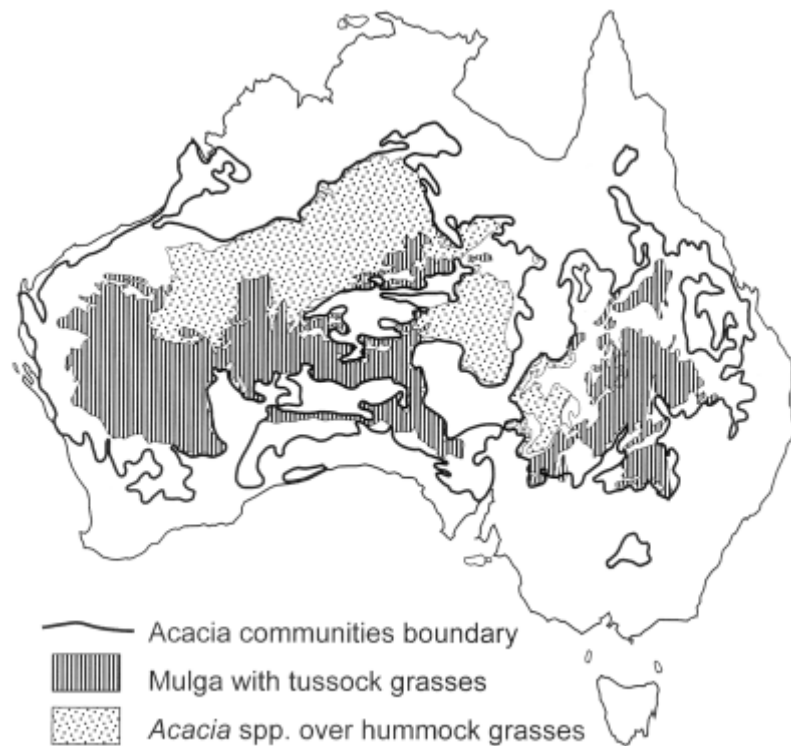


Figure 1.1 Distribution of Mulga dominated plant communities in Australia and the limit for the other *Acacia* communities. The *Acacia* species over hummock grasses is a mix of different desert *Acacias*. Reproduced from Hodgkinson (2002).

In this study I aim to detail the floristic (woody species), soil and fire characteristics of the mulga and spinifex communities at the southern limit of the Tanami Desert; and explore these characteristics for factors that may contribute to the dynamics between these two vegetation communities.

The predominant feature of the landscape at the southern limit of the Tanami Desert is the boundary or edge formed between the mulga communities and the hummock grassland. This is clearly represented in the aerial image below (Figure 1.2). The mulga communities in the study area are dominated by *Acacia aneura* var. *tenuis*, with a discontinuous perennial shrub layer and a seasonally varied composition and density of annual species. The spinifex communities are dominated by the hummock grass *Triodia pungens* with a scatter of perennial species and a flush of annuals following fire and rain. The landscape is relatively flat.



Figure 1.2 A physiognomic boundary between Mulga woodland (dark green) and spinifex hummock grassland (yellow) near the southern edge of the Tanami Desert.

Terminology

Throughout this thesis the word ‘Mulga’ is used as a common name for the trees of the species *Acacia aneura* var. *tenuis* (that dominates the study area), whereas the word ‘mulga’ is used to describe plant communities dominated by Mulga. The word ‘spinifex’ is adopted as a common name for all species of the genus *Triodia* and in this thesis refers to *Triodia pungens*. It is not to be confused with the genus *Spinifex* of coastal distribution. The word ‘boundary’ refers to the area of transition from one vegetation community to another.

Mulga features

Mulga (*Acacia aneura*) is one of the most characteristic plant species of the arid and semi-arid zones of Australia (Johnson and Burrows 1994). Mulga is a leguminous shrub or tree which grows to heights of 3-15 metres. The species exhibits extreme variation in growth form and the size and shape of phyllodes and legumes which has led to considerable work on the taxonomy of the species (Pedley 1973; Randell 1992). The general ecology and biology of Mulga is well documented (Fox 1986; Johnson and Burrows 1994; Latz 1995).

The phytogeographic limits of Mulga are generally controlled by rare summer rainfall in the south and rare winter rainfall in the north, the species being absent in areas of regular winter or summer drought (Nix and Austin 1973). In Central Australia, Mulga is found on a range of landforms and soil types, but most extensively on plains and sand plains of red earth soil adjacent to mountains and hills (Walker and Fogarty 1986; Johnson and Burrows 1994).

Mulga is considered to be a fire sensitive species. However, it withstands less intense fires and recovers quickly if conditions are favourable, and therefore is alternatively referred to as encouraged by fire or even as a fire weed (Griffin 1984). It regenerates from seed and has a variable (related to variety and/or moisture and season) capacity to resprout. Mulga’s ability to dominate other woody species is arguably an artificial subclimax caused by repeated fires. Mulga is argued to have only appeared as a major component of the vegetation 13000 years ago (Smith *et al* 1995). It has been

suggested that the current Mulga/spinifex landscape may be a recently created phenomenon, developed and maintained by indigenous burning practices (Start 1986). So, the present landscape may display the species that are most able to tolerate fire, and although Mulga is not quite as successful as spinifex (when fires are too frequent), it is better than most of the past (previously thought more abundant) fire sensitive species, and thus has managed to dominate (Latz 2007). In this context, the descriptions of Mulga as a fire ‘weed’ or as behaving as fire dependant can be understood. This argument is well beyond the scope of this project, however the point to be made is that the landscape we see today may only be a vague representation of the long past.

It is likely that Aboriginal burning practices contributed to the dynamics of Mulga, however there is no evidence available to support this hypothesis. Certainly Aboriginal burning was extensive in the recent past - many records from explorer’s diaries echo Ernest Giles words that the Aboriginals were ‘about burning, burning, burning; one would think they lived on fire instead of water’(Mulvaney and Kamminga 1999 p.59). Mulga stumps were widely observed in association with spinifex (Cleland 1966). The hypothesis that too frequent fire prevents Mulga from regenerating and gives spinifex the opportunity to establish is biologically sound, although very little unequivocal evidence is available (see further discussion below under ‘The Mulga-spinifex boundary’).

Spinifex features

Hummock grassland communities in arid Australia are dominated by ‘spinifex’ species of the genus *Triodia*. These perennial grasses grow to form rounded hummocks, and rings (depending on the species) if long unburnt. *Triodia* occurs mainly in the arid and semi-arid interior of the continent and is distributed generally north of the Mulga zone although they overlap extensively, and large incursions are known in the south (Suijdendorp 1981). Hummock grasslands cover over 2,000,000 km² or about 22% of the Australian continent (Allan and Southgate 2002). Trees and shrubs are often scattered through this community. These grasses are highly flammable and have been described as fire encouraged (Latz 1995), fire tolerant or fire dependant, as they are able to withstand high intensity fires by regenerating

quickly from seed and rootstock following a fire event (Suijdendorp 1981; Latz 1990). Communities experience regular fire in the order of one every 5-15 years (Suijdendorp 1981; Griffin 1984).

The Mulga-spinifex boundary

The parapatric nature of mulga and spinifex communities today has been argued to be partially an outcome of pre-settlement Aboriginal burning practices (Start 1986; Latz 1995). Where traditional burning regimes are thought to have largely avoided extensive, severe and frequent hot wildfires (Kimber 1983; Griffin and Hodgkinson 1986; Latz 1995; Smyth and James 2003). So, Mulga may have been protected from fire intensities and frequencies beyond its tolerance (Start 1986; Allan and Southgate 2002). Some scientists have raised concern over the vulnerability of Mulga to fire since the interruption and altered nature of traditional Aboriginal burning post-settlement (Griffin and Hodgkinson 1986; Start 1986; Krebs 1989; Latz 1991; Start *et al* 1991; Latz 1995). There is a general concern that fire from adjacent spinifex grasslands is killing Mulga (Cleland 1966; Fox 1980; Latz 1995; Allan and Southgate 2002). However, despite agreement that fire is burning Mulga boundaries (and beyond) at a local scale, there is little evidence of long term retraction of mulga populations on a landscape scale (van Etten 1988; Bowman *et al* 1994; Nano 2005). This remains to be adequately demonstrated.

However, efforts towards understanding this vegetation matrix have identified variables that mediate between these two vegetation communities. These variables have highlighted possible mechanisms that may contribute to the ability (or inability) of mulga boundaries to survive repeated fires from adjacent spinifex hummock grasslands (van Etten 1988; Nano 2005; Bowman, Boggs and Prior 2007).

The environmental gradients most clearly demonstrated to associate with a mulga-spinifex patterned landscape are soil and fire (van Etten 1988; Bowman *et al* 1994). However, there is considerable variation in the extent that these variables appear to regulate the Mulga-spinifex boundaries across different habitats. This raises the possibility that lesser-known mechanisms may contribute to the assembly of mulga and spinifex populations (Nano 2005).

Previous research has recorded soil or other floristic gradients that correspond directly (Bowman *et al* 1994; Nano 2005) or very indirectly (van Etten 1988; Nano 2005) with abrupt mulga-spinifex transitions. Nano (2005) suggested that strong soil differences across mulga-spinifex boundaries mostly have reduced effects from fire, and reduced soil differences across mulga-spinifex boundaries (mostly) have strong effects from fire, on boundary location and regulation in central Australian landscapes. It was considered most rare that a mulga-spinifex boundary had no influence from fire.

The mulga and spinifex communities in the southern Tanami alternate abruptly. This study assumed that given known physiological characteristics (and acknowledged unknown genetics), some condition prevents the mulga and spinifex communities expressing their distribution potentials. Mulga has previously been described to be more 'restricted' than spinifex in its distribution across the landscape (Nano 2005). Like all previous studies on Mulga-spinifex boundaries, this study considers the likely influence of soil and fire on the distribution of the mulga and spinifex communities in the southern Tanami Desert.

Rare parts of the landscape were observed as 'diffuse' boundaries, where mulga and spinifex mixed (see Figure 1.3). This suggested the underlying soil features may be diffusely changing over space, rather than abruptly like the visual vegetation boundaries (as seen in Figure 1.1). Van Etten (1988) reported diffuse Mulga-spinifex boundaries in association with gradual soil gradients and a long absence of fire. Consistent with this, Nano (2005) suggested that the rare occurrence of Mulga integrating with spinifex in central Australian landscapes with weak soil gradients was due to the effect of fire (Nano 2005). Gradual or diffuse soil gradients are representative of landscapes composed of broad environmental gradients (Whittaker 1967). These types of gradients describe ecocline boundary types and have been associated with abruptly alternating Mulga-spinifex transitions (van Etten 1988).



Figure 1.3 An example of diffuse boundaries where Mulga is mixing with spinifex.

By definition, the ecocline boundary type has a gradual transition between communities, where a continuous change in form represents a continuous change in the environment and invariably reflects environmentally complex gradients in the landscape (Whittaker 1967). Whittaker (1967) described how species reach local distribution boundaries in an ‘individualistic’ way, whereby each species is distributed in relation to the total range of environmental factors (including effects of other species) it encounters according to its own genetic, physiological characteristics and population dynamics. As no two species are alike in these characteristics, consequently no two species have the same distribution. This means that communities occurring along environmental gradients show gradual changes in population levels of species along the gradient (van der Maarel 2006). In ecocline boundaries, community boundaries are vague and generally richer in species than the communities they separate.

The lack of a direct soil-vegetation correspondence has been interpreted as evidence for artificially created landscape boundaries in a Western Australian study (van Etten 1988). It has also been suggested to indicate a weaker influence of soil on mulga-spinifex community patterning (Nano 2005). Fire has been implicated as the force shaping the boundaries (van Etten 1988; Bowman, Boggs and Prior 2007). This

study considers the possibility that the essentially 'flat' southern Tanami sandplain study area is composed of gradual soil features with broad transition zones that would reflect more diffuse mulga-spinifex transitions except that fire is making them sharp.

Fire in mulga-spinifex communities is considered a disturbance. Van Etten (1988) referenced Hills and Randall (1968) who described a connection between disturbance and abrupt vegetation boundaries. In support of this, van Leeuwen (1966) associated abrupt boundaries with unstable environments and Forman (1995) suggested that natural disturbances could sharpen an existing boundary, increasing contrast in the landscape. It is consistent with these assertions and van Etten (1988) that the abruptness of the Mulga-spinifex transitions is likely to be strongly fire formed.

With anticipation of gradual and broad soil gradients (in the atmosphere of ecocline boundary types) there comes an expectation that the wider floristic species may have different distributions to the Mulga and spinifex populations. This is supported by Hills and Randall (1968) who described how abrupt vegetation boundaries do not necessarily have corresponding abrupt changes in overall species composition. It is also consistent with the complex environmental gradients that define ecocline boundary types, in that gradual transitions of species and environmental patterning can exist between two distinct vegetation communities (van der Maarel 1976, 1990). So, the spatial distribution of all the woody species in the study area may not necessarily conform to the abrupt Mulga-spinifex transitions. It is likely however, that the distribution of each individual species would partly be an expression of its ability to exist within the fire regime that regularly burns the mulga-spinifex matrix.

Possible dynamics of the Mulga-spinifex boundary

The process most described as causing a retreat of the Mulga edge within the mulga-spinifex matrix is fire frequency. Too frequent a fire from spinifex grasslands is thought to eventually lock Mulga trees in the juvenile stages, stopping their ability to reproduce and therefore exhausting seed banks and their ability to establish themselves after a fire. Consequently, the Mulga tree dies and the new space becomes available for spinifex. Alternatively, the Mulga could persist for generations

with fire, if favourable conditions (fire season/intensity, soil nutrients/moisture, rainfall etc) allowed post-fire persistence. This interaction has been broadly described for tree-grass combinations as the Gulliver's effect by Bond (1996).

Studies that have explored the possibility that frequent fire is permanently burning Mulga away have all agreed that Mulga on the boundary is being burnt and on occasion at high frequencies (van Etten 1988; Bowman *et al* 1994; Nano 2005; Bowman, Boggs and Prior 2007; Bowman, Boggs, Prior *et al* 2007). There is some evidence that Mulga boundaries have permanently retreated on a relatively small scale, over a long time, because of too frequent fire (van Etten 1988). However, recent research emphasizes that Mulga is mostly regenerating after fire. Therefore, despite fire damaged Mulga edges, it appears that mulga-spinifex boundaries may temporarily fluctuate, but are generally stable (Nano 2005; Bowman, Boggs and Prior 2007). This raises the possibility that the Gulliver's effect is essentially restricting Mulga from spinifex space, but not necessarily (too any large extent) creating more space for spinifex to colonize. Bowman, Boggs, Prior *et al* (2007) suggested that a relatively stable vegetation pattern across the landscape could be assumed for the last 1000-2000 years. Although Bowman, Boggs, Prior *et al* (2007) study requires replication across the landscape, it does encourage the consideration that mulga-spinifex boundaries generally may have been stable for a much longer time-scale than previous research in other study areas has been able to suggest.

There was a recognition that Mulga bounding small patches was currently most vulnerable to fire and had a heightened possibility of being converted to spinifex (Bowman, Boggs and Prior 2007; Bowman, Boggs, Prior *et al* 2007). This assertion was qualified with the original concern that Mulga may be replaced by spinifex on the landscape scale given continued change to fire regimes. So, it remains to be more widely monitored over a long period of time before the long term survival of Mulga within expansive spinifex grasslands can be generally claimed.

Mulga structure

I will explore whether the structural profile of Mulga is fire associated and if it varies in relation to fire frequency. Fire has been reported to generate single height stands

in woodlands (Bond and Wilgen 1996). Fire has also been associated with reduced structural complexity in tropical northern Australia (Williams *et al* 1999). Single height stands may indicate fire is structuring the Mulga in the southern Tanami Desert. It has been suggested that frequent firing may cause thick regeneration of Mulga dominated by a single height (Nano 2005). In the study area, high fire frequency or intensity may be creating thicker and younger Mulga stands with little height complexity.

An absence of Mulga in spinifex has been suggested to be consistent with stable boundaries (Nano 2005). I explore this idea in the context of a possible recent boundary retreat.

Biodiversity

The biological diversity of the Mulga–spinifex boundaries is not been specifically defined or known, although the value of the mulga and spinifex communities in Central Australia has been described to some extent.

Mulga vegetation plays a very important ecological role in the landscape and is a critical resource for both indigenous and non-indigenous land managers. Mulga contains rich faunal assemblages of reptiles, ants and birds, some of which are largely confined to these areas (Start *et al* 1991; Cody 1994). Flora and fauna are thought to favour the variety in structure and composition of the understoreys of mulga communities (Start *et al* 1991; Cody 1994). Indigenous people regularly forage in Mulga woodlands for a variety of edible resources and use the wood for cooking and warmth. In particular, the honeyant, which occurs almost exclusively in old growth Mulga, symbolizes the mulga environment and is at the centre of ritual and ceremonial elaboration for people across Central Australia (Devitt 1986; Latz 1995). Pastoralists also occupy a significant portion of Mulga lands. Their need to maximise grazing potential has many and complex implications for Mulga communities (Hodgkinson 2002).

Spinifex grasslands also have considerable biological significance. They provide habitat for a very rich assemblage of reptiles (Pianka 1969), as well as for a range of

mammal and bird fauna, many of which are endemic (eg. Spinifex pigeon, Spinifex Hopping mouse, Emu-wren and Grass-wren). Certain spinifex communities are biologically important, providing shelter for rare species such as the Mala and the Spinifex-bird (Bolton and Latz 1978). It is widely believed that traditional burning by Australian Aboriginals created a patchwork of spinifex habitats in varying degrees of recovery after fire. Concern has been well summarised by Allan and Southgate (2002) that more recent large, intense wildfires in spinifex grasslands has removed the diversity of plants available at any one time across the spinifex grasslands and contributed to the decline in medium sized mammals. Consequently, it is argued that patch burning in spinifex grasslands would promote landscape and faunal diversity.

The functional value of both ecosystems prompts concern about the extent this mulga-spinifex is changing and the effects these might have on landscape health and biodiversity. It is necessary explore the biodiversity of the mulga and spinifex communities in order to begin the process of exploring the effects that fire is having on the quality of these habitats.

Various studies have convincingly argued that a vegetation type dominated by one or two species, with a relatively low floristic diversity, has a fire regime that reinforces the persistence of the dominant species (Hanes 1971; Spencer and Baxter 2006). Given the unquestionable domination of Mulga and spinifex in the southern Tanami and a fire regime that has so far seen a relatively long-standing persistence of these populations, it is conceivable that the floristic diversity within these communities is low. An assessment of floristic diversity for the Mulga-spinifex landscape at the southern limits of the Tanami is needed to provide a reference point to assess this idea.

Species richness of woody perennial vegetation was chosen as the simple measure of floristic diversity in this study. This measure has been suggested as a good representation of total species richness (Sarkar 2002; Sarkar and Margules 2002) and potentially a good estimation for biodiversity (Sarkar 2002; Sarkar and Margules 2002; Clarke 2008). Periodic assessment of the current status of species richness can indicate trends in the abundance and distribution of native perennial vegetation. It is necessary to detect subtle local extinctions, given the substantial impact that these

can have on an ecosystem functioning over time, global extinctions and the loss of ecosystem sustainability (Smyth and James 2003). The description of current woody species richness could begin the process towards monitoring the biodiversity of the Mulga-spinifex ecosystem in the southern Tanami.

It has been suggested that certain species could be used to indicate old growth Mulga (Latz, pers. comm). Based on the observations that some plant species associate with older, less disturbed (burnt) Mulga trees, *Cheilanthes sieberi*, *Spartothamnella teucrifolia* and *Aristida obscura* species were proposed to indicate “old growth Mulga”. An independent test of the association between these species and mulga community structure is not available. I intend to do this. These species presence could be used by land managers in the southern Tanami Desert region as indicators of a stand of old Mulga that should be protected from fire for its unique contribution to landscape diversity.

This thesis

The sharpness of Mulga-spinifex boundaries in the southern Tanami will be explored for its relationship to soil, other woody species and fire gradients. This thesis sampled at a broad scale to detail the composition of the Mulga and spinifex communities at large. It sampled well into Mulga and spinifex vegetation types in an attempt to increase the space between the communities, away from the boundary zone, and to optimize the contrast between these communities, allowing the detection of shallow environmental gradients.

The following questions are asked. Was there a fire gradient across the Mulga-spinifex boundary? Was there an abrupt floristic and soil gradient (or condition induced by plants) across the abrupt sand-plain Mulga-spinifex boundaries? Was there an effect of fire associated with the spectrum of floristics and soil conditions across the Mulga-spinifex transition? Is it possible to detect a combination of fire related plant functional traits across the Mulga-spinifex transition? These questions are addressed in Chapter 3 where fire histories of the study sites were compared across vegetation types. And Chapter 4 where a floristic survey and soil (surface) measurements were made and described in terms of their gradients across the abrupt

Mulga-spinifex landscape boundary. The plant functional traits related to persisting with fire are considered for the most frequently occurring species associated with Mulga and spinifex vegetation types.

Nano (2005) recommended that the effect of fire on the quality of the Mulga habitat should be a research priority. The structural diversity of the Mulga stands in the Southern Tanami is not known. Are more frequently burnt Mulga stands less diverse? Does the season of a fire have an effect on the structural dynamics of Mulga? Does the structural diversity of a Mulga stand contribute to the ability of Mulga to persist after a fire? These issues are considered in Chapter 5 where the structural diversity of Mulga stands was sampled and analysed in the context of fire frequency and season.

The number of woody species in Mulga, mixed and spinifex communities is established to compare the biodiversity of species across the Mulga-spinifex mosaics. Does the proposed ecocline boundary type have greater species richness in the 'transition' compared to the two communities it separates? These issues are considered in Chapter 6 where species richness is compared across the Mulga-mixed-spinifex vegetation sequence to establish the level of biodiversity (of woody species). The frequency of three 'fire sensitive' species was recorded to investigate their potential as indicator species for long unburnt Mulga.

This project utilizes serial Landsat imagery to target data collection and analyse serial fire behaviour relating to sites surveyed. This project will contribute to the conservation of biodiversity, sustainable rangeland production and help define appropriate fire regimes for the long term integrity of Mt Denison Mulga/spinifex boundaries.

CHAPTER 2: STUDY AREA and METHODS



...mulga patches



...a mulga-spinifex boundary

Study Area

Location

The study area is on Mt Denison pastoral station (22°07'50 S, 132°04'54 E) on the southern edge of the Tanami Desert and 350 km north west of Alice Springs (Fig. 2.1). The area (Figure 2.2) was selected because it is accessible and has a mosaic of Mulga patches in spinifex expanses on an apparently uniform sand plain. The area also has a well documented fire history. Throughout the study area (approximately 512km²) up to 70 Mulga patches (ranging in size from 0.002km² to 25km²) occur throughout spinifex grasslands. The physiography of the region is characterized by the Lander River along the far eastern boundary with the Yindjirbi Range and the Giles Range to the east, beyond the Lander. The Tanami Desert is to the north and west of the study area.

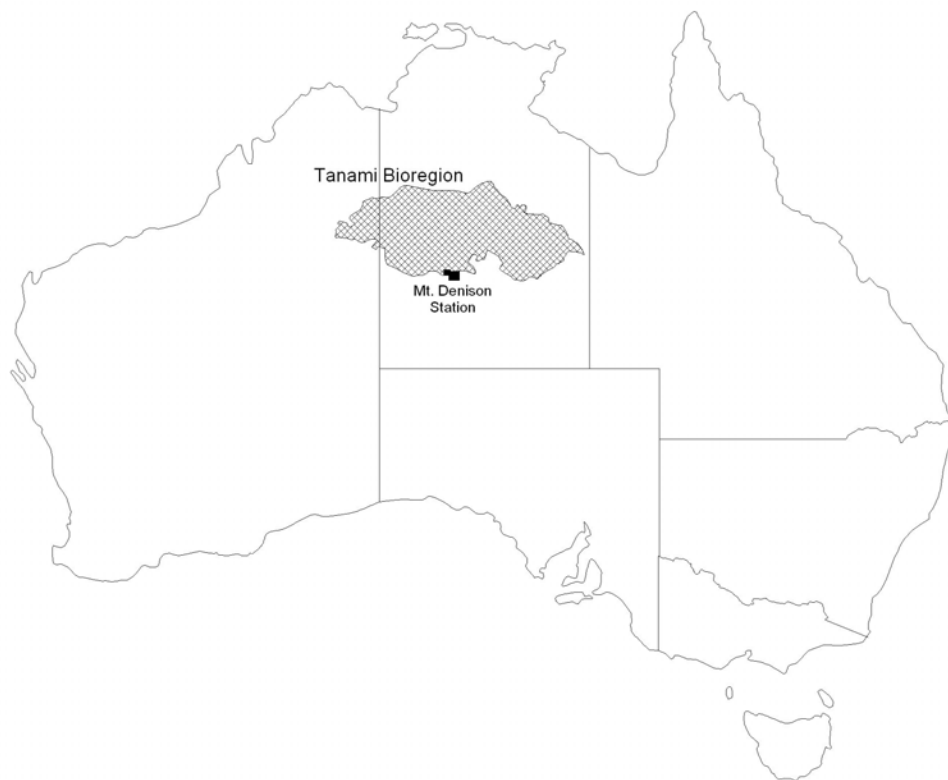


Figure 2.1 Map of the study area in relation to the Tanami desert in the Northern Territory of Australia.

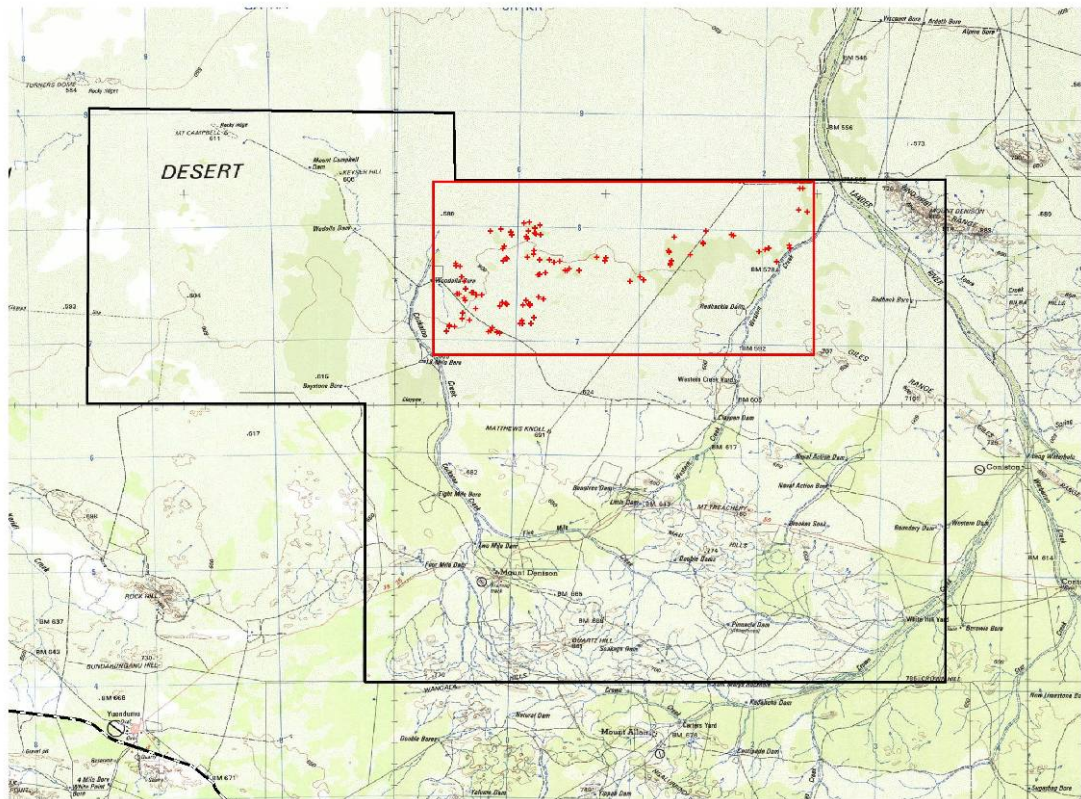


Figure 2.2 Mt Denison station showing the study area (red box) with study sites (red marks). Taken from the Mt Peake map sheet [1:250 000, sheet 53-05, NATMAP Topographic map series]. In this representation, 15mm = 5km.

Geology

Red sands and earths predominate in the study area, with alluvial deposits along adjacent floodplains. Redhackle Granite with subordinate Lander Rock Formation (sandstone and siltstone) dominates the study area. Emerging rock material seen throughout the study region suggests the sand sheet is shallow. Stratiform mafic rocks are also interpreted as having Lander Rock Formation occurring locally, particularly in the north of the study area. A fault line has been interpreted east/west through the study area (from airborne magnetic data) which differentiates the sandstone and granite (pers. comm. Nigel Donnellan).

Climate

Mt Denison station has an average annual rainfall of 363mm but is typically central Australian with erratic and extremely variable annual rain (Figure 2.3). While zero rainfall can be experienced in all calendar months, significant totals are also possible in all months, but are more likely in summer (Figure 2.4). It is most likely the decaying tropical cyclones or the monsoon trough from the north, that move well south into the central regions, bringing the widespread rain and thunderstorms typical of the summer season (The Regional Institute, 2005).

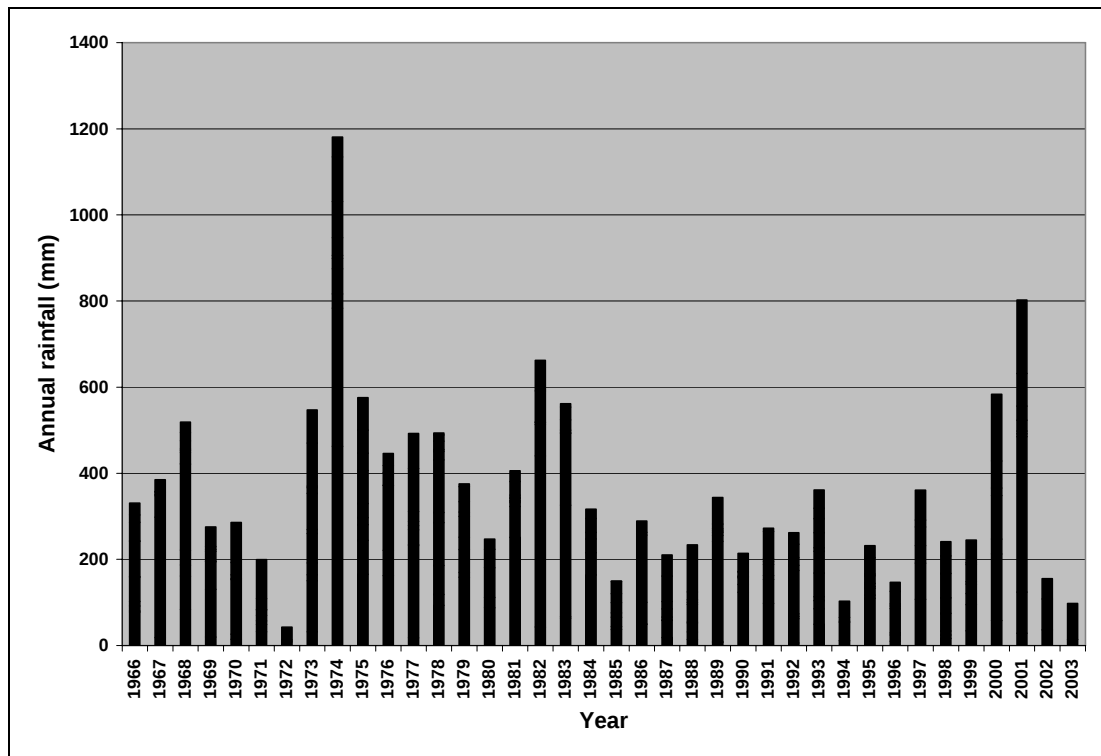


Figure 2.3 Annual rainfall Mt Denison station 1966-2005. Taken from the Bureau of Meteorology, unpublished historical weather database. Rainfall data was recorded at Mt Denison Station homestead which is approximately 30km south of the study area.

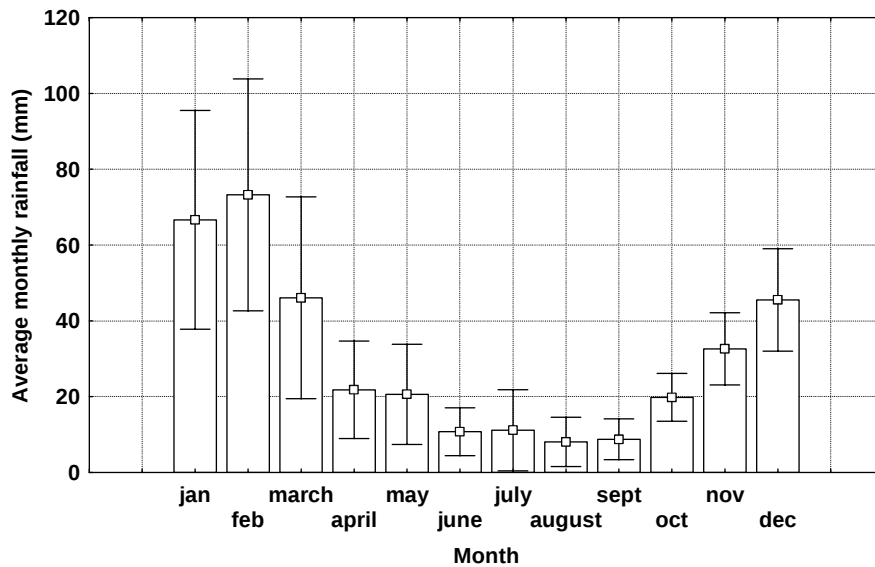


Figure 2.4 Mean (and standard deviation) of monthly rainfall (from 1966-2003) for Mt Denison Station. Taken from the Bureau of Metereology, unpublished historical weather database.

Average monthly maximum temperatures at Yuendumu, 45 km north-east of the study area, range from 40°C in summer to 26°C in winter, whilst average minimums range from 21°C in summer to 5°C in winter (Fig. 2.5). Winters (June to August) are cool and summers (December to February) hot. Frosts occur occasionally. Winds are most frequent from the east and humidity is mostly low.

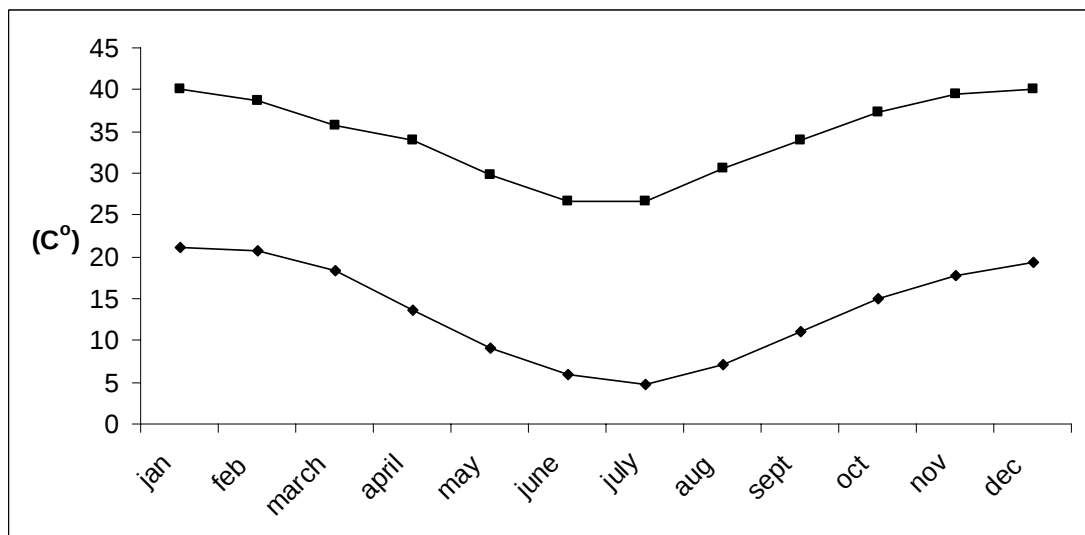


Figure 2.5 Average monthly minimum and maximum temperatures for Yuendumu Community. Taken from the Bureau of Metereology, unpublished historical weather database.

Methods (in the field)

Vegetation survey

To characterize the vegetation of the Mt Denison study area, 105 plots were placed in either mulga, spinifex or mixed mulga with spinifex vegetation types. Sampling occurred in 42 Mulga plots, 39 spinifex plots and 24 mixed plots. Mulga plots were defined as having predominately Mulga (*Acacia aneura* var. *tenuis*) trees with less than 1% spinifex cover, and spinifex plots were defined as having predominately spinifex (*Triodia pungens*) with less than 1% Mulga tree cover. The mixed vegetation type was defined by having cover of more than 5% (cover) of both spinifex and Mulga trees interspersed.

Landsat images were used to locate Mulga patches large enough to sample and to locate a wide range of fire ages for each vegetation type. The final location for a plot was decided on once in the field, ensuring each plot was placed in vegetation of the same fire age. A stratified sampling system targeted the Mulga-spinifex boundary and varying distances from the boundary (up to 500+m, which was rare in Mulga given mostly patches were relatively small). Mixed plots were located near, but never across the boundary, such that the entire plot consistently included greater than 5% cover of both spinifex and Mulga.

The plot size was 80m x 20m, which previous research (van Leeuwen unpublished data as referenced by van Leeuwen (1994)) indicated to be the optimum size for sampling 95% of the perennial flora in a Western Australian mulga woodland. Patches of Mulga smaller than 1600m² was not sampled although patches this small were numerous and frequently examined to give context to the study area.

For each plot, each long-lived perennial species and three aggregate categories of short-lived plants (sub-shrubs, perennial grasses, and herbs and annuals) were recorded as [modified Braun-Blanquet] cover scores: 1=<1%, 2=1-5%, 3=6-10%, 4=11-25%, 5=26-50%, 6=51-75% and 7=76-100%. Cover scores were also recorded for litter (leaf litter and dead plant matter on the ground) and bare ground. Species were identified by myself with the support of the Alice Springs Herbarium, with

nomenclature following the online resource

<http://www.nt.gov.au/nreta/wildlife/plants/checklist.html> - March 2007.

For each Mulga and mixed plot the numbers of Mulga trees (dead and alive considered separately) were counted in height classes: seedling or re-sprout (<50cm), juvenile (51cm-1m), 1m-3m, 3m-5m, 5m+ thin (stem <15cm diameter at base) and 5m+ thick (stem >15cm diameter at base). The height categories were selected to give an indication of the growth/regrowth profile of mulga stands as they relate to fire histories. Although Mulga apparently does not have morphological features which indicate exact age for individuals (Winkworth 1973) it was decided that for the purpose of this study it was reasonable to infer an 'age' profile based on the heights of Mulga trees and relate this data to fire histories.

Soil Survey

Crusting/Fragmentation/Termite/Ants

The bare ground in each plot was sampled using 100 step-points. At each step the surface was described as one of: sand, gravel, soil crust, biological crust (early stage) and biological crust (well developed). See Appendix 1 for examples of different crusts. If a step landed on spinifex or litter, it was disregarded and another step taken.

The crust in each plot was sampled using another 100 step-points. At each step the crust continuity was described within a 20cm² frame as one of: fragmented, slightly continuous, moderately continuous and highly continuous (see Appendix 1 for examples of different continuities). Again, if a step landed on spinifex, litter or pure sand, it was disregarded and a further step was taken.

For each plot, the number of tower termite mounds, round-form termite mounds and Mulga ant nest mounds (*Polyrachis* sp.) were counted.

Texture

In each plot the field texture was determined following the procedure of Handreck and Black (1999). A surface soil sample (at maximum depth of <10cm) was

moistened and kneaded until there was no apparent change in the way the soil felt. The sample was then inspected to see if the sand particles were visible. If not, then it was noted if sand was felt. Then the sample was squeezed hard to see if a cast formed (Figure 2.6a), and if so whether it held together or fell apart. Finally the sample was squeezed out before thumb and forefinger with a sliding motion and the length of self-supporting ribbon that formed was noted (Figure 2.6b and Figure 2.6c). Two samples were determined for each plot for confidence. A third sample was determined if the first 2 differed. The most frequent texture grade was recorded for the plot. The texture grades were: sandy, loamy sand, clayey sand, sandy loam, fine sandy loam and sandy clay loam.



Figure 2.6 Determining soil texture: **a.** Making a caste from soil sample, **b.** Making a ribbon from soil sample, **c.** Measuring the ribbon from soil sample.

Bulk density

Two samples of soil were removed from each plot for the measurement of bulk density (mass/volume) using a steel pipe of 117.1cm³ volume (below the slit in the pipe). The depth of the soil sample removed was 7cm, measured from the surface of the soil (hammered to the slit in pipe) to end of pipe (see Figure 2.7). The 2 samples for each plot were kept separate and averaged after the soil analysis was finished.



a.



b.



c.

Figure 2.7 Collecting soil sample for bulk density assessment: **a.** hammering steel pipe into soil, **b.** removing soil from around the pipe, **c.** removing the soil sample.

Methods (Analysis)

Soil

Bulk density

The samples were dried overnight in an oven at about 100⁰C. The mass of each sample was measured with an electronic balance to the nearest milligram. The bulk density was calculated as Mass/Volume. Values from the two samples were averaged to provide a value for each plot.

pH/Electrical conductivity/Nitrates

The soil samples collected for the bulk density measure were also used for analysis of pH, electrical conductivity (EC) and the concentration of nitrates, using the methods and interpretation of Tregear and Beardsell (1997). Twenty grams of air-dry soil was mixed vigorously with 100mL of distilled water three times over half an hour. The slurry was poured through a filter into a clean jar. The pH of the clear extract was measured using the Hanna pHep3 pH meter to 2 decimal places. The electrical conductivity (a measure of the salinity of the water) of the same clear extract was measured for each soil sample using a Hanna Dist 4 plus Electrical conductivity meter to 2 decimal places. The presence of nitrates was measured using an analytical nitrate test strip (Merckoquant brand). For each sample a strip was dipped in the same extract used for pH and EC measurements. The reaction zone of the strip was noted for colour and compared to a scale indicating the concentration of nitrates.

Fire History

Fourteen Landsat images covered the fire activity in the study area for the period 1980-2004. The date of images purchased (by Bushfires Council) before 2000 was determined by a time sequence that related to a vegetation analysis project (indirectly related to fire events). These images were opportunistically scanned by Bushfires Council for fire scars and these scars were 'back' dated using Landsat Quick-look

images. This meant that at times, the most accurate date allocated to a fire may be a range of months. The date of images after 2000 was determined by actual fire events that were detected using Landsat Quick-look images and more accurately dated with purchased Landsat images.

Plot locations were projected onto the fire images using the Geographic Information Services (GIS) computer program ArcView 9.0. Images were then layered over one another for the period 1980-2004, each one visually examined for the number of fires and the minimum interval between fires in each plot. Interpreted fire histories were frequently checked against field records and photographs with the support of Grant Allan from Alice Springs Bushfires Council. This process identified significant errors, where satellite image interpretation for fire histories, did not match field observations. This was especially so for boundary plots where fire scars can be ambiguous, often appearing to coincide with vegetation boundaries but not discretely. A difference image was created (by Grant Allan, Bushfires Council, Alice Springs) to aid interpretation of plots that were unclear. The ‘differences’ between consecutive images were most strongly highlighted and increased confidence in identification of fire activity.

Data

Characteristics of the vegetation

Long-lived perennials were classified according to the percent of plots recorded in each vegetation type. Mean, maximum and minimum cover scores were identified for each species in each vegetation type.

Rainfall (from the Bureau of Meteorology, unpublished historical weather database for Mt Denison homestead) for 12 months and 24 months before the fire date was tabulated.

Ordinations

I used ordinations to identify floristic patterns in the vegetation and their environmental correlates. The cover classes data on all 53 long lived perennials was used for the first ordination, removing Mulga and spinifex (but retaining all other) cover classes data for the second ordination. These analyses were done using the windows version of the Pc-ord software program (MjM 2006). The Non-metric multidimensional scaling (NMS) method of ordination was used. The NMS Scree Plot was routinely checked for the recommended dimensionality and its success in analyses compared to a randomized data set. The Multi-Response Permutation Procedure (MRPP) was used to evaluate the separation between the pre-defined Mulga, mixed and spinifex groups.

Both ordinations had a joint-plot of all the species fitted, with an additional joint-plot fitted to the first ordination of the environmental measures. Environmental measures used were: surface descriptors (sand, gravel, soil crust, biological crust (early stage) and biological crust (well developed), fragmented, slightly continuous, moderately continuous and highly continuous), distance to Mulga edge, texture, bulk density, pH, number of termites (round and tower mounds) and ants and time since last fire. Texture (sandy=1, loamy sand=2, clayey sand=3, sandy loam=4, fine sandy loam=5 and sandy clay loam=6) and distance to Mulga edge (0-10=1, 11-50=2, 51-200=3, 201-500=4 and 500+=5) were converted to numerical scales.

The joint plot is a diagram of radiating lines and was used to show the relationship between different species or environmental variables and the scatter of plots on the ordination. The angle and length of the line describe the direction and strength of the relationship. The relative scaling of the vectors is determined by the *r* value; the absolute scaling is arbitrary.

Tabulation of functional attributes of species driving the ordinations

The species identified as most strongly driving the ordinations were explored for functional traits (time to seed after fire, length of life, response to fire and re-sprouting type) classified according to the Northern Territory Ecological Attributes

database (unpublished) and tabulated according to association with Mulga, mixed or spinifex vegetation.

Graphing environmental variables identified from the ordinations

The environmental variables identified as strongly associating with Mulga or spinifex plots (number of termites, sandiness of surface, texture, biological crusting and time since fire) were graphed to identify the variation (and possible gradation) from Mulga, mixed to spinifex vegetation types.

Modelling the Mulga-spinifex gradient

I used a Generalized Linear Model (GLM) to relate environmental variables to a measure of the Mulga-spinifex gradient. The measure was the strong gradient (in the first ordination) from Mulga to spinifex. This gradient was rotated parallel to the x-axis and the x-axis co-ordinates then used as a response variable in the GLM.

A correlation matrix was consulted to identify and remove strongly correlated continuous independent variables from the modelling exercise. Surface (sandiness and continuousness) measures and time since last fire were deleted because they correlated (above 0.5) with other retained variables (and were decided to be well represented within the retained variables). The response variable was checked for normality. The relationship of the independent variables (gravel, soil crusting, Mulga edge, pH, bulk density, and number of fires) with the response variable were assessed for non-linearity. Gravel and soil crusting were found to have non-linear relationships with the response variable and so were arcsine transformed (because this transformation deals well with percent data). The distribution of the independent variables was also checked for extreme outliers in the data that may excessively influence the results. No cases needed transforming based on this.

One GLM was performed with several runs. The Generalized Linear/Nonlinear models function in STATISTICA7 software was used. A poisson distribution with an identity link function was chosen. The GLM runs were; Fire (number of fires), Soil (biological crusting, gravel, soil crusting, texture, pH, and bulk density), Fire and

Soil (number of fires, gravel, soil crusting, pH, bulk density and texture) and all possible characters (biological crusting, gravel, soil crusting, pH, bulk density, texture, distance to Mulga edge and number of fires).

The best subsets based on the Akaike Information Criterion (AIC) was used to select the best supported combination of variables (Burnham and Anderson 2002) within and between runs. The lower AIC values indicate more support for a model, where delta values <2 infer a high level of support and delta values of 2-10 infer weak support. Delta is the difference between the AIC value for the best-supported model and the alternative models. The deviance explained was calculated for each best subset for each run. The relative strength of the contribution of each predictor variable in a model was calculated (by iteratively removing each variable and identifying the relative loss of deviance explained attributable to each) and ordered for their importance in the model.

Mulga demographics

The modal height class of (living Mulga) for each plot was identified. The height profiles for plots in each modal class were then summarized. The Shannon-Weiner index was used to explore the height structural diversity of each of the different modal classes.

Modelling Mulga height classes

GLM 1

I used a GLM to relate environmental variables to a measure of the height class structure of Mulga plots. The measure was based on the spread of Mulga height classes for each plot, called a skewness measure. This was calculated according to the equation in Krebs (1989). The skewness measure was checked for normal distribution and was acceptable. The models were explored for their statistical contribution to the Mulga skewness measure (where an increasing positive skewness represented increasing dominance of smaller plants and an increasing negative skewness represented increasing dominance of larger plants).

The remaining independent variables (gravel, Mulga edge, texture, number of fires and fire season) were assessed for non-linearity of their relationship with the response variable. Gravel (had a non-linear relationship with the response variable) and so was arcsine transformed (because this transformation deals well with percent data). The distribution of the independent variables was also checked for extreme outliers in the data that may excessively influence the results. In consideration of a small sample size (n=42), texture and 'distance to Mulga edge' variables were collapsed into categorical variables (with 2 categories, and one parameter), in an effort to reduce the options within each variable and increase the power of the model.

From a preliminary modelling exercise (using all independent variables) it was noted that pH, bulk density and gravel were substituting for each other. It was decided to remove pH and bulk density, while retaining gravel.

The Generalized Linear/Nonlinear models function in STATISTICA7 software was used. A normal distribution with an identity link function was chosen. Evaluation and identification of the most convincing models was undertaken as per description (above) for the GLM for the Mulga-spinifex gradient.

GLM 2

I used a GLM to relate environmental variables to the frequency of seedlings ($\log_{10}[x+0.375]$ -transformed) in Mulga plots. A gamma distribution with a log link function was chosen. The environmental variables used were texture, time since last fire and 'distance to Mulga edge'. All the independent variables were collapsed into categorical variables (with 2 categories, and one parameter), in an effort to reduce the options within each variable and increase the power of the model.

The Generalized Linear/Nonlinear models function in STATISTICA7 software was used. Evaluation and identification of the most convincing models was done as per description (above) for the GLM for the Mulga-spinifex gradient.

Biodiversity

Mean and cumulative woody species richness of Mulga, mixed and spinifex vegetation were calculated.

The frequency of occurrence of hypothesized 'indicator' species for 'old growth Mulga' was compared across Mulga, mixed and spinifex plots. The presence/absence of indicator species in burnt and unburnt Mulga plots (for the 24 year fire history) was compared using the Fisher exact test.

CHAPTER 3: FIRE



...recently burnt mulga

Fire in the study area

There were 97 fires that burnt within the study area during the study period 1980-2004, detected from Landsat images. The fires burnt areas in the wider region that ranged in size from 50m²-5716km² (fires burning areas smaller than 50m² were detected but not included).

Fire history for study plots

Fourteen of the fires in the study area burnt plots (Figure 3.1). The mean number of plots burnt by a fire was 13.6 with a standard deviation of 16.0 (and a minimum of 1 and a maximum of 59 plots burnt by a single fire). The fires burning the 2 largest proportions of plots (56% and 31%) in the study period were in the summer season. One fire in winter burnt 22% of plots with all other known fires in any season burning mostly less than 10% of plots. A fire burning more than 50% of plots happened once in the study period and was followed by fire events that generally burnt less than 10% of plots for the next 16 years.

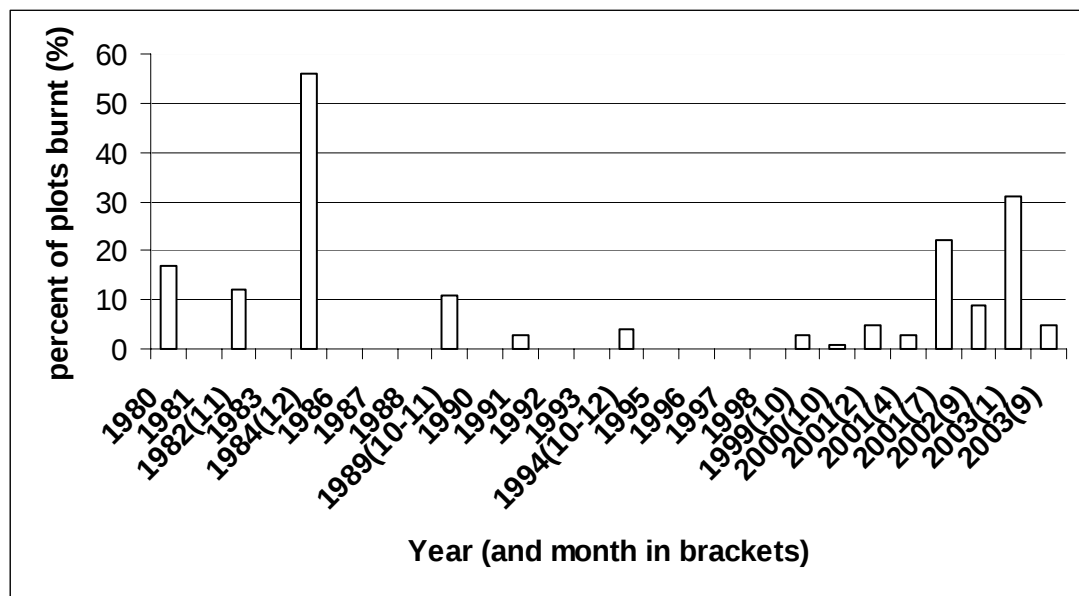


Figure 3.1 The percent of plots burnt in the study area by the year (and month if known) for each fire for the study period 1980-2004 identified from LANDSAT imagery.

There was a positive trend for above average rainfall to precede fires that burn larger proportions of plots, although it was weak (Figure 3.2, Spearman's rank one-tailed

$r_s=0.44$, $n=14$, $P=0.05$). Above average rainfalls for the 24 months before a fire event did not always result in large portions of the study area been burnt.

The mean annual rainfall 12 months before a fire (397ml, std dev 211, $n=14$) was not significantly different to the long term mean annual rainfall of 363ml (using t -test for single means, $P=0.55$). The mean rainfall 24 months before a fire (815ml, std dev 260ml, $n=14$) was not significantly different from the average mean rainfall for 24 months of 726ml (using t -test for single means, $P=0.23$).

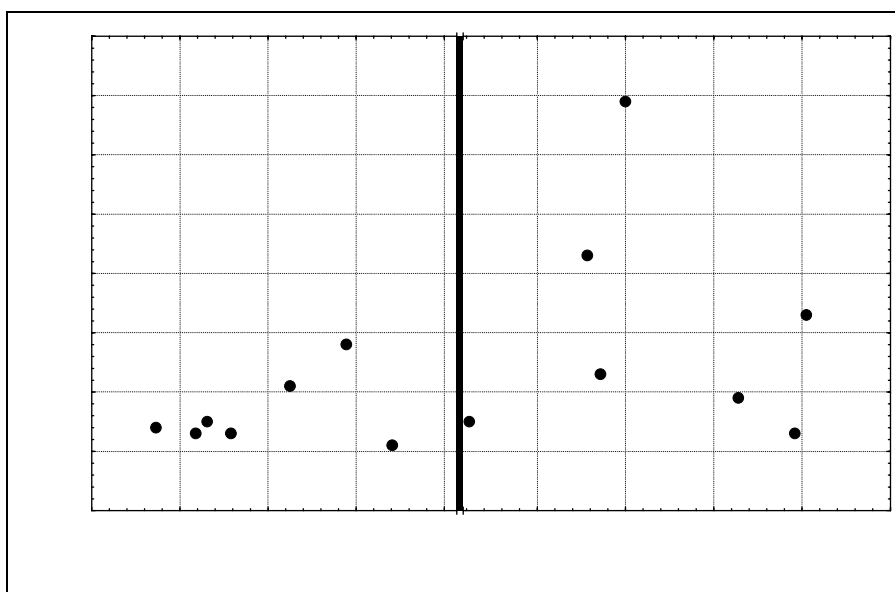


Figure 3.2 The percent of plots burnt (during the study period 1980-2004) plotted against the rainfall 24 months before each fire event. The mean rainfall 24 months before a fire is indicated by the black line at 815mls.

Fire was observed to often not cross the Mulga-spinifex boundary. Although this was inconsistent as a Mulga-spinifex boundary in the field could appear completely unburnt, partly trickled into and largely burnt. So Mulga patches exposed to the same fire were not affected evenly. In contrast to this, spinifex plots tended to burn more widely (less patchily) and clearly more often than Mulga or mixed vegetation (Figure 3.3). However, these are generalizations and much variation (in both vegetation types) of fire behaviour was noted.

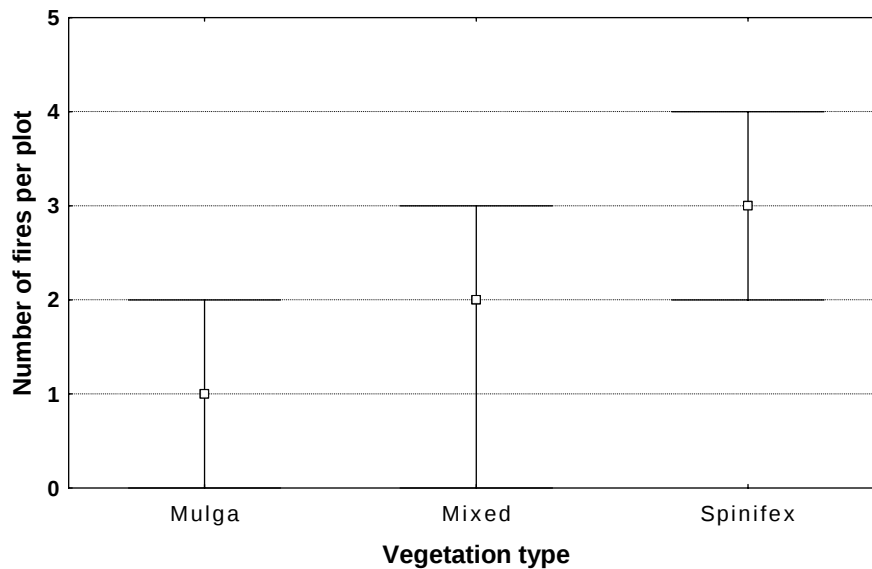


Figure 3.3 Fire frequencies (median with 10% and 90% percentiles) identified from LANDSAT imagery for the period 1980-2004 in Mulga, mixed and spinifex vegetation plots. The vegetation types differed significantly (Kruskal-Wallis $H_{2,105}=44.8$, $P < 0.00001$; Multiple comparisons of P -values (two tailed): Mulga V mixed, $P=0.13$; Mulga V spinifex, $P=0.000001$; mixed V spinifex, $P=0.001$)

Spinifex plots had mostly experienced a return of fire within 5 years at some time. Mulga plots were mostly either not burnt or burnt once in the 24 year study period (Figure 3.4). A summer fire (December 1984) burnt most of the single burn Mulga plots (data not shown).

Spinifex plots that had a short interval between fires, were mostly followed by a longer time before the next fire (Figure 3.5, Spearman's rank two-tailed $r_s=-0.83$, $n=42$, $P=0.05$).

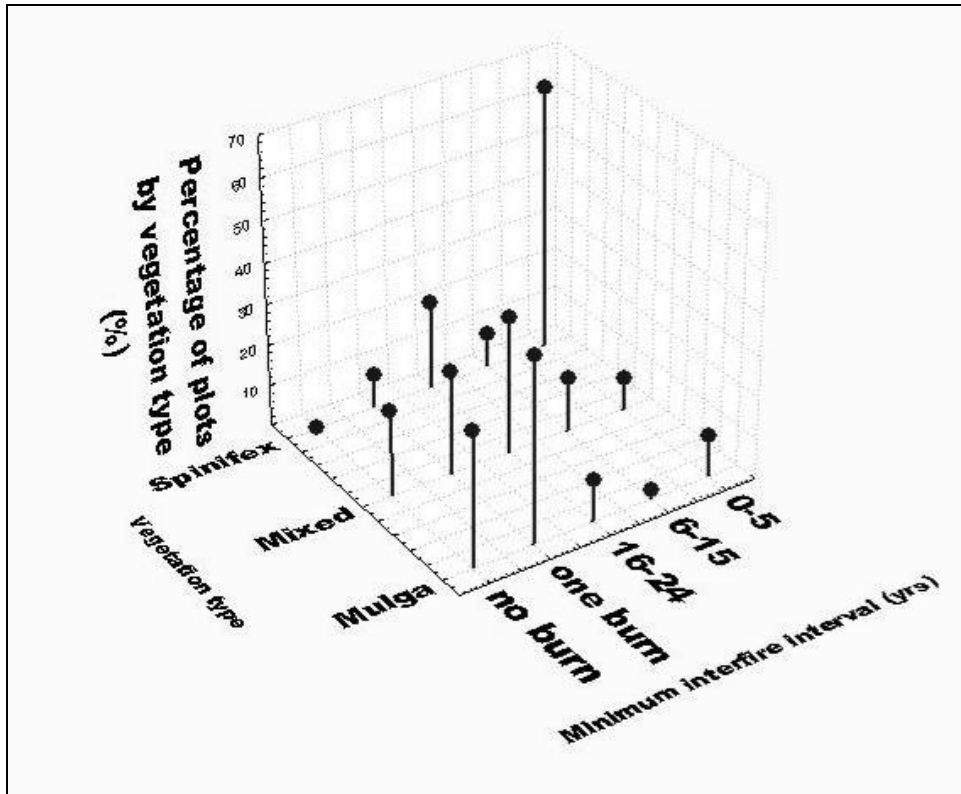


Figure 3.4 Minimum inter-fire interval identified from LANDSAT images for Mulga, mixed and spinifex vegetation types, including two open categories for plots with no observed interval (because plot did not burn or had only one burn in the study period).

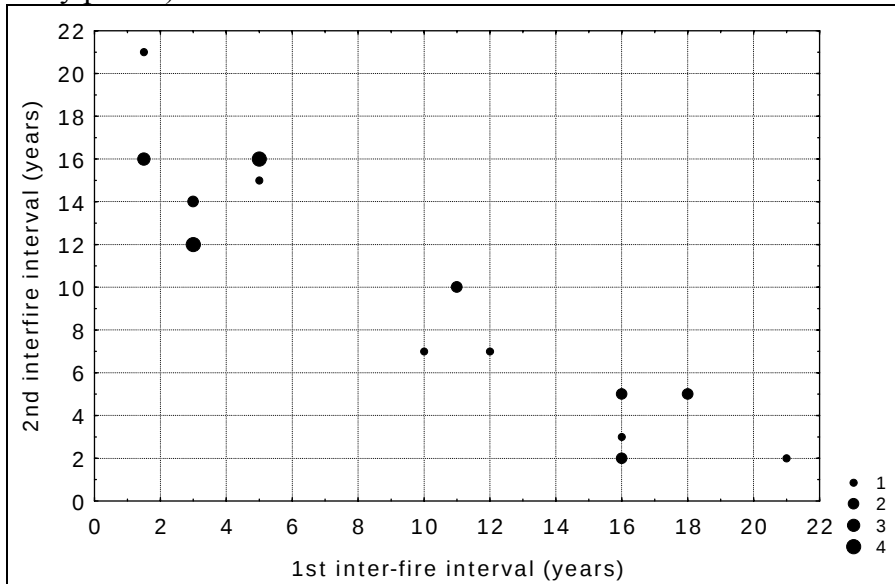
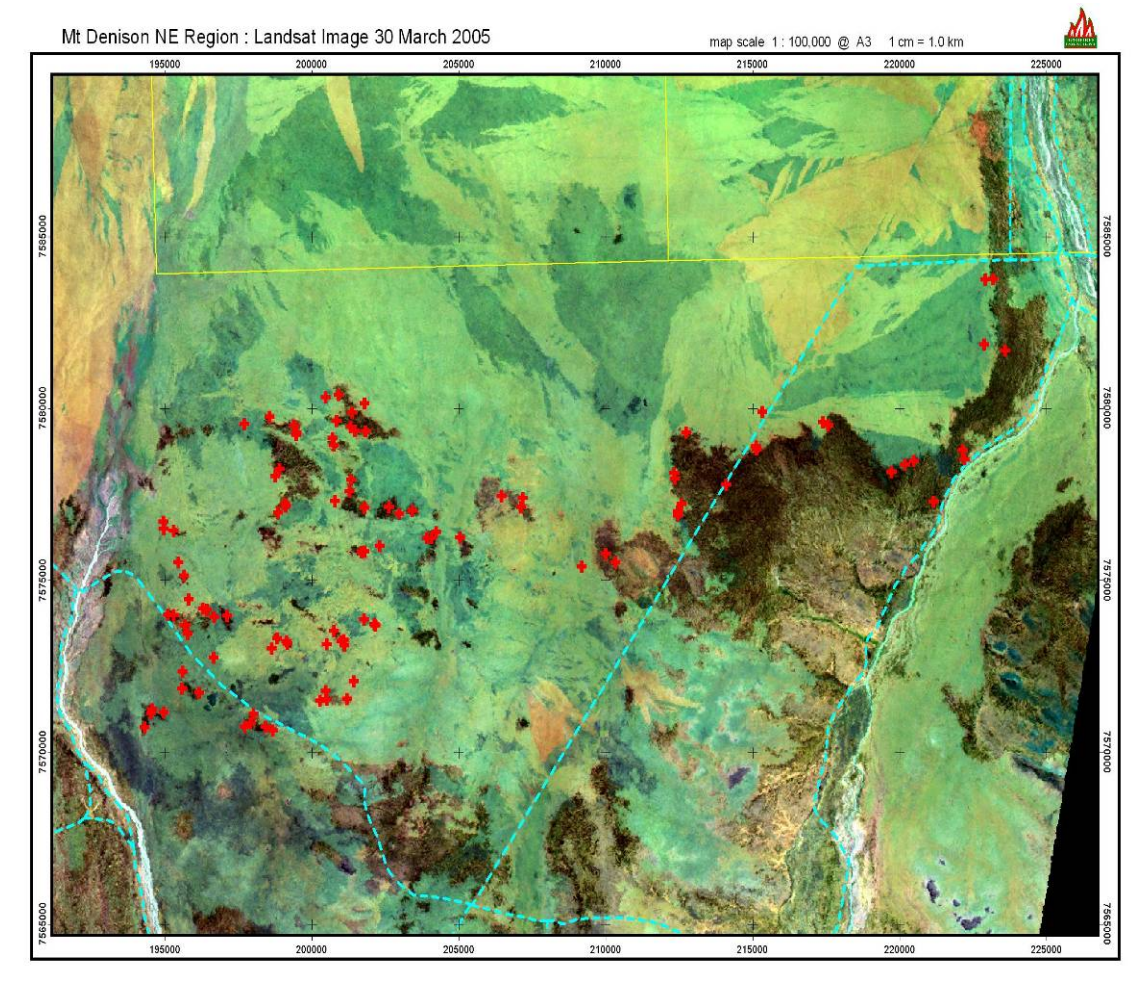


Figure 3.5 The time between the 1st inter-fire interval compared to the 2nd inter-fire interval for spinifex plots, identified from LANDSAT imagery. An increase in bubble size indicates an increase the number of spinifex plots that had that particular 1st and 2nd interfire interval sequence.

CHAPTER 4:

FEATURES OF MULGA AND SPINIFEX VEGETATION



Mt Denison station study region. Darker brown/green area is mulga patches within (various shades of) lighter green spinifex grasslands. Lighter green and pale brown/red areas are more recently burnt areas. Red crosses represent study plots

This chapter examines the pattern of change for woody species, surface soil variables and recent fire history across the transition from Mulga to spinifex. The floristic and soil gradients measured across the Mulga-spinifex boundary are compared to the abrupt Mulga-spinifex physiognomic boundary in the southern Tanami landscape (as seen in Figure 4.1). A total of 105 plots were surveyed, 42 in Mulga, 39 in spinifex and 24 in the mixed vegetation type. The mixed vegetation type was generally found in the boundary region between spinifex (Figure 4.2-a) and Mulga vegetation (Figure 4.2-b) and was a relatively even spatial mix of spinifex and Mulga trees (Figure 4.2-c, d, e for examples). General observation revealed that it was a minor component of the landscape compared to ‘pure’ Mulga and spinifex.



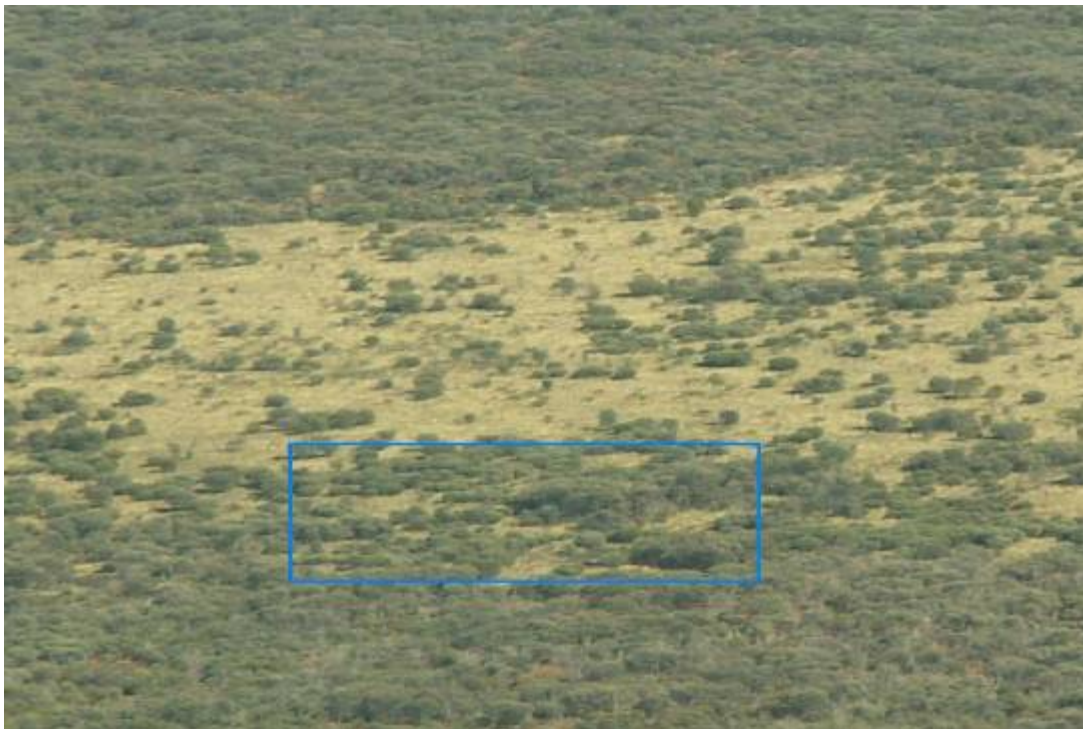
Figure 4.1 An aerial photo of the boundary between Mulga woodland (dark green) and spinifex grassland (yellow) on the southern edge of the Tanami sand plain.



a.



b.



c.



d.



e.

Figure 4.2. Images of: **a.** Typical spinifex vegetation. **b.** Typical Mulga vegetation. **c.** An aerial photo of a mixed vegetation site (blue box), where Mulga trees and spinifex grass are evenly mixed and no one vegetation is dominating. **d.** Mixed vegetation **e.** Mixed vegetation

Floristics

Fifty three long lived perennials were recorded with a mean of 11.1 species per plot (range 4 – 22) (Table 4.1). Sixty eight percent of species were shared across the Mulga-spinifex boundary (appearing in all vegetation types). Few species were widespread and abundant, most were local and infrequent. In total, 93% of species were found in less than half the plots with average cover scores of less than 1%. Only two species, other than Mulga and spinifex, were recorded in more than 50% of the plots: *Senna artemisioides helmsii* in all vegetation types but more so in spinifex, and *Eremophila latrobei* in all vegetation types but more so in Mulga. Other than Mulga and spinifex, only 2 species had an average cover score of greater than 1% and one of these species was recorded only once.

Four species were recorded in Mulga plots only and 4 species were recorded in spinifex plots only (Table 4.1). Most of these species were recorded only once and all species had a median cover score of <1%. No species was recorded in mixed plots only. The species exclusive to Mulga or spinifex were rare except for *Sarcostemma viminalis australe* which was recorded in 10% of Mulga plots.

Four species were recorded in Mulga and mixed plots but absent from spinifex, the most frequently occurring species being *Psyrax attenuata* (Table 4.1). Four species were recorded in spinifex and mixed plots but absent from Mulga, the most frequently occurring species being *Eucalyptus gamophylla*. All of these species had a median cover of <1% with a frequency of records in 2-26% of plots.

Mulga and spinifex were clearly present in their own vegetation types at near maximum cover percentages to within meters of the boundary (Figure 4.3). The occasional Mulga in spinifex vegetation and the more frequent spinifex in Mulga vegetation were at 1% cover scores. All common species for each vegetation type (except for Mulga and spinifex) were shared across the boundary (Table 4.1), such that the Mulga edge did not correspond to an abrupt change in other species.

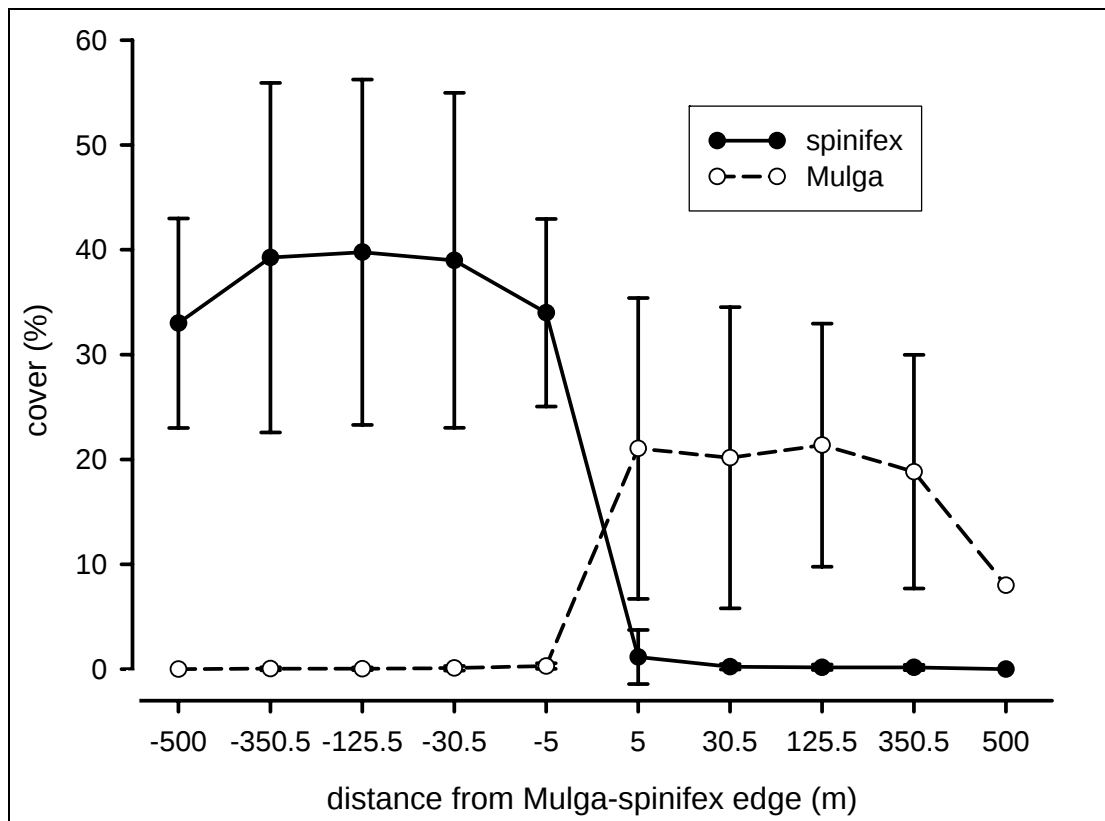


Figure 4.3 Mean cover ($\pm$ standard deviation) for Mulga and spinifex in Mulga (positive distance measure) and spinifex (negative distance measure) plots.

Table 4.1 The frequency and cover of long lived perennials recorded in study area plots, sorted by frequency in spinifex plots. The median cover class is presented with the minimum and maximum in brackets. The cover class without brackets was a single recording. The species in bold were strongly correlated with the ordinations as indicated in Figures 4.4-4.5 (*=additional to Figure 4.4 from Figure 4.5; ** additional to Figure 4.4 and 4.5 from ordination not shown using presence/absence data for species other than Mulga and spinifex).

	SPINIFEX		MIXED		MULGA		% all
SPECIES	% plots	Cover	% plots	Cover	% plots	Cover	
<i>Psyrax attenuate</i> var. <i>myrmecophila</i>	0		33	1(1-1)	45	1(1-2)	26
<i>Spartothamnella teucrifolia</i>	0		21	1(1-2)	31	1(1-2)	17
<i>Acacia cuthbertsonii</i>	0		8	1(1-1)	19	1(1-2)	10
<i>Sarcostemma viminalis australe</i>	0		0		10	1(1-2)	4
<i>Senna artemisioides filifolia</i>	0		13	1(1-1)	5	1(1-1)	5
<i>Acacia minyura</i>	0		0		2	1	1
<i>Canthium linearis</i>	0		0		2	1(1-1)	1
<i>Senna petalo</i>	0		0		2	1	1
<i>Rhyncharrhena linearis</i>	3	1	25	1(1-1)	41	1(1-1)	23
<i>Eremophila gilesii</i>	3	1(1-1)	29	1(1-2)	36	1(1-5)	22
<i>Einadia nutans</i>	3	1	13	1(1-1)	7	1(1-1)	7
<i>Grevillea striata</i>	3	2	0		2	2	2
<i>Clerodendrum floribundum</i>	3	1	0		0		1
<i>Ipomoea costata</i>	3	1	0		0		1
<i>Melaleuca lasiandra</i>	3	1	0		0		1
<i>Ventilago viminalis</i>	3	1	0		0		1
<i>Acacia melleodora</i>	3	1(1-1)	4	1	0		2
<i>Dodonaea petiolaris</i>	3	1	4	1	0		2
<i>Hakea divaricata</i>	3	1	4	1	0		2
<i>Tinospora smilacina</i>	5	1(1-1)	21	1(1-1)	19	1(1-1)	15
<i>Enchylaena tomentosa</i>	5	1(1-1)	13	1(1-1)	17	1(1-1)	12
<i>Carissa lanceolata</i>	5	1(1-1)	8	1(1-2)	7	1(1-1)	7
<i>Corymbia aparrerinja</i>	5	2(2-2)	0		2	1	3
<i>Rhagodia eremaea</i>	8	1(1-1)	21	1(1-1)	29	1(1-1)	19
<i>Senna sturtii</i>	8	1(1-1)	17	1(1-1)	10	1(1-1)	11
<i>Scaevola spinescens</i>	8	1(1-1)	4	1	2	1	5
<i>Acacia anisotrocarpa</i>	10	1(1-2)	4	1	5	1(1-1)	7
<i>Acacia kempeana</i>	13	1(1-1)	54	1(1-3)	38	1(1-4)	32
<i>Condonocarpus continifolius</i>	13	1(1-1)	25	1(1-1)	2	1	12
<i>Acacia aneura</i> var. <i>tenuis</i>	15	1(1-1)	100	3(1-5)	100	4(1-5)	69
<i>Eucalyptus gamophylla</i>**	18	1(1-2)	4	1	0		8
<i>Acacia colei</i>	21	1(1-2)	8	1(1-1)	2	1	11
<i>Acacia estrophiolata</i>	26	1(1-2)	4	2	5	1(1-1)	12
<i>Senna artemisioides oligophylla</i>	31	1(1-2)	50	1(1-2)	33	1(1-1)	35
<i>Atalaya hemiglaucula</i>**	33	1(1-2)	25	1(1-2)	19	1(1-2)	26
<i>Santalum lanceolatum</i>	33	1(1-2)	13	1(1-1)	2	1(1-1)	16
<i>Eremophila longifolia</i>**	36	1(1-1)	25	1(1-1)	14	1(1-2)	25
<i>Hakea chordophylla</i>	36	1(1-1)	21	1(1-1)	12	1(1-1)	23
<i>Ptilotus obovatus</i>	44	1(1-1)	42	1(1-1)	41	1(1-1)	42
<i>Acacia adsurgens</i>*	44	1(1-3)	38	1(1-1)	14	1(1-2)	31
<i>Eremophila latrobei</i>	46	1(1-2)	92	1(1-2)	86	1(1-3)	72
<i>Senna artemisioides artemisioides</i>	46	1(1-1)	42	1(1-1)	21	1(1-1)	36
<i>Acacia ligulata</i>	46	1(1-2)	21	1(1-1)	10	1(1-1)	26
<i>Senna artemisioides helmsii</i>	49	1(1-1)	79	1(1-2)	74	1(1-6)	66
<i>Corymbia opaca</i>**	49	1(1-2)	33	1(1-1)	12	1(1-1)	30
<i>Acacia pruinocarpa</i>*	54	1(1-2)	67	1(1-2)	17	1(1-1)	42
<i>Acacia inaequilatera</i>	54	1(1-2)	29	1(1-1)	7	1(1-1)	30
<i>Acacia tenuissima</i>*	56	1(1-2)	33	1(1-1)	24	1(1-1)	39
<i>Acacia coriacea</i>	62	1(1-3)	25	1(1-1)	7	1(1-1)	32
<i>Anthobolus leptomerioides</i>	64	1(1-2)	42	1(1-2)	26	1(1-1)	44
<i>Hakea macrocarpa</i>	69	1(1-1)	38	1(1-1)	17	1(1-2)	42
<i>Gossypium australe</i>	79	1(1-2)	38	1(1-1)	21	1(1-1)	48
<i>Triodia pungens</i>	100	5(4-6)	96	4(2-6)	45	1(1-2)	77

An ordination of all long lived perennials by their cover scores (Figure 4.4) demonstrated a clear, graded separation of Mulga, mixed and spinifex plots, the separation being driven by a number of species but most strongly by Mulga and spinifex. The vector for species richness (not shown) was weakly correlated with the other species as it appeared as a very short vector at $r^2=0.22$. This confirms that species composition is driving the ordination rather than species richness. The graded separation remained recognizable (although Mulga and spinifex plots merged more) when the ordination was repeated with Mulga and spinifex excluded both with cover score data (Figure 4.5) and presence/absence data (not shown, MRPP $T = 22.5$, $P < 0.000001$). The mixed plots overlapped with Mulga and less so with spinifex plots in the absence of the Mulga and spinifex scores.

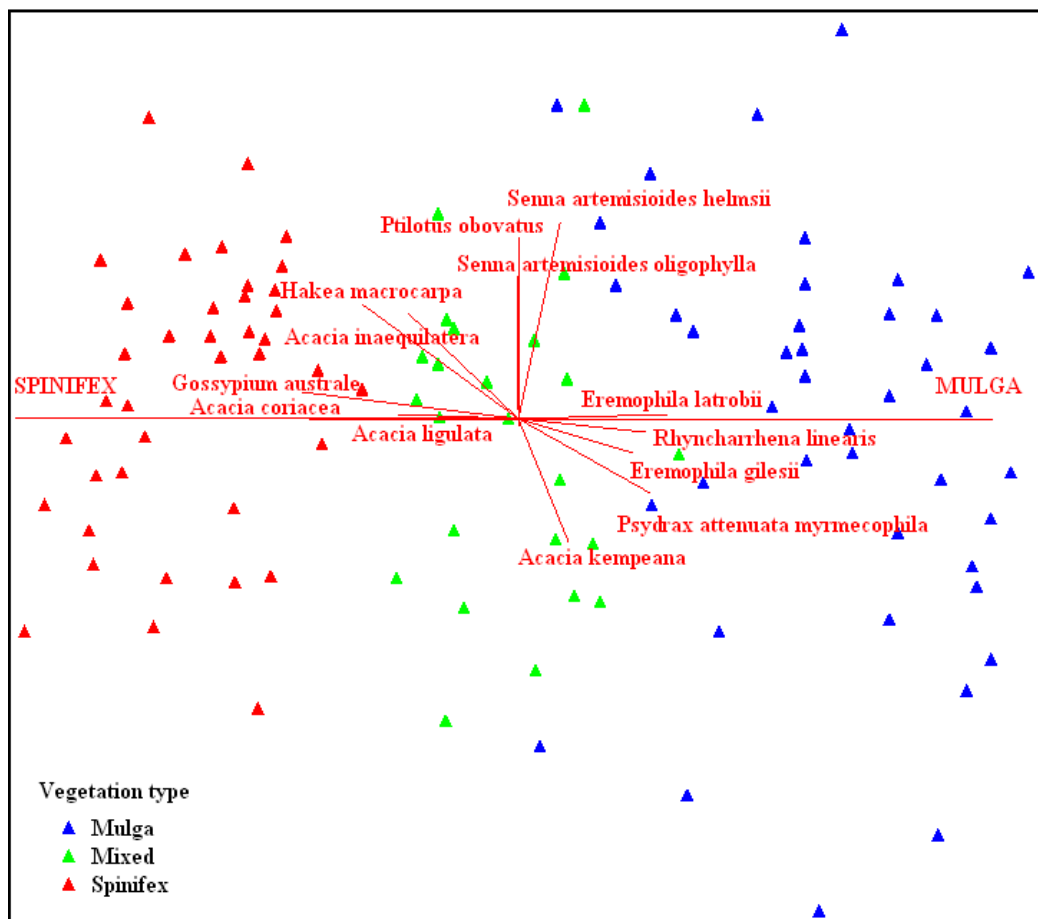


Figure 4.4 The first two dimensions of a three dimensional ordination of 105 vegetation plots on a Mulga-spinifex sand plain using species cover classes. The three vegetation types differed significantly (MRPP $T = -43.9$, $P < 0.00000$). The (joint plot) vectors ($r^2 > 0.17$) angle and length show the species direction and strength of the relationship to the Mulga-spinifex spectrum.

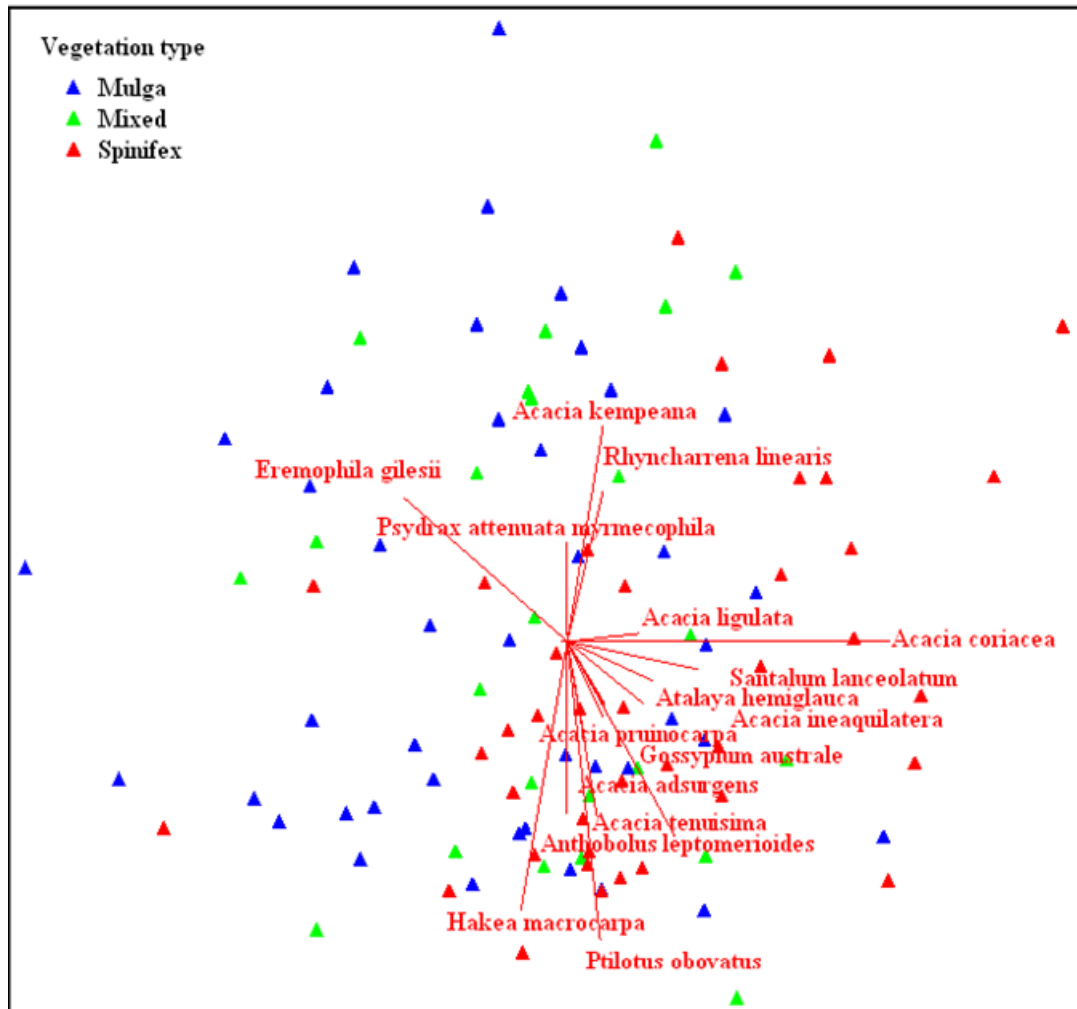


Figure 4.5 The first two dimensions of a three dimensional ordination of 105 vegetation plots on a Mulga-spinifex sand plain using species cover scores other than Mulga and spinifex. (MRPP $T = 23.0$, $P < 0.000001$). The angle and length of the vectors ($r^2 > 0.17$) show the direction and strength of the relationship of species to the Mulga-spinifex spectrum

The species other than Mulga and spinifex that were prominent in driving the ordinations occurred in all vegetation types (Table 4.1-bolded species), with the exception of *Psydrax attenuata myrmecophila*, which was absent from spinifex and *Eucalyptus gamophylla* which was absent from Mulga vegetation.

Analysis by ordination failed to identify convincing floristic patterns within Mulga as solutions were barely different from random solutions as shown by NMS scree plot (not shown).

Functional Traits

The key functional traits (life expectancy, time to seed after fire and re-sprouting type and mechanism) for the species driving the ordination (highlighted species in Table 4.1) did not separate the species into distinct vegetation types (Mulga, mixed or spinifex) (Table 4.2). The species associated with either Mulga or spinifex had the same range of life histories from short lived to long lived perennials. All the species seeded within 5 years after a fire except Mulga. The response of Mulga associated species to fire varied from seeder to variable resprouter to resprouter. This was the same as spinifex associated species. The mechanism to resprout after a fire was equally varied within either Mulga or spinifex associated species as much as comparing Mulga and spinifex associated species.

Table 4.2 The functional attributes (from the Northern Territory Ecological Attributes Database-unpublished) of the species identified as strongly influencing the ordinations, arranged according to their primary vegetation type. Attribute: **Life history** = expected length of life; **Seeding** = time to seed post-fire (or * = observed time to seed in the field); **Fire response** = S (seeder), VR (variable resprouter), R (resprouter) of an adult; **Resprouter type** = BSB (basal stem buds), ES (epicormic shoots) and RS (root suckers) and USO (underground storage organs). *art.* = artemisioides

Species	Lifespan (years)	Seeding (yrs)	Fire response	Resprout
MULGA ASSOCIATED				
<i>Acacia aneura</i> var. <i>tenuis</i> (Mulga)	>20	5-15	S+VR	?
<i>Psyrax attenuate</i> var. <i>myrmecophila</i>	>20	6-10*	VR	RS+BSB
<i>Acacia kempeana</i>	11-20, >20	2-3	S+VR	BSB+ES+RS+none
<i>Eremophila gilesii</i>	6-20	2-3	VR	BSB
<i>Eremophila latrobei</i>	>20	2-3?	R	BSB
<i>Rhyncharrhena linearis</i>	6-20, >20	1	R	USO
MIXED ASSOCIATED				
<i>Senna art. artemisioides</i>	11-20, >20	2-3	VR	BSB
<i>Ptilotus obovatus</i>	2-10	1	R	BSB
<i>Senna art. oligophylla</i>	11-20, >20	2-3	VR	BSB
SPINIFEX				
<i>Triodia pungens</i> (spinifex)	>20?	1	VR	?
<i>Acacia coriacea</i>	>20	1-3	R	BSB+ES
<i>Acacia inaequilatera</i>	11-20, >20	2-3	S+R	BSB+ES
<i>Acacia ligulata</i>	4-20	2-3	S+R	BSB
<i>Acacia tenuissima</i>	>20	2-3	VR	RS
<i>Corymbia opaca</i>	>20	2-5	R	BSB+ES
<i>Gossypium australe</i>	4-20	1	R	?
<i>Hakea macrocarpa</i>	>20	1	R	BSB+ES
<i>Acacia adsurgens</i>	4-20	1-2	S	BSB
<i>Acacia pruinocarpa</i>	>20	2-5	R	BSB+ES
<i>Eucalyptus gamophylla</i>	>20	2-3-4	R	BSB
<i>Atalaya hemiglauc</i>	>20	?	R	RS+BSB
<i>Anthobolus leptomerioides</i>	>20	2-3,4-5	R	RS

Surface soil characteristics

The floristic gradient in Figure 4.1 corresponded with a number of environmental gradients (Figure 4.6). Tower termite mounds were more frequent in spinifex (Figure 4.7); sandiness of the surface soil was greater in spinifex (Figure 4.8); biological crusting covered more of the surface soil in Mulga than spinifex vegetation (Figure 4.9), even when Mulga and spinifex had the same time since the last fire (Figure 4.10). Biological crusting increased significantly with time since last fire for both Mulga and spinifex vegetation. Surface soil texture was heavier in Mulga (Figure 4.11), however there was a clear spread of texture grades that did not allow discreet classification of vegetation groups according to soil texture group. The texture of spinifex plots became sandier (Fig. 4.12) and in Mulga plots became heavier (Fig. 4.13) with increased distance from the Mulga edge, however these very weak gradients indicate the textural boundary was diffuse. Bulk density and pH were not significantly different between the vegetation types (one-factor ANOVAS pH: $F=0.62, df=2, 102; P=0.54$; Bulk density: $F=0.82, df=2, 102; P=0.44$; see Table 3.3). No nitrates were detected (by the analytic technique used) in any of the samples.

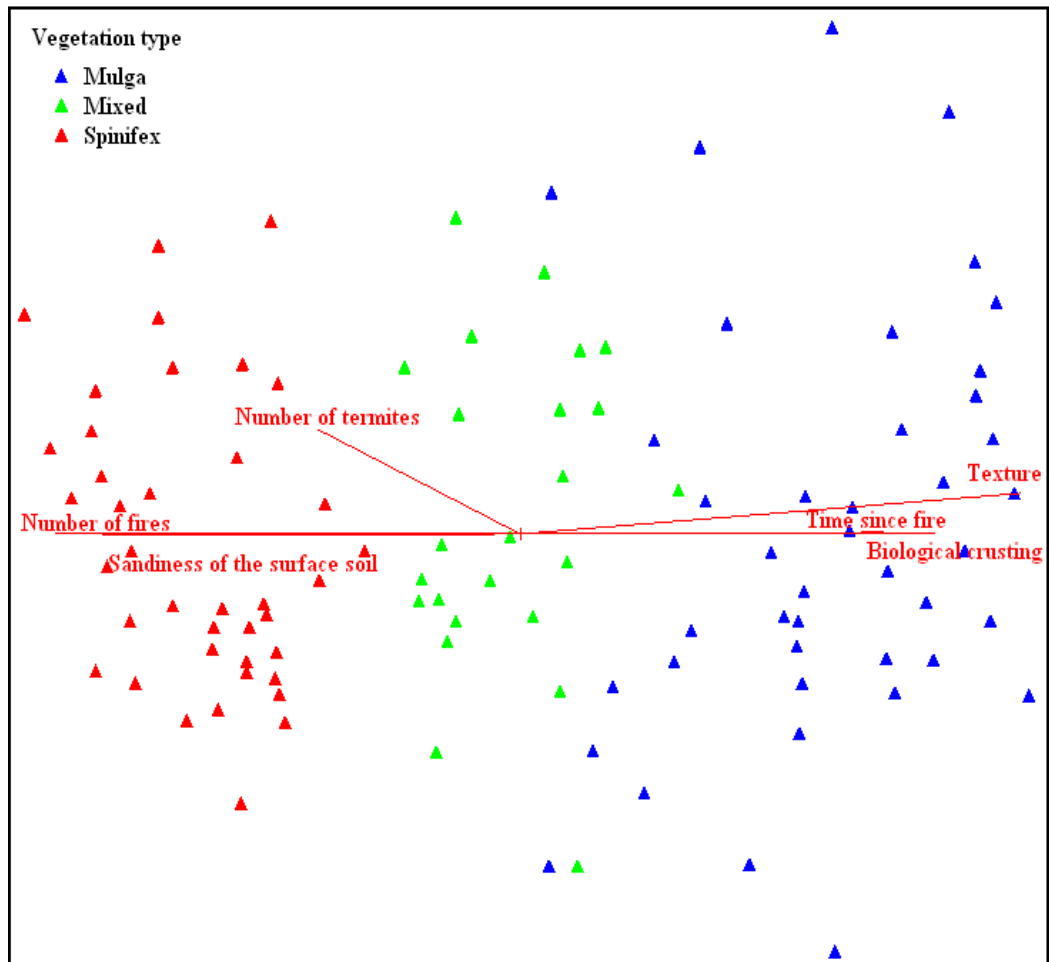


Figure 4.6 Ordination of 105 vegetation plots on a Mulga-spinifex sand plain using species cover scores (Fig. 4.4) with environmental variables as a bi-plot. The (joint plot) vectors ($r^2 \geq 0.17$) angle and length show the environmental variables direction and strength of the relationship to the Mulga-spinifex spectrum

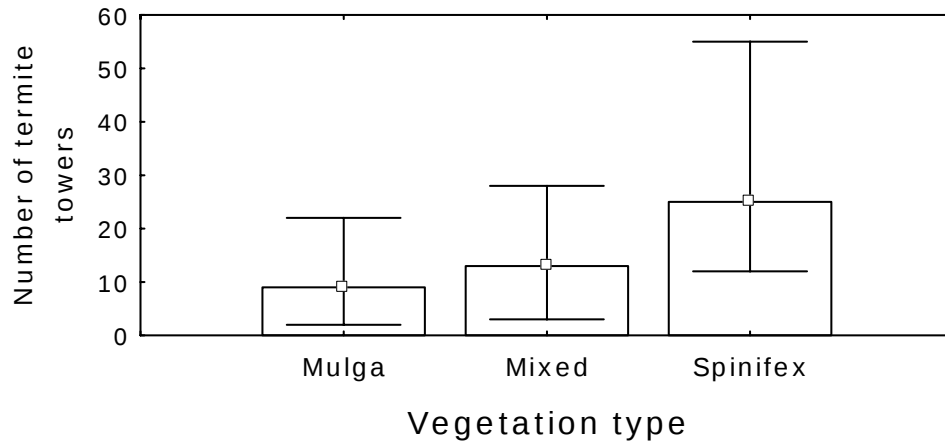


Figure 4.7 Number of tower termite mounds (median with 10% and 90% percentiles) counted in Mulga, mixed and spinifex vegetation plots. The vegetation types differed significantly (Kruskal-Wallis- $H_{2,105} = 33.7$, $P < 0.00000005$).

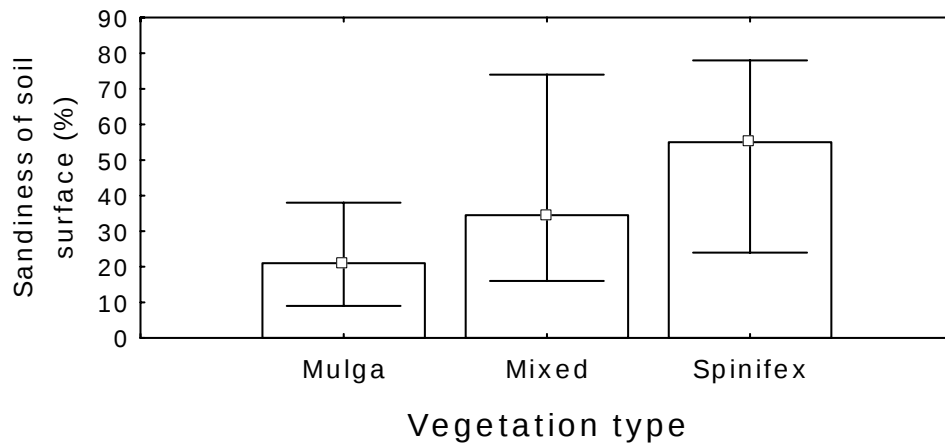


Figure 4.8 Cover of sand on the surface of surface soil (median with 10% and 90% percentiles) in Mulga, mixed and spinifex vegetation. The vegetation types differed significantly (Kruskal-Wallis $-H_{2,105} = 40.4531$, $P < 0.000000002$).

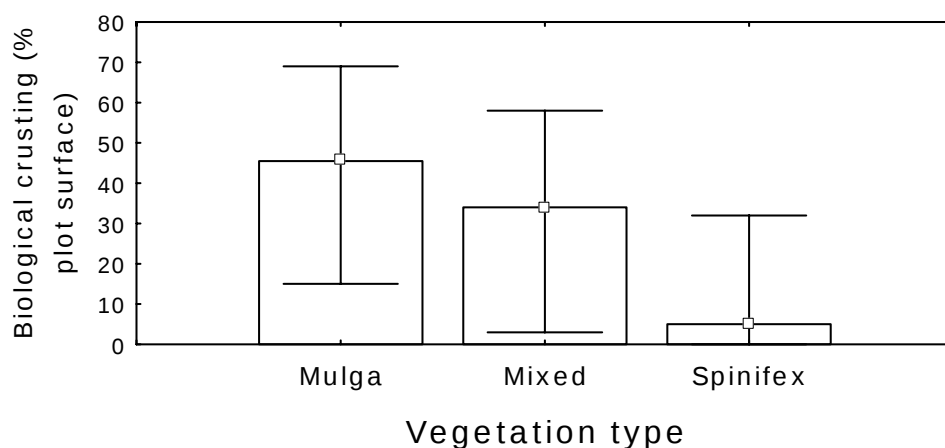


Figure 4.9 Biological crusting (Median with 10% and 90% percentiles) in Mulga, mixed and spinifex vegetation. The vegetation types differed significantly (Kruskal-Wallis- $H_{2,105} = 40.4$, $P < 0.000000002$). Mulga and mixed vegetation had similar biological crusting (Multiple Comparisons P values (2-tailed): 0.22) where Mulga and mixed differed from spinifex vegetation (Multiple Comparisons P values (2-tailed); MulgaVspinifex: 0.000001, mixedVspinifex: 0.0009).

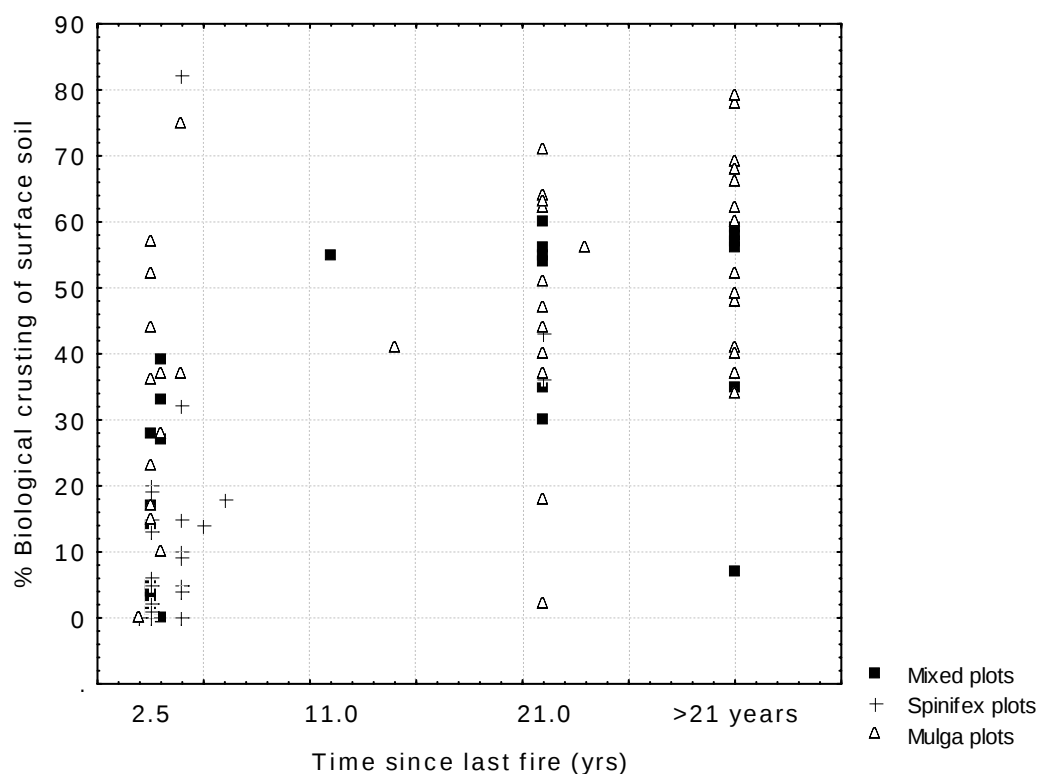


Figure 4.10 The percent of plot surface covered with biological crusting against time since the last fire in Mulga ($r_s=0.48$, $n=42$, $P=0.001$), mixed ($r_s=0.70$, $n=24$, $P=0.0002$) and spinifex ($r_s=0.41$, $n=39$, $P=0.009$) vegetation types.

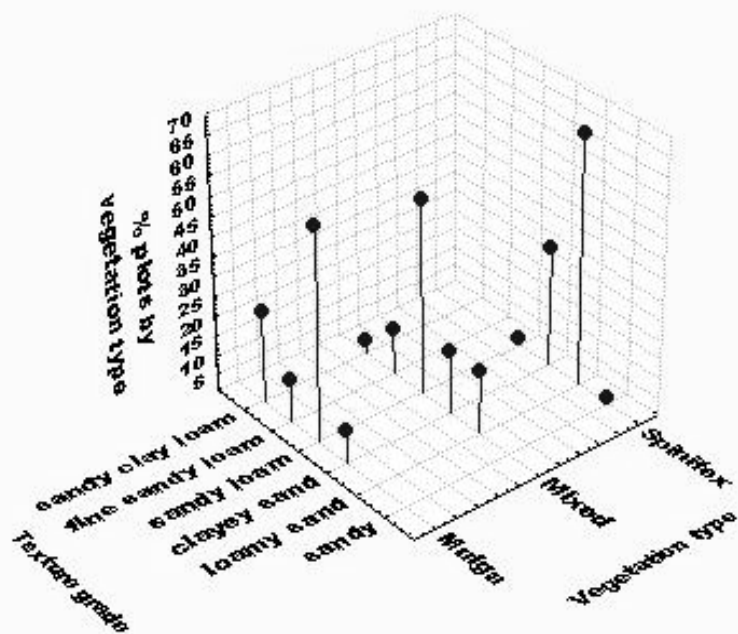


Figure 4.11 The spread of texture grades across Mulga, mixed and spinifex vegetation types. The vegetation types differed significantly (Kruskal-Wallis- $H_{2,105} = 63.4$, $P<0.00001$).

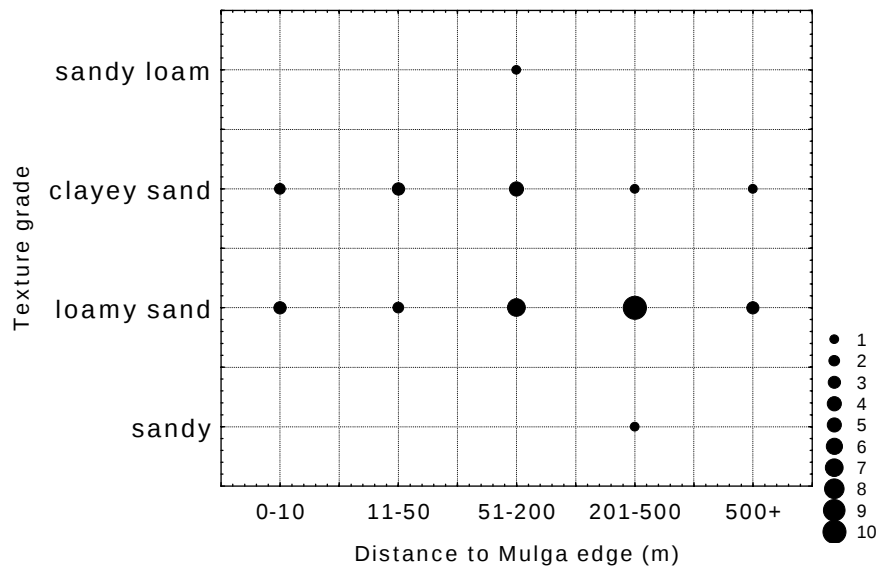


Figure 4.12 Comparison of spinifex plot texture grades against distance from Mulga-spinifex boundary. The texture was sandier with increasing distance from the Mulga boundary ($r_s=0.3$, $n=39$, $P=0.05$). An increase in bubble size indicates an increase number of samples taken of that texture at that distance from the Mulga-spinifex boundary.

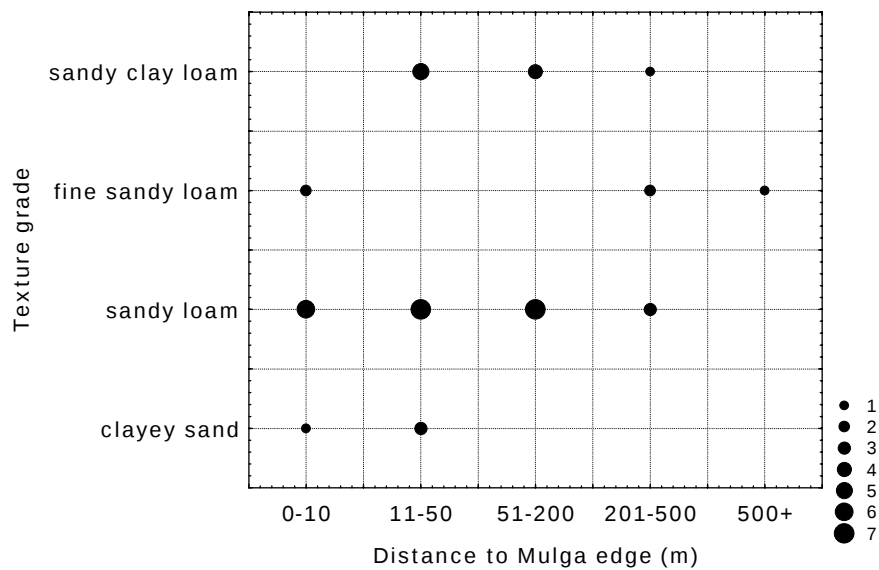


Figure 4.13 Mulga plot texture against distance from Mulga-spinifex boundary. The texture was heavier with increasing distance from the Mulga boundary ($r_s=0.25$, $n=42$, $P=0.05$). An increase in bubble size indicates an increase number of samples taken of that texture at that distance from the Mulga-spinifex boundary.

Table 4.3 The Mean, Standard Deviation and Standard Error for pH and Bulk density measures in Mulga, mixed and spinifex soil samples.

	pH	SD.	Bulk density	SD.
Mulga	6.91	0.35	1.50	0.081
Mixed	6.90	0.28	1.50	0.082
Spinifex	6.84	0.29	1.52	0.070

Modelling the Mulga-spinifex spectrum

The number of recorded fires contributed to 45% of the overall goodness of fit to the model expressing the floristic gradient across the Mulga-spinifex mosaic (Table 4.4, run 1) but the addition of soil variables accounted for an additional 25% of the deviance (run 3). However, removing fire and running soil variables alone (run 2) only slightly reduced the explanatory power compared to the fire and soil combined run. Run 4 had variables in the best supported model that were the same as the variables combined from the fire alone and soil alone runs. An increased measure of Texture, Biological crusting and Gravel variables in Mulga vegetation were in all the best supported models, with an increased measure of fire in spinifex vegetation adding slightly to the explanatory power of the model. Support for the second subset of variables across runs 2-4 was strong ($\Delta_I < 0.9$) and indicated an increase of soil crusting in spinifex vegetation (see figure 4.14, run 2-4) both with and without fire. However, the addition of greater pH, Bulk density and 'distance to Mulga edge' in spinifex vegetation provided minor improvement to the explanatory effect of the model and increased support for the first two subsets of variables, in the presence of fire ($\Delta_I > 1.3$).

Table 4.4 **Generalized Linear Model runs 1-4** (and their respective best subsets as measured by the Akaike Information Criterion) explored for their statistical contribution to the Mulga-spinifex spectrum (deviance explained). **GLM run 1**= Fire, **GLM run 2**= Soil, **GLM run 3**= Fire and Soil and **GLM run 4**= All possible variables. The predictor variables for each model are ordered in decreasing order of contribution to the model. The response variable ranged from Mulga to spinifex, where a positive (+) symbol indicates more in Mulga vegetation and a negative (-) symbol indicates more in spinifex vegetation. A measure of the variable is indicated as it relates to the floristic gradient. Δ_I = difference in AIC value relative to the most strongly supported model.

Generalized Linear Model run	AIC	Δ_I	Deviance explained (%)
1. Number of fires(-)	212.6		45
2. Texture(+), Biological crusting(+), Gravel(+)	157.9	0	68.6
Texture(+), Biological crusting(+), Gravel(+), Soil crusting(-)	158.7	0.8	69.0
Texture(+), Biological crusting(+), Gravel(+), pH(-)	158.7	0.8	69.0
3. Texture(+), Biological crusting(+), Gravel(+), Number of fires(-)	155.3	0	69.9
Texture(+), Biological crusting(+), Gravel(+), Number of fires(-), Soil crusting(-)	156.1	0.8	70.3
Texture(+), Biological crusting(+), Gravel(+), Number of fires(-), pH(-)	156.7	1.4	70.1
Texture(+), Biological crusting(+), Gravel(+), Number of fires(-), Bulk density(-)	157.2	1.9	70.0
4. Texture(+), Biological crusting(+), Gravel(+), Number of fires(-)	155.3	0	69.9
Texture(+), Biological crusting(+), Gravel(+), Number of fires(-), Soil crusting(-)	156.1	0.8	70.3
Texture(+), Biological crusting(+), Gravel(+), Number of fires(-), pH(-)	156.7	1.4	70.1
Texture(+), Biological crusting(+), Gravel(+), Number of fires(-), M-edge(-)	156.8	1.5	70.1
Texture(+), Biological crusting(+), Gravel(+), Number of fires(-), Bulk density(-)	157.2	1.9	70.0

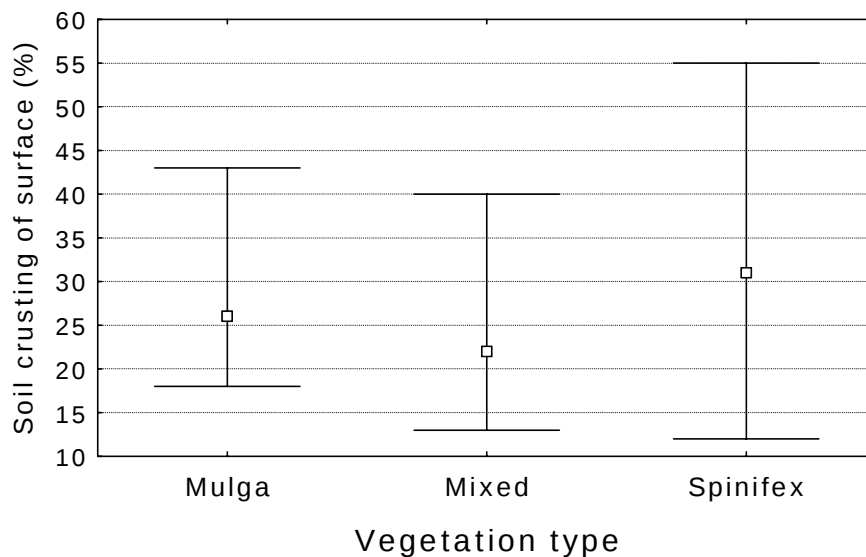


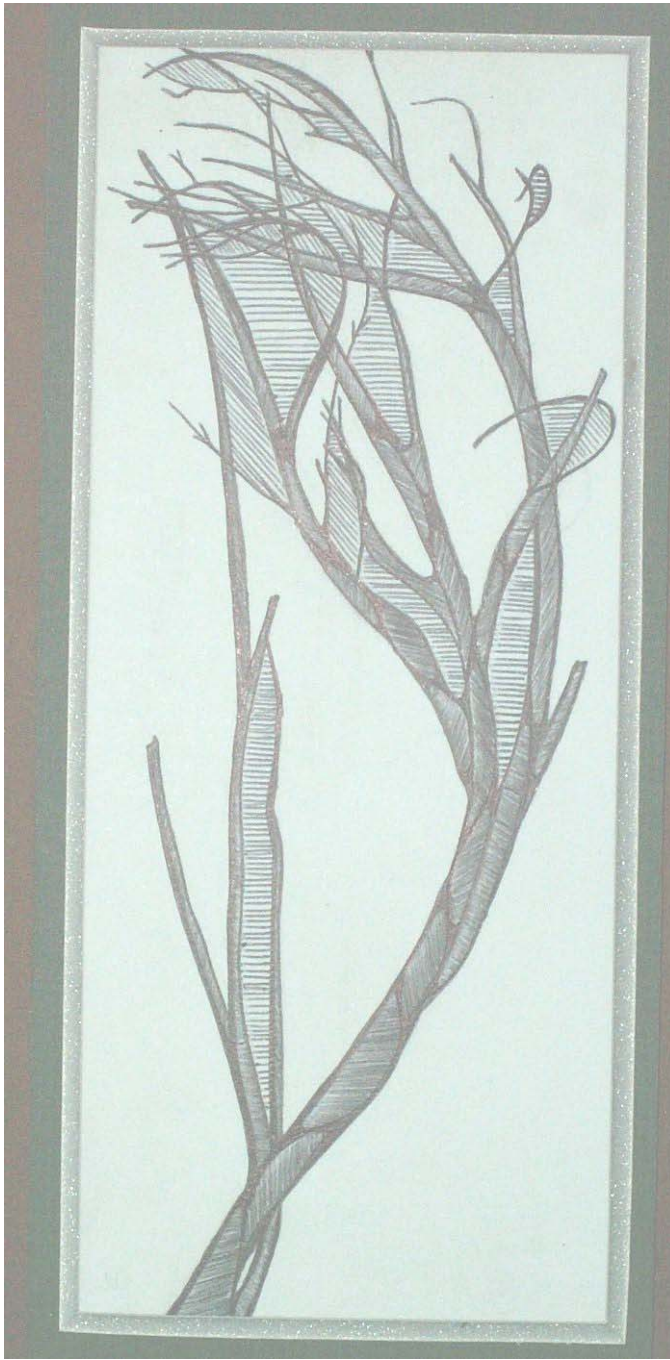
Figure 4.14 Soil crusting (Median with 10% and 90% percentiles) in Mulga, mixed and spinifex vegetation. The vegetation types differed significantly (Kruskal-Wallis- $H_{2,105} = 7.9, P=0.0195$).

Conclusions

In the southern Tanami landscape the Mulga edge is a sharp physiognomic boundary. The transition zone from Mulga to spinifex is narrow, rarely exceeding 10 meters (field observation). However, the floristic and soil differences between the dominant Mulga and spinifex communities are more diffuse, indicating that the gradation of species and environmental variables across the Mulga-spinifex boundary is subtle, complex and clearly not abrupt. Thus, the landscape is overwhelmingly characterized by the Mulga and spinifex keystone species.

Modelling of the mulga spinifex boundary indicated that the number of fires is a significant factor that is clearly interacting and influencing the floristic patterning and soil gradients identified in this study.

CHAPTER 5: MULGA DEMOGRAPHICS



The Mulga tree

Warren McCaskill

A study of the structure of Mulga is presented with attention to the relationship between the diversity of height structures and the most frequently occurring (modal) height class for each Mulga plot. The Mulga skewness measure is explored for environmental correlates.

Height structural profiles and diversity

Seedlings were present in all Mulga plots but only frequent in plots dominated by Mulga <1m tall (Figure 5.1). Sixty percent of the Mulga plots were dominated by the intermediate height classes (between 1-5metres). Less than 20% of plots were dominated by 'old' Mulga trees (>5metres), although the exact age of these trees is not known. Burnt Mulga stumps and charcoal was observed in every Mulga plot so the description of 'old (growth) Mulga' refers to 'not recently burnt', rather than of any definite long biological age. The tendency was for Mulga plots dominated by more developed trees to have a more diverse structure of heights (Figure 5.2), although no significant difference in the Shannon-Weiner diversity index was found between different modal classes (Kruskal-Wallis test: $H_{4,42} = 7.32$, $P = 0.12$). Generally, Mulga plots were dominated by their modal class and lacked strong representation of the other height classes, this being least true for the tallest height class. The least diverse height structure in the study area was recorded for almost half of the seedling modal height class plots.

The frequency of dead Mulga trees was not significantly different across the different modal classes (Kruskal-Wallis test: $H_{4,42} = 2.9$, $P = 0.57$). Dead Mulga trees of heights more than 1m were consistently present across the modal classes. Dead 5m+ Mulga trees were more abundant than living 5m+ trees in all modal classes except for 5m+ and 1-3m.

The mixed vegetation Seedling modal class had almost no other height classes represented with a tendency for more dead young trees (Figure 5.3). The frequency of each modal height class sampled was not significantly different between Mulga and mixed vegetation types ($\chi^2 = 6.65$, $df=4$, $P=0.17$).

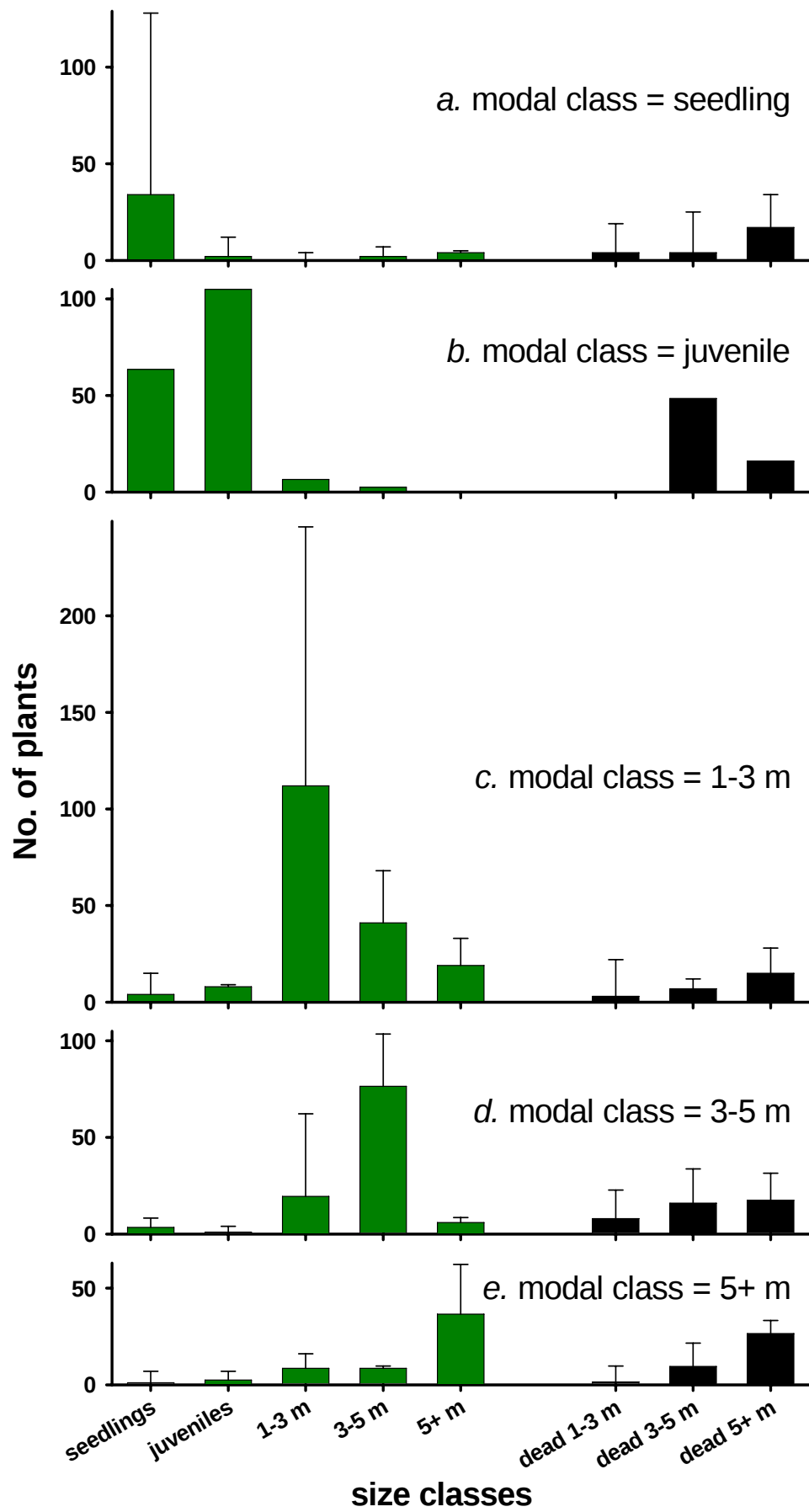


Figure 5.1 (previous page) The height structure (median and 75th percentile) for living and dead Mulga trees in Mulga vegetation in plots grouped by their modal height class of living Mulga plants; a: n=7, b: n=2, c: n=15, d: n=10 and e: n=8.

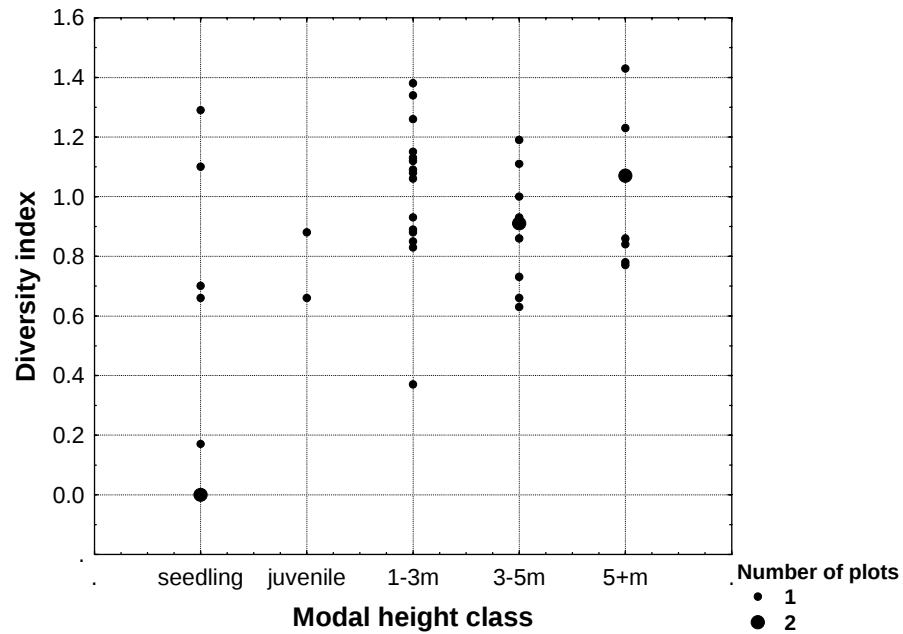


Figure 5.2 The Shannon-Weiner diversity index for Mulga plots with different modal height classes.

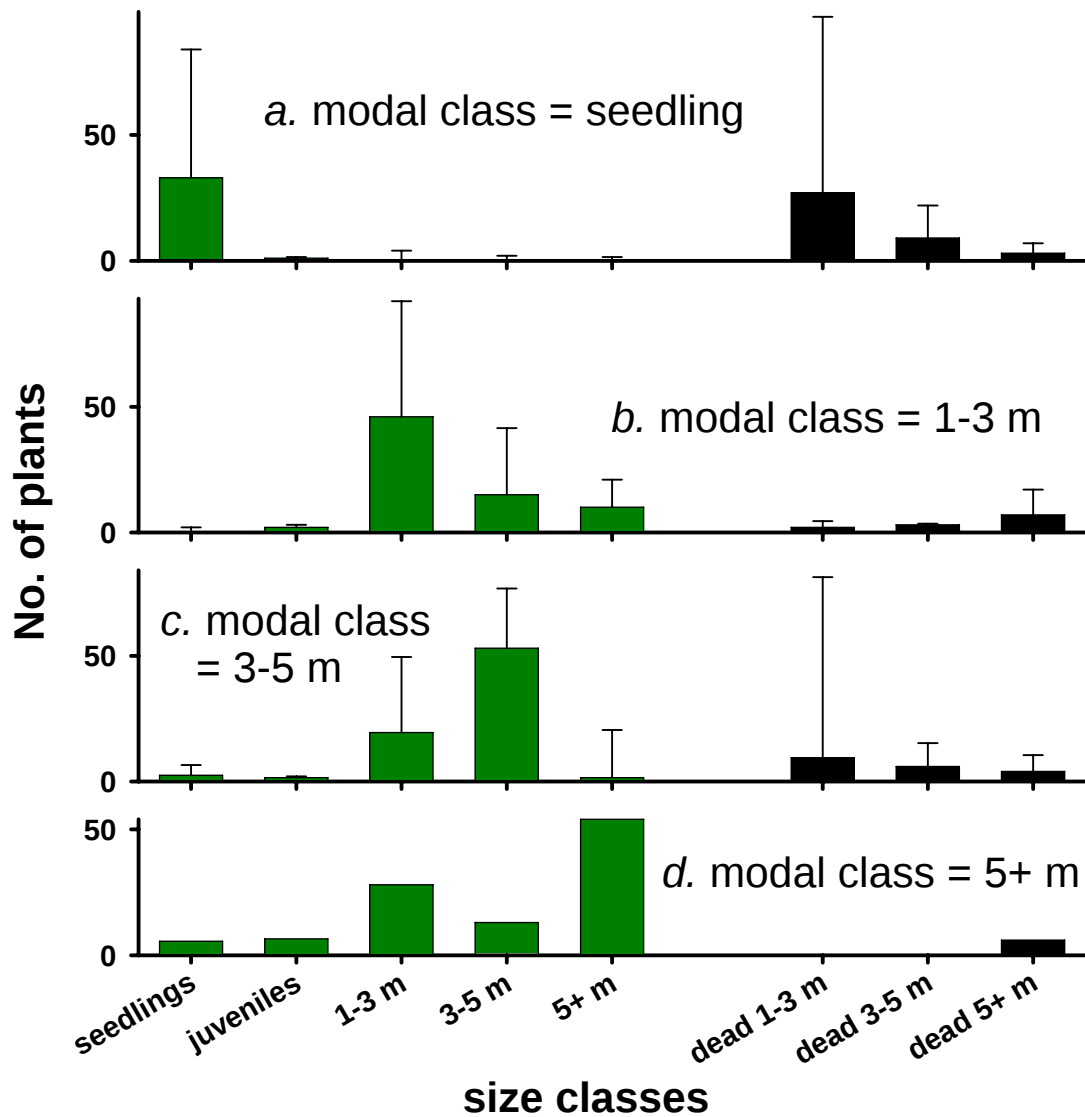


Figure 5.3 The height structure (median and 75th percentile) for living and dead Mulga trees in Mixed vegetation in plots grouped by their modal height class of living Mulga plants; a: n=9, b: n=5, c: n=8 and d: n=2.

Modelling Mulga demographics

The four best supported models ($\Delta_{aic} < 2.0$), expressing the variation in height structure of Mulga stands, all included the number of fires and fire season (Table 5.1). The number of fires and fire season accounted for almost 30% of the deviance in the models for Mulga skewness. Plots that were burnt more frequently, tended to be dominated by smaller Mulga trees (Figure 5.4). Plots that were burnt by summer fires also tended to be dominated by smaller Mulga trees (Figure 5.5). The weaker additional effects of the distance from the Mulga-spinifex boundary and texture

accounted for a further 5% of deviance explained. Mulga plots further away from the Mulga-spinifex boundary, tended to be dominated by taller Mulga trees (Figure 5.6). Mulga plots on finer texture grades had a weak tendency to support taller trees (Figure 5.7).

The four Mulga plots that were burnt twice in less than five years, had numerous (50-200) fire-killed mulga of all heights, few remaining older plants, and very few (less than 10) seedlings.

Table 5.1 The five best supported models and their contribution to the Mulga skewness measure. A positive Mulga skewness indicated a dominance of smaller plants and a negative Mulga skewness indicated a dominance of larger plants. The predictor variables are ordered for their importance in the model.

Model	AIC	Δ_{aic}	Deviance explained (%)
No. of Fires(+), Fire season, Texture(-)	159.4	0	33.7
No. of Fires(+), Fire season	159.9	0.5	29.6
No. of Fires(+), Fire season, Distance to Mulga edge(+)	160.6	1.2	31.8
No. of Fires(+), Fire season, Distance to Mulga edge(+), Texture(-)	160.6	1.2	34.9
No. of Fires(+)	163.2	3.8	16.3

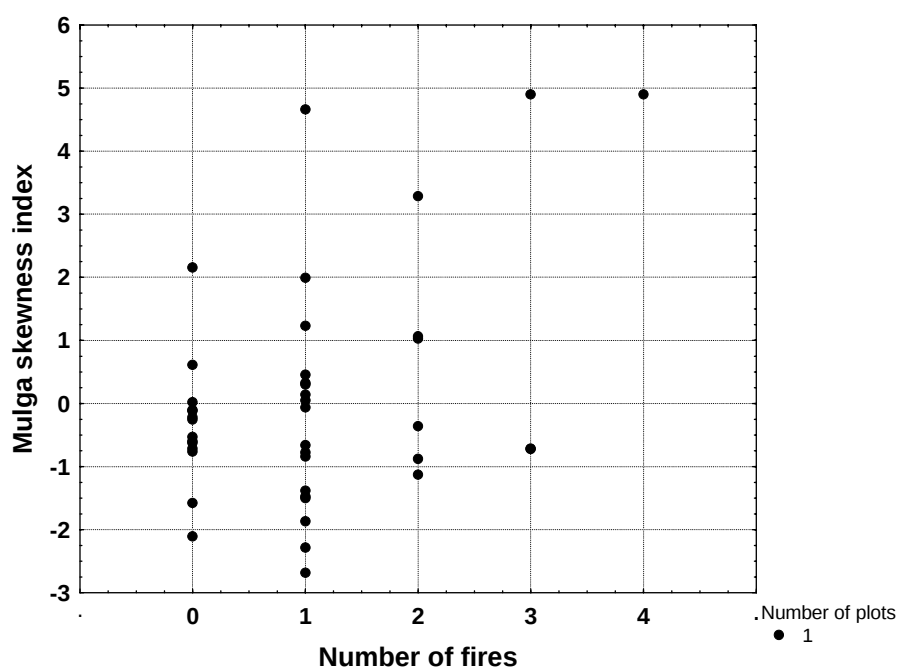


Figure 5.4 The Mulga skewness index for fire frequencies in Mulga vegetation plots.

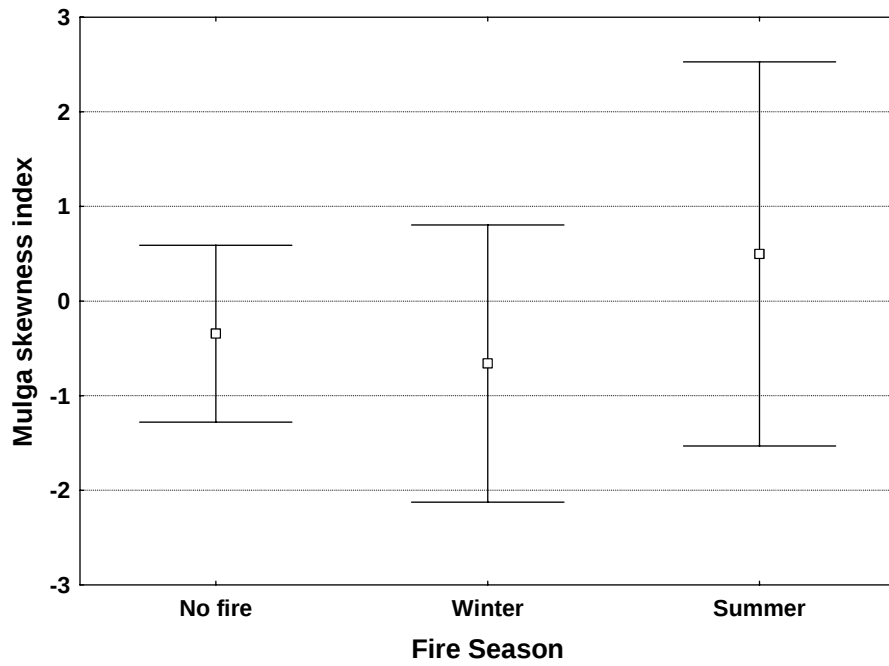


Figure 5.5 The mean and standard deviation of Mulga skewness for Fire season (Winter: April-Sept, Summer: Oct-March).

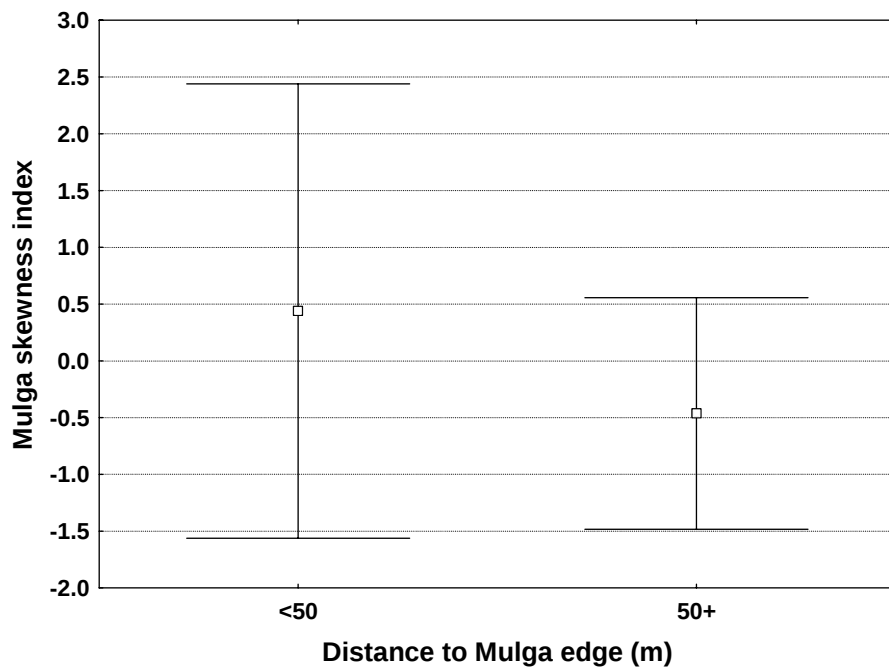


Figure 5.6 The mean and standard deviation of Mulga skewness for Mulga vegetation plots close and further from the Mulga-spinifex boundary.

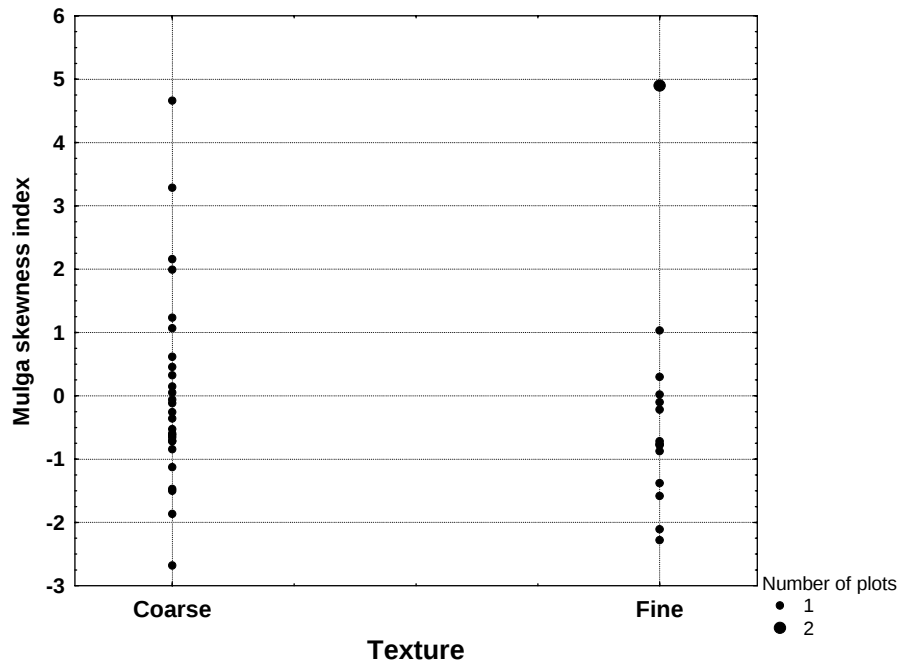


Figure 5.7 The Mulga skewness index for coarse (clayey sand and sandy loam) and fine (fine sandy loam and sandy clay loam) texture classes in Mulga vegetation plots.

The time since the last fire accounted for almost 43% of the deviance of the models for Mulga seedling frequency (Table 5.2). An additional effect of texture and distance from the Mulga edge accounted for an additional 5% deviance. Seedlings were strongly associated with Mulga plots that had been recently burnt (Figure 5.8). There was a weak trend for more seedlings on coarse textured soil (Figure 5.9) and an increase in number of seedlings with distance from Mulga edge (as identified from the direction of effects in the GLM results). The distance from the Mulga edge contributed a further 2% deviance to the explanatory power of the model, although this effect was not seen when graphically represented.

Table 5.2 The best supported models ($\Delta_{aic} < 2.0$) and their contribution to the frequency of Mulga seedlings.

Model	AIC	Δ_{aic}	Deviance explained (%)
Time since last fire, Texture (+)	60.0	0	46.5
Time since last fire, Texture (+), Distance to Mulga edge	60.7	0.7	48.4
Time since last fire	61.2	1.2	42.8

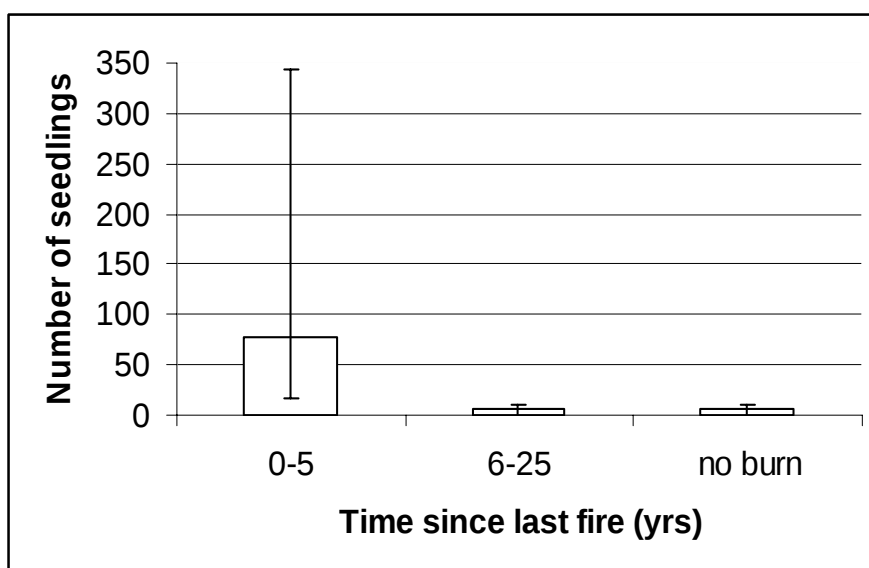


Figure 5.8 The mean and standard deviation of numbers of seedlings in Mulga plots of different fire ages.

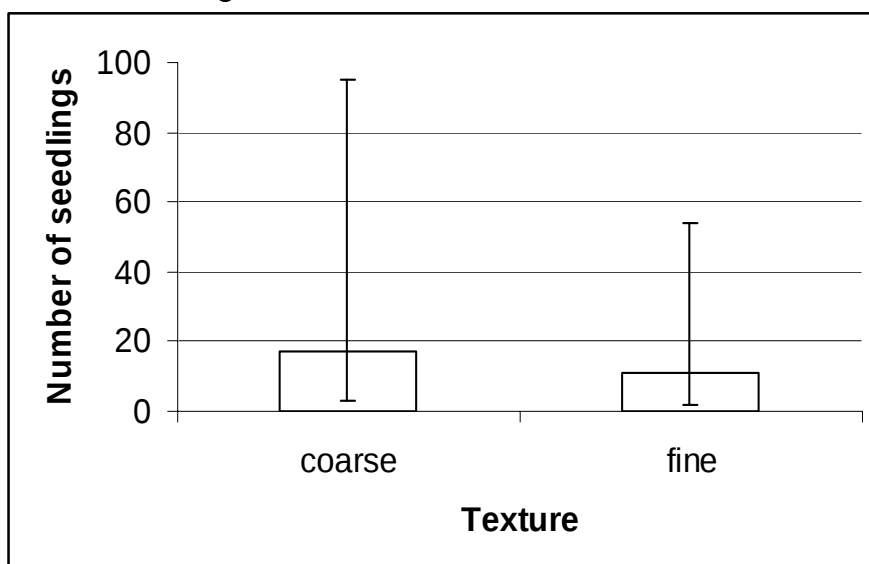


Figure 5.9 The mean and standard deviation of numbers of seedlings in coarse (clayey sand and sandy loam) and fine (fine sandy loam and sandy clay loam) textured Mulga plots.

Conclusions

There was a trend for Mulga plots with a more diverse range of height structure to have had less fire. Furthermore, plots dominated by smaller Mulga tended to have had more frequent fire and/or summer fires. There was an association of taller Mulga trees, on finer textured soils, with increased distance from the Mula-spinifex boundary. Seedlings strongly dominated in recently burnt plots and were more associated with coarse textured soils.

The results demonstrate that Mulga closer to the Mulga-spinifex boundary is less diverse (structurally), has less tall trees, experiences more fire and has a soil-fire interaction.

CHAPTER 6: BIODIVERSITY



Cheilanthes sieberi



Aristida obscura



Spartothamnella teucrifolia

This chapter compares the local and landscape levels of woody species diversity for the Mulga, mixed and spinifex vegetation types in order to explore the possibility that species richness differs at the plot scale compared with the landscape scale. Species that are suggested to indicate ‘old growth Mulga’ are analysed for their presence across the vegetation types. The fire sensitivity of indicator species is considered by comparing the species frequency of presence in burnt and unburnt plots.

Species Richness

Species richness of woody plants plus spinifex in Mulga, mixed and spinifex vegetation plots, at the local (*alpha*) diversity level (Whittaker 1977), was least in Mulga plots (Figure 6.1). However, species richness, considered as a cumulative species count within vegetation type, measures beta diversity, and shows that Mulga vegetation was as diverse as spinifex at the landscape scale (Figure 6.2). The suggestion is that the mixed vegetation type has the greatest woody species richness at the landscape scale, although a small sample size limits this assertion.

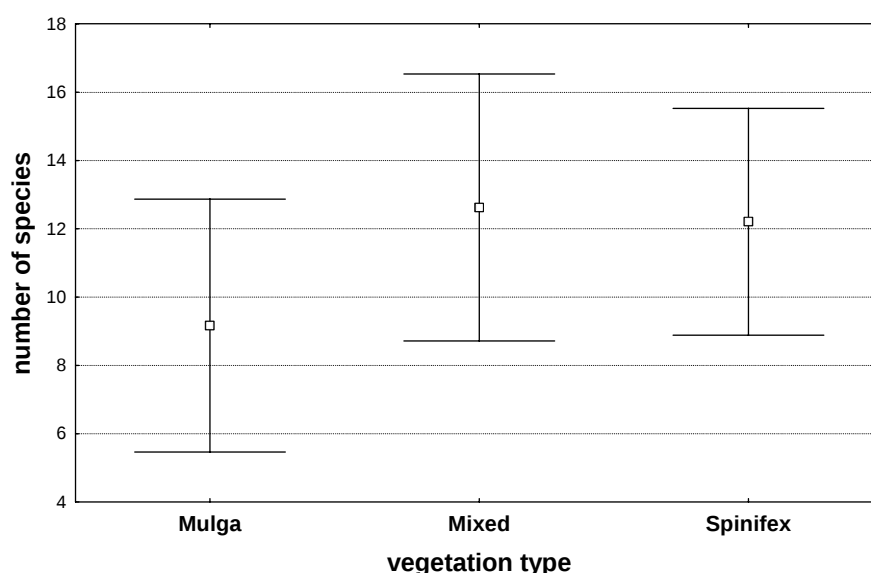


Figure 6.1 The mean and standard deviation of the species richness of woody plants plus spinifex in Mulga, mixed and spinifex plots. Species richness differed significantly between the vegetation types (Kruskal-Wallis- $H_{2,105}=16.6$, $P=0.0002$).

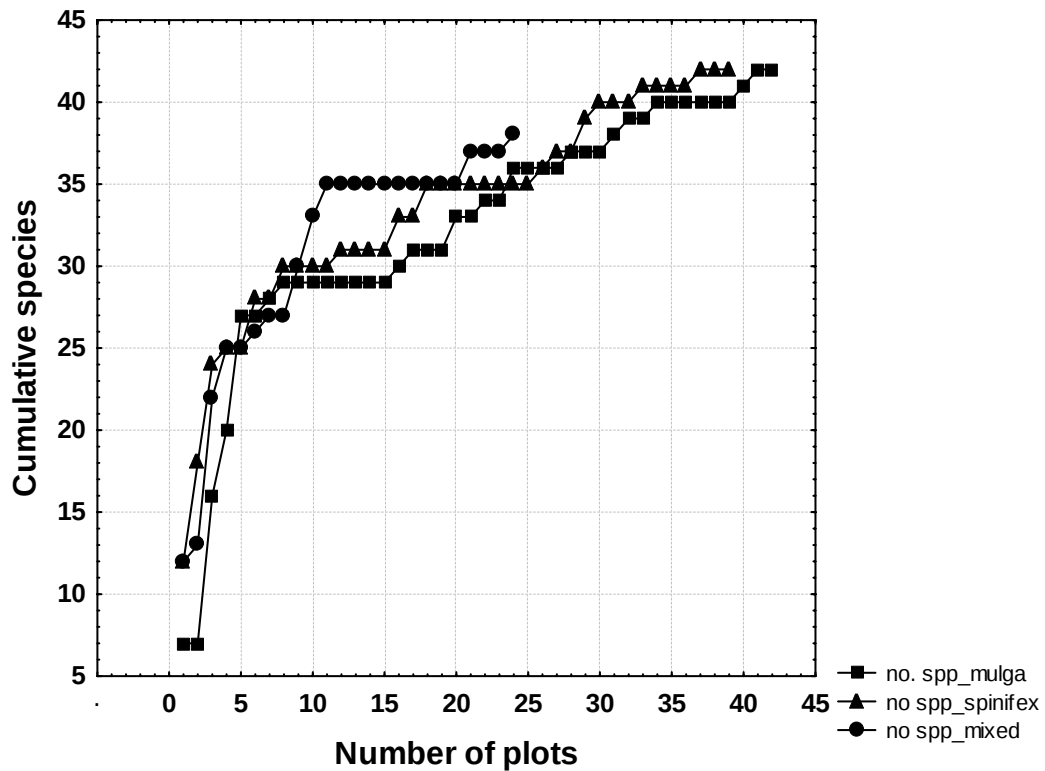


Figure 6.2 The cumulative number of species as plot number increases for Mulga, mixed and Spinifex vegetation.

Indicator species

Species considered especially sensitive to frequent fire and proposed as indicator species of old growth Mulga were all absent from spinifex vegetation but recorded from both Mulga and mixed vegetation (Table 6.1). No effect of fire was found for *Cheilanthes sieberi* and *Aristida obscura* but *Spartothamnella teucrifolia* was significantly more frequent in burnt plots (Table 6.2). There were more tall ‘old’ Mulga trees at sites where *Cheilanthes sieberi* (Mann Whitney *U* Test $P=0.01$) and *Aristida obscura* (Mann Whitney *U* Test $P=0.03$) were present. This was not the case for *Spartothamnella teucrifolia* (Mann Whitney *U* Test $P=0.25$).

Table 6.1 The percent of plots that indicator species were recorded in Mulga, mixed and Spinifex vegetation.

SPECIES	SPINIFEX (n=39)	MIXED (n=24)	MULGA (n=42)
<i>Cheilanthes sieberi</i>	0	33%	57%
<i>Aristida obscura</i>	0	21%	31%
<i>Spartothamnella teucrifolia</i>	0	0	26%

Table 6.2 The percent frequency of indicator species in burnt (in the study period) and unburnt plots.

SPECIES	% in unburnt plots	% in burnt plots	Fisher exact test (P value)
<i>Cheilanthes sieberi</i>	43	51	0.36
<i>Aristida obscura</i>	16	17	0.61
<i>Spartothamnella teucrifolia</i>	11	36	0.03

Conclusions

Individual spinifex plots have a greater diversity of woody species than Mulga plots, but at the landscape scale Mulga and spinifex vegetation were very similar in species alpha diversity. It is possible that Mulga and spinifex vegetation types are equally stable. There was a slight trend for mixed vegetation to have increased woody species richness across the landscape.

The suggested indicator species for ‘old growth’ Mulga were not recorded from spinifex vegetation. The frequency of indicator species in burnt and unburnt plots (for the study period) was not significantly different, except for *Spartothamnella teucrifolia*, which was more frequent in burnt plots. There was a trend for more taller ‘old’ Mulga trees at sites where *Cheilanthes sieberi* and *Aristida obscura* were present.

CHAPTER 7: DISCUSSION



stylized mulga
Warren McCaskill

Fire on the southern edge of the Tanami Desert

During the 25-year period for which fire records were available, spinifex, mixed and mulga vegetation in the study area was burnt on approximately three, two and one occasion respectively. A short period between spinifex fires (2-3 years) was always followed by a longer period before the next fire (15-16 years), yielding great variation in the fire return cycles. I cannot be confident about the typical range of the fire return intervals for Mulga as most plots were burnt only once during the study period. A small number of Mulga plots were repeatedly burnt, the repeat fires occurring in summer. Most fires in any vegetation type were during the warmer half of the year.

Spinifex has been reported to have fire return times ranging from 3-30 years depending on rainfall (Allan and Southgate 2002), and from 5-15 years (Suijdendorp 1981; Griffin 1984). Fire return times in *Acacia*-wooded landscapes have been reported as every 30-50 years (Allan and Southgate 2002), or potentially every 10-50 years (Walker 1981). Fire is possible any season of the year but more likely during the warmer months from September-March (Griffin *et al* 1983; Allan and Southgate 2002). These reports are consistent with results obtained in this study which show that Mulga is burnt less frequently than spinifex.

The differences in fire frequencies between Mulga and spinifex in the study area could be attributable to differences in flammability, rates of fuel accumulation and/or fuel continuity. The fuel in spinifex communities is primarily spinifex itself, which is highly flammable (Latz 1995). Following above average rainfall, this may be supplemented by large amounts of short-lived grasses such as *Aristida* spp. (Griffin 1984; Allan and Southgate 2002), rendering fires at intervals possibly as short as 2-3 years. Spinifex has also been reported to return to 'closed community of hummock grasslands within 2 to 3 years from fire' at which point there was no growth of ephemerals (Suijdendorp 1981). Spinifex accumulates fuel and increases the connectivity of clumps to quite high levels with time (Suijdendorp 1981; Allan and Southgate 2002). In the study area, older spinifex sites had cover scores between 51-75%.

In contrast, Mulga itself is not so flammable and the litter for *Acacia aneura* var. *tenuis* is classified as flammable, both with and without flammable compounds. The fuels to carry fire through mulga vegetation are mostly thought to be annual and short lived perennial grasses, which occur in large amounts for only a short time following high rainfall (Allan and Southgate 2002). The highly variable distribution of fuel, likely related to the heterogeneous soil conditions within mulga soils (Griffin 1984; Griffin and Friedel 1984; Tongway and Ludwig 1989, 1990; Allan and Southgate 2002; Dunkerley 2002), can create highly variable fire burning behaviour inside mulga vegetation.

In summary, the fuel characteristics of mulga and spinifex differ markedly and in a way that much more readily promotes fire in spinifex vegetation. These characteristics are also strongly influenced by rainfall before and between fires. Differential susceptibility to fire is likely to have consequences for the relationship between the two vegetation types.

Contrasts and gradients in the mulga-spinifex mosaic

Floristics

The most striking contrast in the landscape was the sharp delineation of vegetation dominated by mulga and spinifex. Spinifex provides the matrix in which Mulga patches are embedded, suggesting that Mulga has the narrower niche in this landscape.

By far the strongest floristic difference between these two vegetation types was the scarcity of spinifex in Mulga plots, and of Mulga in spinifex plots. The landscape was overwhelmingly characterized by the presence of these two species. Indeed, the mulga-spinifex boundaries did not delineate discrete floristic communities. Most other woody species occurred on both sides of the boundary in relatively low abundance. Removing the influence of the Mulga and spinifex species in the ordination analysis reduced the distinction between the vegetation types and revealed a complex series of subtle floristic gradients.

Mulga soils have been reported to suppress spinifex and regenerating spinifex suppresses mulga seedlings (Nano 2005). Furthermore, shade suppresses spinifex growth (van Etten 1988; Nano 2005). Mulga's systematic use of and conservation for water (Tongway and Ludwig 1990) and mostly unknown chemical/physical combatants of fallen leaf litter may be contributing to Mulga's its ability to exclude spinifex and other species from flourishing within its niche. It seems likely that under current conditions, Mulga and spinifex are highly competitive both with each other and other species.

That the sharp boundary is characterised by just two species suggests that the system drivers can be related directly to their ecology. Analysis by ordination and modelling identified higher fire frequency in spinifex as the strongest environmental correlate of the vegetation types, with some support for a correlation with soil texture and soil surface and biological crusting. The possible role of these factors will be explored in subsequent sub-sections.

Fire

In a previous section, I argued that differences between vegetation types contribute to their markedly different fire regimes. In this section, I consider evidence that the converse is also the case: that fire has a major role in influencing the mulga-spinifex mosaic. A major role for fire in shaping this mosaic was recognised by van Etten (1988), Bowman *et al* (1994), Nano (2005) and Bowman, Boggs and Prior (2007).

Both spinifex and mulga can regenerate from seed and re-sprout after fire, though rates vary with species and the nature of the fire (see *Fire in the southern Tanami Desert* section). Within species, variation in mortality and regeneration is likely to be in response to variation in the frequency, intensity and timing of fires.

Spinifex, including *Triodia pungens* in the study area, almost invariably regenerates vigorously following fire (pers. comm. Peter Latz and Grant Allan). It was observed to mostly resprout. This species has been reported as an obligate seeder in a study at Ayers Rock and to mostly resprout in northern Queensland, with suggestions that resprouting varies according to the nature of fires which in turn vary with rainfall

(Rice and Westoby 1999). No other studies were found that could shed light on the influence of the frequency, intensity or seasonality of the fire for this or other *Triodia* species.

Mulga is frequently killed by fire (Fox 1980; Start 1986; Latz 1995), but can re-sprout in some circumstances, perhaps where fires are less intense. Intense fires are known to stimulate mass germination of Mulga seed (Fox 1980; Hodgkinson and Griffin 1982), although a lack of follow-up rain can destroy the seedling cohort (Hodgkinson 1991). Germination is reported as primarily a function of soil moisture and temperatures (Fox 1980; Hodgkinson 1991). An absence of seedlings after fire has been associated with a presence of seeds in the surface soil (Fox 1980) or alternately as their absence there (Hodgkinson 1991). Very little is known about the soil seed bank dynamics of Mulga and how they may alter with fire.

The variety of Mulga in the study area, *Acacia aneura* var. *tenuis*, is estimated to take 5-15 years to produce seed after fire (NT Ecological Attributes database, unpublished). In a counterpoint to concerns about the adverse effects of fire on Mulga (eg. Start 1986, van Etten 1988, Latz 1995), the variety *tenuis* has been classified as a potential fire weed (NT Ecological Attributes database, unpublished) because of its ability to regenerate and dominate after fire if conditions are favourable.

Bond and Wilgen (1996) provided a general description for the relationship between trees and grass in fire-prone environments in which trees are "held hostage" by grass. It is known as the Gulliver effect. It is argued that highly flammable grass recovers quickly from burning and has rapid growth rates compared to trees which take longer to mature. At the regeneration phase, the 'Gullivers struggle to emerge from the herbaceous layer as juveniles' (Bond and Wilgen 1996 p161). Seedling growth is suppressed and frequent fire eventually kills the Gulliver. In the absence of fire, the Gullivers grow and it is possible that the vegetation will change to woodland.

Spinifex is highly flammable and may expose nearby Mulga to repeated fire at short intervals. Almost all spinifex plots were burnt twice in a short time during the history of fire records in this study. Mulga that germinates in spinifex-dominated vegetation

is likely to be burnt before it produces seed, so fire may eliminate the seed bank and largely prevent the establishment of Mulga in spinifex vegetation.

However, I am less convinced that spinifex fires create many opportunities for the species to colonise mulga vegetation in the study area. Firstly, few Mulga plots were re-burnt at short intervals. My data suggest that spinifex fires frequently do not carry into Mulga. Secondly, as spinifex plots burnt twice in a short time were subsequently not burnt for 15-16 years, I speculate that even if an adjacent stand of Mulga is repeatedly burnt, it is frequently likely to have an opportunity to mature and restore seed banks before the next fire. And as fuels to carry fire in Mulga are generated by high rainfall in the warmer season, there is a reasonable chance that fires will coincide with the high temperatures and adequate soil moisture needed to germinate and successfully establish Mulga seedlings.

In summary, it is likely that mulga is generally maintaining its position in the landscape by successfully regenerating after the lower frequency of fires that enter mulga patches. Soil differences across the mulga-spinifex mosaic may also be involved and will be discussed in the next sub-section.

Soils

The mulga-spinifex boundary sat sharply across a very gradual soil surface textural gradient, and the vegetation types differed in the degree of biological and physical surface soil (non-biological) crusting. Mulga was on slightly heavier textured and less crusted soil on average and spinifex on slightly sandier soil with greater surface crusting, but these differences were far from categoric. I found no difference between vegetation types in pH, nitrates or salinity in surface soil. The texture difference is consistent with the findings of Bowman, Boggs, Prior *et al* (2007). However, van Etten (1988) and Bowman, Boggs, Prior *et al* (2007) found that nitrates were greater in soil under mulga than spinifex. The different finding for nitrates could be because I used a different analytical technique or because nitrate levels are so variable across the landscape.

Because the soil texture gradient was subtle and variable, it is unlikely to be a direct or primary cause of the sharp boundary and distinction between mulga and spinifex vegetation, but it could be a contributing factor. Soil texture differences could also be influenced by fire histories and/or by the vegetation, possibilities that need not exclude soil also contributing causally to the mosaic. There is some evidence from other studies with which to evaluate these possibilities.

Mulga is known to contribute to the condition of soil, increasing surface stability, improving the nitrogen economy and retention of soil moisture (Winkworth 1973; Tongway and Ludwig 1990; Eldridge and Bradstock 1994; Dunkerley 2002). Nodulation occurs in Mulga roots and the nitrogen fixing capacity is thought to contribute significantly to the nitrogen economy of Mulga (Winkworth 1973). In contrast, fire is known to degrade and reduce the clay content of soil (Warcup 1983; Fayos 1997). The higher levels of soil crusting in the spinifex vegetation occurred notwithstanding more frequent mobile surface sand which may have covered the crusting, causing it to be underestimated. Soil crusting is likely to reduce penetration of moisture and inhibit the emergence of seedlings (Belnap *et al* 2001).

Thus, there is a real possibility that the mulga-spinifex mosaic is a self-reinforcing system in that mulga promotes soil favourable for its growth - and excludes fire, whilst high fire frequencies degrade soils in spinifex areas. The reinforcement is complete if, as a result, mulga is better able to regenerate following fire where it had previously been able to modify soil conditions in its favour, and where it regenerates most vigorously it is subsequently more likely to exclude fire.

I interpret the gradual soil gradient as characteristic of the ecocline boundary type (see introduction). Forman (1995) suggested that natural disturbances could sharpen an existing boundary, increasing contrast in the landscape. Van Etten (1988) also found gradual soil gradients and suggested it indicated an ecocline boundary type despite sharp mulga-spinifex boundaries.

Biological crusting may also be part of, and perhaps contribute to the reinforcement of existing vegetation. The species composition of the biological crusting observed in this study may be mainly cyanobacteria (pers. comm. David Eldridge), with darker

samples representing greater concentrations of cyanobacteria and maybe more species. Sandy soil inhibits filament growth (Belnap and Eldridge 2001), and since sandiness is associated with higher fire frequencies in this mosaic, the lower level of biological crusting in spinifex could be the product of frequent fire (Eldridge and Bradstock 1994). Furthermore, biological crusting may recover more rapidly after fire in Mulga than spinifex because it is able to develop and diversify better with the protection of shrub and tree canopies that provide shade and reduce wind speeds at the soil surface (Danin *et al* 1989).

In summary, the soil textural gradient is associated with the mulga-spinifex mosaic and likely to be influenced by both vegetation and fire. Contrasts in biological and soil crusting could alter soil conditions and contribute to the ability (or inability) of Mulga to maintain itself in the face of fire.

Plant functional traits

The woody species other than mulga that occurred in the study area not only mostly occurred in both mulga and spinifex vegetation, but generally shared functional life history and regeneration traits. There was a paucity of obligate seeders among the more frequently recorded woody species, *Acacia adsurgens* (associated with spinifex) being the only example. This is in contrast to Nano (2005), who found obligate seeders to be mostly associated with Mulga habitat, but consistent in that re-sprouters (and variable re-sprouters) did not favour one habitat.

The lack of obligate seeders in mulga vegetation is somewhat surprising given that the woody species most frequent in mulga mostly had shorter post-fire seeding times than Mulga (as well as an ability to re-sprout). It is less surprising that obligate seeders were absent from spinifex given high fire frequencies in that vegetation. Nevertheless, all woody species present in spinifex vegetation had both the capacity to seed rapidly after fire and to re-sprout. This illustrates the generality that all species present in the mosaic, whether in spinifex or mulga, must be able to persist in a fire-prone ecosystem.

The low abundance of all woody species other than mulga (and the low abundance of spinifex) in mulga vegetation may be the result of Mulga's ability to effectively suppress or compete with other species (see floristics). Along with coping with fire, re-sprouting traits may ensure persistence in a (mulga) environment where establishment from seed is difficult for any competitor - the persistence niche of Bond and Midgley (2001).

In summary, all woody species in the study area had seed biology and regeneration strategies that allow them to live in a flammable landscape. Re-sprouting may favour persistence in the face of intense competition from Mulga as well as from fire.

Fire and the structure of Mulga

The analysis of height diversity showed that mulga with more tall (and thus, presumably, old) trees, tended to be 'inside' the Mulga patch away from the boundary, and to have the most even representation of Mulga trees in all size classes. Mulga at or near the boundary tended to experience more frequent fires and/or more summer fires.

An abundance of seedlings in the study area was associated with recent fires, and a stand of Mulga with the same height is assumed to be the result of a mass germination following a fire (eg. Fox 1980). Mulga can also germinate without the stimulation of fire (Preece 1971; Nano 2005), but such germination is scattered rather than mass. Scattered seedlings were noted in this study and some germination may have occurred independent of fire. Stochastic fire behaviour and post-fire rainfall are other factors that may contribute to variable mulga demographics and complicate the interpretation of structural snap-shots such as undertaken in this study. However, most of the mulga structural profiles featured an abundance of a single height class and consequently are likely to be the result of germination following fire. Only a small proportion of the landscape had 'older' mulga that was structurally diverse. Thus, most of the mulga vegetation of the southern Tanami Desert appears to have been structured by fire. However, fire may not be pre-eminent in structuring mulga in all central Australian environments, as Nano (2005) frequently found Mulga

seedlings and younger age classes even in stands otherwise dominated by a single, taller height class..

Mass recruitment may permit Mulga to develop dense canopies and dominate the landscape, thus inhibiting spinifex and reinforcing boundaries. It is unclear whether this mechanism and the resulting uniform-age stands are viable in the longer term. It is possible that reduced structural diversity may reduce options (seeding *cf* re-sprouting) to cope with future fires.

A small number of sites in this study had numerous fire-killed trees and no seedlings, raising doubts about the ability of Mulga to persist there. These sites were associated with a short fire-return time and are consistent with the notion that Mulga is frequently dependant on maturation to produce seed in-between fires. This is also consistent with Bowman et al's (in press) suggestion that, whilst most mulga-spinifex boundaries in the study area are stable, small-scale changes in the form of conversion of mulga to spinifex are occurring.

In summary, Mulga on the boundary with spinifex is more frequently burnt, generating younger, less structurally diverse mulga. Changes in fire regimes are likely to alter the structure of mulga stands, the biodiversity implications of which are considered in the next section.

Biodiversity implications

The species richness of woody plants was higher in spinifex than mulga vegetation at the local scale, but similar at the landscape scale. Higher species richness at the plot scale in spinifex could arise because the woody plant niche is otherwise vacant in spinifex vegetation but filled by a potentially highly competitive species – Mulga – elsewhere.

It is possible that habitat segregation of woody species in this landscape may only be evident at a considerable distances from the boundary and was thus not detected in this study in which sampling occurred within 500m of the boundary. The slight trend for higher species richness in mixed vegetation is consistent with the suggestion that

ecocline boundaries generally have greater species numbers (van der Maarel 2006). Few species were exclusive to either mulga or spinifex vegetation, and none to mixed vegetation.

It has been suggested that the grass *Aristida obscura*, the fern *Cheilanthes sieberi* and the woody long-lived perennial *Spartothamnella teucriflora* are associated with long unburnt Mulga (Latz in press). In this study, these species were found only in mulga, but occurred in a range of mulga structural groups including some interpreted as having been burnt recently and more than once. Clearly, these species have some tolerance of fire, although the degree of tolerance and whether populations have changed in response to recent changes in fire regimes remains unknown.

The lack of long unburnt ('old growth') Mulga in the study area has implications for structural diversity within Mulga habitat, which may have implications for some bird species (Woinarski and Recher 1997). However, no evidence was obtained in this study that there are any implications of current fire regimes for plant species. Further study may be warranted.

No woody species other than Mulga was abundant in this landscape, so that landscape function is overwhelmingly dependant on the energy flow and matter recycling of Mulga and spinifex. However, the other species, even the infrequent ones, may become critical in the functioning of this landscape under changed conditions (Grime 1998). In this context, the species richness of the dominant communities is valuable and could well play a critical role in future changes that emerge in this environment (van der Maarel 2006).

A dynamic relationship

Is the mulga-spinifex mosaic stable?

There is evidence that mulga-spinifex mosaic in the study area have had generally stable boundaries for the last half century (Bowman, Boggs and Prior 2007) and indeed for the last 1000 years (Bowman, Boggs, Prior *et al* 2007). This may be also be true for a wider area of central Australia (Bowman *et al* 1994; Nano 2005). Given

the frequency of fire in the region and the demonstrable sensitivities of Mulga to it, these reports are perhaps surprising, even more so in that these vegetation types are often interspersed at a remarkably fine scale.

The vegetation boundaries in the study area were mostly sharp and the occurrence of Mulga and spinifex mostly exclusive to opposite sides of the boundaries, suggesting a remarkable incompatibility. This incompatibility does not appear to represent any marked differences in realised or fundamental niche with respect to soils, so it seems likely that some form of competitive exclusion is involved. The relatively dense mulga canopy inhibits spinifex growth through shading (van Etten 1988, Nano 2005). Mulga soils suppress the growth of spinifex, and spinifex suppresses mulga seedlings (Nano 2005). These antagonisms are, I propose, enhanced in the landscape by feedback loops involving soils and fire.

I have previously cited (in *Soils* section of this chapter) evidence that Mulga enhances soil but fire degrades it. It is also clear that spinifex has much greater tolerance of fire than does Mulga. By its flammability, spinifex encourages the spread of fire, whilst in comparison, Mulga and particularly dense Mulga that may suppress the growth of annual grasses, inhibits it. Enhancement of the soil may permit Mulga to regenerate more rapidly after fire at sites it previously occupied than in areas previously occupied by spinifex, thus not only re-establishing its dominance but reducing the likelihood of subsequent incursions of fire from nearby spinifex stands. Thus, subtle and non-discrete differences in soil preferences are consolidated into self-perpetuating stands of antagonistic species.

It is noteworthy that the mixed vegetation type is scarce in the study area. It may well be a short-lived transitional state in which, given current high fire frequencies, mulga is being converted to spinifex. Were fire excluded, Mulga might well be able to establish dominance in mixed vegetation to the eventual exclusion of spinifex.

Given the evidently pre-eminent role of fire in maintaining this mosaic, it follows that major changes in fire regimes could shift the balance between spinifex and mulga.

Past - present – future

Acacia is thought to have appeared in Australia no earlier than the Miocene, but nevertheless has had a long history of speciation in Australia. Seasonal climates and associated fires in the mid-Tertiary may have encouraged its evolution and diversification (Pedley 1973; Griffin and Hodgkinson 1986; van Oosterzee 1991). The appearance of Mulga as a major component of the arid-zone vegetation is argued to have happened around 13000 years ago (Smith *et al* 1995), possibly and rather ironically given current circumstances, aided by an increase in burning from early Australians (Latz 1995). Spinifex, endemic to Australia, probably dates from the break-up of Gondwana (van Oosterzee 1991), previously less common (Jacobs 1982) and has a long evolutionary relationship with fire (Suijdendorp 1981).

It has been suggested that the current Mulga/spinifex mosaic may be a recently created phenomenon, developed and maintained by indigenous burning practices (Start 1986) that are thought to have largely prevented extensive, frequent and hot wildfires (Kimber 1983; Griffin and Hodgkinson 1986; Latz 1995; Smyth and James 2003). This may have protected Mulga from fire intensities and frequencies beyond its tolerance (Start 1986; Allan and Southgate 2002).

Concern that the recent replacement of traditional Aboriginal burning practices with less frequent but more intense and extensive fires (Hodgkinson, 2002) may be causing a retraction of Mulga (Griffin and Hodgkinson 1986; Start 1986; Krebs 1989; Latz 1991; Start *et al* 1991; Latz 1995) may not be warranted (van Etten 1988; Bowman *et al* 1994; Nano 2005). However, it is conceivable that current fires regimes may be driving a structural shift within mulga that has undesirable consequences for biological diversity and possibly, in the longer term, for Mulga's capacity to persist. This and previous studies are far from the last word on the stability or otherwise of mulga - spinifex boundaries and their implications for biodiversity and management.

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APPENDIX 1: Examples of different soil surface descriptors

Sand



Soil crust



Early biological crust



Well developed biological crust



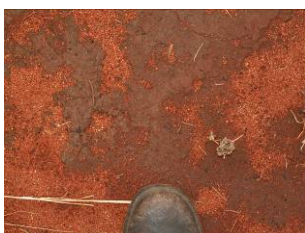
Fragmented



Slightly continuous



Moderately continuous



Highly continuous

