Optimum Management of White Cypress Pine (*Callitris glaucophylla*): Individuals to Landscapes

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A thesis submitted for the degree of Doctor of Philosophy

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December 2008

For Monica

28/11/1984 – 07/01/2009

A contribution to dreams cut short.

Declaration

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any assistance received in the preparation of this thesis, as well as all sources consulted have been duly acknowledged in this thesis.

The contribution of all co-authors to publications included as part of this thesis has been identified where required and does not exceed the usual assistance that would be expected in the role of supervisor, statistical advisor, etc.



Melinda T. McHenry

December 2008.

Acknowledgements

I am indebted to my supervisors Dr. Brian Wilson, Dr. Peter Lockwood, Dr. Chris Guppy and Professor Brian Sindel. I have been most fortunate to have received unwavering support from my supervisory team, each of whom have supported me throughout the logistical, technical and financial challenges central to the completion of such a project. I would especially like to thank Dr. Wilson for his ongoing assistance with all aspects of the project and for providing me with industry exposure, which has helped broaden my understanding of the challenges facing natural resource management.

This project would never have been completed without the substantial technical assistance provided by John Lemon, who I now consider to be a great friend even despite our heated conversations about soil sampling in even hotter weather! At this point I must also thank Andrew Harrison for giving up many weekends and holidays to assist me with sampling and menial laboratory tasks. I am eternally grateful for Andrew's technical expertise and patience. Finally, to Christiaan O'Brien and Stephen Parker who have remained great friends and who managed to stay smiling even whilst sieving over 1000 litter samples!

To the numerous contributors to this research, I extend my sincere thanks. Leanne Lisle (UNE), David Donnelly and Vicki Fermor (NSW Department of Environment and Climate Change) provided substantial laboratory and technical expertise to various sections of the project. Greg Chamberlain and David Edmonds (UNE) assisted with the management experiment. Dr. Lachlan Copeland (UNE) lent his enormous knowledge of NSW plants to the management experiment and Dr. Ivor Growns (NSW Department of Water and Energy) and Dr. Matthew Tighe (UNE) applied their equally substantial statistical knowledge to some very challenging data throughout the project.

I would like to thank the staff in the former NSW Department of Natural Resources (now DWE, DECC and the Catchment Management Authority) building on campus for their support and assistance throughout the project, especially Dr. Ian Oliver, Mr. Alan Ede, Ms. Tara Schalk, Ms. Sally Croker and Mr. Mark Dahm. A special mention must go to Dr. Chris Nadolny for his ongoing interest in the project and for always being on hand to provide answers to my questions. Thanks must also go to Dr. Nadolny for always being the source of stimulating discussion on many environmental issues.

Finally, special thanks must go to the landholders who have allowed me access to their properties and their homes for the past four years. Bill and Narelle Croker and The Hynes Family also provided me with historical data about their properties and the region. Bill and Vicki Newton and their children have become great friends and have assisted in every way from feeding hungry field assistants, looking after the children and even assisting with field work themselves.

In the final stages of this project I made the transition to the Agronomy Department at UNE and found everyone to be most welcoming and supportive. I am especially grateful to Dr. John Stanley and Dr. Paul Kristiansen for some philosophical and technical discussions of the topic, and also to Craig Birchall and Elizabeth Davies for assisting with the document production process.

After a project like this one often considers their faith and their good fortune. I have been blessed with the most beautiful children that any person could wish for, Yvette and Pearce. There have been times in which it has been a struggle to maintain a balance between work and family, but I am never conflicted. This is for you my darlings - I owe everything that I have achieved to the joy of having you in my life.

Abstract

Woody vegetation thickening and encroachment is a global issue of both environmental and economic significance. On the North Western Slopes and Plains of New South Wales, Australia, the indigenous conifer *Callitris glaucophylla* Joy Thomps. & L.A.S. Johnson (White Cypress Pine) regenerates prolifically, especially in previously cleared agricultural landscapes. The species is recognised in state legislation as '*Invasive Native Scrub*' and strategies to manage the species in a manner that *improves or maintains* on-farm environmental condition are now required by law. The primary objective of this study was to address some of the present knowledge gaps that exist regarding the role and function of the species in a range of configurations in agricultural landscapes of the region. A secondary objective was to draw upon data resulting from this project to suggest optimum management strategies for the species under a variety of scenarios. The investigative approach taken in this study employed a combination of field surveys, field experiments and glasshouse trial, each of which were concerned with describing and/or manipulating the effects of the species on soil and vegetation parameters.

As a prelude to this project, a small pilot study was used to identify soil and vegetation parameters most likely to respond to changes in the management of the species. This study used a paired site approach to revisit sites thinned or maintained as controls since 2000 by Greening Australia and compared them with adjacent cleared areas as yet un-colonised by *C. glaucophylla.* In general, soil and vegetation parameters varied due to site and land-use or their interaction. There was a general trend of increased litter cover from cleared zones through to control zones across all sites, whilst vegetative groundcover decreased with increasing tree cover. The diversity of vegetative groups was linked to site effects. Soil C, N, S and ext. P were generally more abundant in the mineral soil of treed areas and were

significantly less abundant in cleared zones, although soil pH was significantly more acid in control plots than thinned or cleared areas. The study also identified two possible economic benefits of the species for landholders. The growth of trees in thinned plots in the five years since management suggested that it may have farm-forestry potential. This growth, in conjunction with the carbon content of all other site components resulted in an estimated total site carbon that was much higher in thinned and control plots than cleared areas and hence the carbon trading potential for the species in a agricultural setting was also suggested. The results of this study indicated that, for the parameters studied, thinning maintained environmental condition.

The *New South Wales Native Vegetation Act 2004* ('The Act') regulates the management of dense *C. glaucophylla* on the North Western Slopes and Plains of NSW. Individuals and stands can be managed freely provided that they have grown since 1990, and those individuals existing prior to 1990 which require clearing permission and must satisfy the maintain or improve test. Some stakeholders are opposed to the guidelines of the act because mature trees, which existed prior to 1990, potentially supply much more seed to the surrounding managed pasture than juvenile, post-1990 'regrowth'. Other stakeholder groups also believe that the species is inherently detrimental to pasture productivity and soil health, especially soil stability. The first two field surveys in this study were designed to describe the effects of *C. glaucophylla* trees on soils and vegetation in two spatial configurations (individual trees and dense stands) and for individual trees, two age / size classes (small/juvenile and large/mature).

There existed localised enhancements beneath the canopies of both small and large trees for soil that were driven primarily by soil extractable phosphorous, carbon and pH as well as litter biomass. These canopy enhancements were spatially restricted to the radius of the tree canopy, that is, smaller trees had a smaller zone of influence. It appeared from the results of this study that trees employed the 'biological pumping' mechanism that increased surface soil

pH via the deposition of anion-rich litter. Vegetative cover was reduced next to trees of both sizes although there were large site-related fluctuations in groundcover due to weed incursions. The potentially large seed sources of large trees as well as the effect of individual trees on pasture cover were areas of concern worthy of further study.

In dense stands it was difficult to relate soil and vegetation spatial patterns to tree distribution and tree size. Across all study sites, only one strong positive relationship existed between litter biomass, soil pH and tree size/distribution, at the relatively flat Yallaroi site. Again the biological pumping mechanism was proposed to explain this relationship. The strong negative effects of stand intra-specific competition resulted in a net decrease in vascular plant cover in the understorey, which, combined with the sloping topography of most of the study sites, presumably resulted mass transport of litter away from the stand during rainfall events. Acidic, lower nutrient soils beneath dense stands relative to the canopy zone of individual trees and even adjacent managed paddocks suggested that the lack of accumulated litter interfered with the biological pumping process. Therefore, strong competitive interactions within dense *C. glaucophylla* populations and between stands and understorey plants created nutrient depauperate zones with adverse outcomes for ecology and production.

The processes underpinning 'lock-up' (extremely slowed growth of individuals in a dense stand) and the effects of plant density on soil fertility and nutrient uptake were investigated further in a glasshouse experiment which compared plant phenology and plant/soil nutrient stature in three different planting densities (one, twenty-five and forty seedlings per pot). Growth and demographic analysis revealed that high-density stands approached 'lock-up' by the end of the 630-day trial, and nitrogen uptake in high-density stands slowed substantially, indicating nitrogen limitation. Instead of population regulation via self-thinning, individuals in high-density stands exhibited a 'plastic' morphological response, increasing root: shoot ratios and maintaining extremely slow biomass increase in response to declining soil resource

levels, and limiting lateral foliage growth to minimise spatial interference. Limited size variation of individual seedlings within pots, slow growth and negligible mortality rates suggested that competition between *C. glaucophylla* plants in high density stands was almost exclusively for below-ground resources. For this reason, it was concluded that intra-specific competition in high density stands resulted in limited size variation, and hence competition and nutrient acquisition in dense stands occurred independently of plant size (size symmetric competition). These results had very important implications for the field, because without the capacity to interfere with each other spatially, individuals in dense *C. glaucophylla* populations are unlikely to self-thin and hence require active management for population maintenance.

The final investigation in this project assessed the short-term (almost three-year) effects of thinning, clearing and retaining dense stands with or without periodic grazing from domestic livestock. Both thinning and clearing resulted in increases in soil C, N, ext. P and higher soil pH, irrespective of grazing regime, and this was attributed to the retention of felled timber on the soil surface, which was a progressive source of nutrients to the soil. Vascular plant cover increased substantially following thinning and clearing, but the composition of the understorey changed over time and gradually many species were replaced by the invasive exotic perennial Coolatai Grass (*Hyparrhenia hirta*). This effect was more severe in un-grazed plots, which lacked 'intermediate disturbance regimes' from grazing animals, who reduced the severity of *H. hirta* infestations and therefore maximised species richness. Conversely, reductions in groundcover in grazed plots coincided with an increase in *C. glaucophylla* re-establishment relative to un-grazed plots. It was concluded that thinning and clearing dense *C. glaucophylla* stands only produced substantial environmental benefits if soil stability and adequate groundcover were maintained. On-going management of secondary weed incursions and regeneration events were required in order to maintain a managed state and prevent transition back to a dense woody state.

In conclusion this study provided new insight into the impacts of *C. glaucophylla* regeneration at a variety of spatial scales, from individuals to landscapes. The key findings were:

1. At the level of individual tree, plants enhance their surrounding environment in a manner analogous to many other tree species worldwide, but the risk of prolific seedling re-establishment into surrounding paddocks is high if adequate groundcover is not maintained.
2. Nutrient cycling and surface soil chemistry in dense stands depends heavily on the fate of litter. The effects of intra-specific competition most likely impede litter production, and any litter that is produced is often lost due to lateral transport and the absence of vascular plant cover. Hence there is an anisotropic distribution of resources in dense stands that may result in perpetual nutrient deficits.
3. This study has demonstrated that 'lock-up' is a real process which enables individual plants to persist in low-nutrient environments, and that the factors most limiting to plant growth at high densities most likely soil nitrogen and hence the temporal availability of water. High survival rates and reduced growth rates of individuals in dense stands result in environments unsuitable for sufficient plant cover to persist in the understorey.
4. Treatment of stands through thinning and clearing maintains or improves upon the environmental condition of dense stands, however the long-term benefits are negligible if felled timber is not retained, and grazing management is poor.

This thesis has provided new insight into the ecological processes governing the spatial distribution of resources in agro-ecological landscapes where *C. glaucophylla* comprises a substantial component of the over storey vegetation community. Further work must now concentrate on nutrient cycling and its role in agro-ecological landscape function.

Publications Arising from this Thesis

McHenry MT, Wilson BR, Lemon JM, Donnelly DE and Growns IO (2006) Soil and vegetation response to thinning White Cypress Pine (*Callitris glaucophylla*) on the north-western slopes of New South Wales, Australia. *Plant and Soil* **285**: 225 -235.

McHenry MT, Wilson BR, Lockwood PV, Guppy C, Sindel BM, Tighe M, Growns IO, Lemon JM (2009) The impact of individual *Callitris glaucophylla* (White Cypress Pine) trees on soils and pastures on the north-western slopes of NSW, Australia. *The Rangeland Journal* **31 (3)**: 1-21.

McHenry MT, Tighe M, Wilson BR, Lockwood PV, Guppy C, Sindel BM (2009) Restoration barriers to the management of dense White Cypress Pine (*Callitris glaucophylla*) regeneration on agricultural land in Australia. *Journal of Vegetation Science* (in press).

List of Abbreviations used throughout the Thesis

GENERAL ABBREVIATONS

INS	Invasive Native Scrub
NSW	New South Wales (Australia)
NWS	North-Western Slopes (of NSW)
C	Total Carbon (%)
	as determined by LECO
N	Total Nitrogen (%)
	as determined by LECO
S	Total Sulfur (%)
	as determined by LECO
Ext. P	Extractable Phosphorus (mg/kg)
	as determined by Olsen method
LDW	Litter Dry Weight (g)
DBHOB	Diameter at Breast Height (1.3 m)
	determined Over Bark

STATISTICAL ABBREVIATIONS

ANOVA	Analysis of Variance
ANCOVA	Analysis of Co-Variance
GLM	General Linear Model
df	Degrees of Freedom

Levels of significance for critical *f*- and *t*-tests:

*	$p < 0.001$
**	$0.001 < p < 0.010$
***	$0.010 < p < 0.050$

Please be advised that this thesis contains chapters which have been either published or submitted for publication.

The accepted version(s) of the following chapter(s) have been retained:

McHenry, M. T., Wilson, B. R., Lemon, J. M., Donnelly, D. E., & Growns, I. G. (2006). Soil and vegetation response to thinning White Cypress Pine (Callitris glaucophylla) on the North Western Slopes of New South Wales, Australia. *Plant and Soil*, 285(1-2), 245–255. doi:10.1007/s11104-006-9011-9

McHenry, M. T., Wilson, B. R., Lockwood, P. V., Guppy, C. N., Sindel, B. M., Tighe, M. K., … Lemon, J. M. (2009). The impact of individual Callitris glaucophylla (white cypress pine) trees on agricultural soils and pastures of the north-western slopes of NSW, Australia. *The Rangeland Journal*, 31(3), 321. doi:10.1071/rj08052

No proof of publication could be located for the following chapters:

Chapter 1: Introduction
Chapter 3: Study Area
Chapter 5: Regrowth Trees
Chapter 6: Demography
Chapter 7: Management Experiment
Chapter 8: Summary and Conclusions

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Chapter 1. Introduction

1.1. General Introduction

Vegetation thickening has occurred in a range of environments across the world (Boer and Stafford Smith 2003; Eldridge and Simpson 2002; Gifford and Howden 2001; Harrington 1991; Johnson *et al.* 1993; Walker and Noy-Meir 1982; Williams and Ashton 1987). Vegetation thickening occurs as part of a natural phase of disturbance and recovery (Gifford and Howden 2001). Ecological disturbances such as altered grazing regimes and changes in the populations of introduced and native herbivores (Boer and Stafford Smith 2003; Eldridge and Simpson 2002; Walker *et al.* 1981), the exclusion or re-introduction of fire (Boer and Stafford Smith 2003; Harrington 1991) and climate change (Johnson *et al.* 1993) have been proposed as causes of vegetation thickening in managed landscapes. In addition, woody vegetation is now encroaching on environments that may not previously have supported such populations and communities in the past (Gifford and Howden 2001).

Over much of eastern Australia, extensive clearing for agriculture and development has resulted in an overall decline in native vegetation cover (Martin *et al.* 2004; Reid and Landsberg 2000). In some regions however, these modifications have also created conditions that encourage vigorous regeneration of native trees and shrubs. Dense, mono-specific stands of native trees and shrubs (e.g. *Eucalyptus* spp., *Eremophila* spp. and *Callitris* spp.) (Plate 1) now occupy large areas of the agricultural landscape. This regeneration is considered to be a significant environmental problem especially in the dryland grazing/cropping regions west of the Great Dividing Range (Cobar Vegetation Management Committee 2006). Increasingly, published research highlights and lends support to the notion that dense woody vegetation restricts routine agricultural activity, due to the suppression of ground-cover, depletion of water and nutrient resources for pasture plants, environmental degradation and soil erosion (Booth 1985; Burrows 1986; Eldridge *et al.* 2003; Harris *et al.* 2003)



Plate 1. Woody vegetation thickening in North-West NSW; left – *Eucalyptus coolabah* Blakely & Jacobs near Rowena (Image courtesy of John Lemon), right – *Callitris glaucophylla* near Tamworth. Both species are believed to impede normal farming activities and are on the *Invasive Native Scrub* list in various parts of NSW.

In NSW, the appropriate management of native vegetation is guided by the *New South Wales Native Vegetation Act* (2003). A considerable focus of this legislation has been directed at native species which are considered to be *invasive native scrub* (INS), that is, native species which have spread rapidly within their centre of origin and:

1. have invaded plant communities previously devoid of the species, and;
2. may regenerate prolifically following natural or artificial disturbances such as fire, clearing or grazing.

An important legislative distinction has been made between 'remnant' vegetation, and vegetation which can be managed with few restrictions if it can be proved that it is *regrowth* which has established on previously cleared land after 1990 (1983 in the NSW western division). Clearing of pre-1990 INS must be approved through a Property Vegetation Plan (PVP). Treatments of INS approved with PVP should *improve or maintain* environmental outcomes (the 'environmental test'). In 2008, 44 species were listed as INS in NSW, mostly in the western and central western regions of the state. For most of these species, there are few demographic data available to measure the success or failure of a regrowth management activity against, nor is it clear which treatment strategies would represent the best compromise between ecological diversity, ecosystem stability and agricultural productivity.

In order to manage INS effectively, it is necessary to examine the role and functions of native vegetation and regrowth in the landscape and to assess the impacts of retaining such vegetation. By clarifying the role of trees with respect to soil condition, ground-storey vegetation and other landscape function components, more effective methods can be developed to optimise the integration of native vegetation into production systems. In this thesis I present research findings relating to the ecology and management of a common INS species *Callitris glaucophylla* Joy Thompson and L. A. S. Johnson[1] (Cupressaceae – 'White Cypress Pine') in agricultural landscapes of north-west NSW, at a range of spatial scales from individual trees through to dense stands.

1.2. *Callitris glaucophylla*

1.2.1. Ecology, distribution and population structure

Callitris glaucophylla is an indigenous Australian conifer, with a distribution across all mainland states in Australia, primarily in the 350 – 700 mm rainfall belt (Figure 1). Individuals can tolerate extreme periods of drought (Attiwill and Clayton-Greene 1984; Bowman and Latz 1993; Thompson and Eldridge 2005b; Zeppel and Eamus 2008), but are susceptible to water-logging (Harris *et al.* 2003; Humphreys *et al.* 2001) and may also be fire intolerant (Bowman and Harris 1995). Although the species is sometimes found on higher nutrient clays, it is more common on well-drained sands and rocky skeletal soils, often of low nutrient status (Hart 1995; Johnston and Jennings 1991; Thompson and Eldridge 2005b).

Individuals may grow to 30 m tall and have a distinct conical shape that is modified in dense stands (Lacey 1973). Seeds are produced in 6-valved cones (Garden 1956) which are dropped e*n masse,* especially in early summer (Nov-Dec) (Lacey 1973) (Plate 2).

[1] *Callitris glaucophylla* Joy Thompson & L.A.S. Johnson is the recognised nomenclature for White Cypress Pine (after Thompson & Johnson 1986). The species has previously been known as *C. hugelii* (Carriére) Franco (Garden 1957), *C. columellaris* F. Muell (Blake 1958) and *C. glauca* R. T. Baker and H. G. Sm. (Thompson 1961). The latter was deemed to be a misapplied synonym that had been later corrected by the original authors (Brown *et al.* 1908, 1913 in Thompson & Johnson 1986).

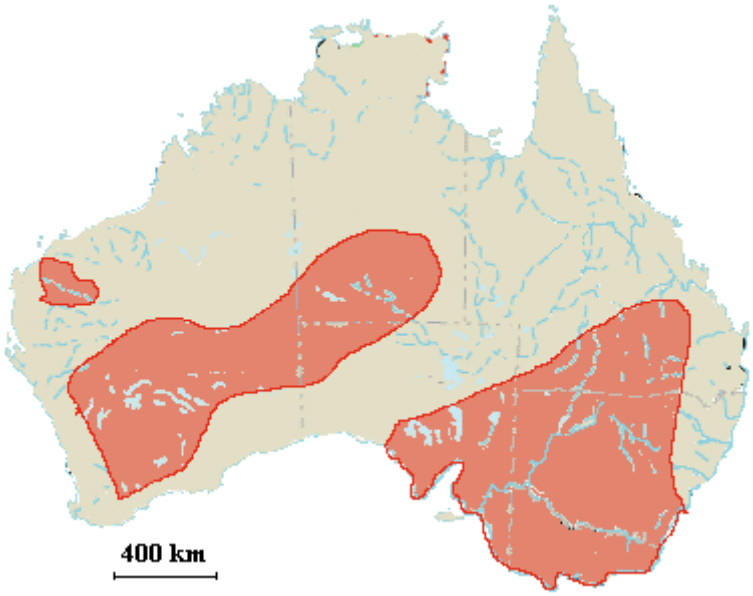


Figure 1. Distribution of *Callitris glaucophylla* (red) across mainland Australia (after Bowman and Latz 1983).

Extensive use has been made of *C. glaucophylla* timber in construction (Curby *et al.* 2001) due to its structural quality (Grant *et al.* 1991), resistance to termite infestation (Gay and Evans 1968; Thompson and Eldridge 2005b) and its prevalence in areas of limited rainfall and soil fertility. *Callitris glaucophylla* has often been maintained by commercial logging as the dominant species in low closed forests in NSW and QLD (Horne 1990; Johnston and Jennings 1991), although a significant reduction in the use of the species for timber products occurred after the rezoning of the Pilliga State Forests (NW NSW) in 2005 for conservation purposes.

Callitris glaucophylla exists naturally as a solitary tree in savannah land or as a canopy species in Eucalypt-dominated sclerophyll forest or woodlands (Bowman and Harris 1995). There are conflicting opinions regarding the pre-European community composition and population density of Eucalypt woodlands of the North Western Slopes and Plains of NSW of which *C. glaucophylla* is now a significant component (Norris *et al.* 1991; Rolls 1981). Prior to European settlement, most *C. glaucophylla* woodland probably had a multiple-age structure



Plate 2. The cones are pivotal to the identification of *C. glaucophylla* (foreground of bottom image). The outer covering is smooth and shiny (top left) and the columella (central stalk in the freshly opened cone – top right) is a single lobe.

where existing large trees would limit the regeneration and growth of other trees and shrubs beneath them, which was maintained by natural disturbances and self-thinning. During the past two centuries however, woodlands have been cleared or substantially altered over extensive areas of the state and subsequent agricultural land management has produced relatively large areas where conditions are suitable for seedling establishment. As a consequence, large stands of single-aged regrowth are now more common in the landscape (Eldridge et al. 2003) (Plate 3).



Plate 3. (top) Dense *C. glaucophylla* at Upper Moore Creek, near Tamworth. Photo: John Lemon; (bottom) A thinned, single-aged stand at Emerald Hill.

1.2.2. Factors influencing regeneration of C. glaucophylla *in agricultural landscapes*

Two contrasting regeneration patterns and therefore management regimes exist for *C. glaucophylla* in eastern Australia. In the south of the state, which has a winter-dominant rainfall pattern ('Mediterranean' climate), spontaneous regeneration of species such as *C. glaucophylla* is rare and various strategies have been employed in order to reverse tree decline (Spooner *et al.* 2002; Spooner and Briggs 2008). Most recently, pine populations on sand hills in the Riverina, Murray-Darling depression and South-Western Slopes bioregion of NSW have been declared endangered ecological communities under the *NSW Threatened Species Conservation Act 1995.* In contrast, to the north of the state and in southern QLD, where the climate is increasingly dominated by summer rainfall, dense *C. glaucophylla* stands are a prominent feature of many agricultural landscapes and therefore require different management regimes. The reasons for the abrupt change in the behaviour of the species are unclear, but it is likely that a combination of ecological characteristics, different pastoral activities and contrasting climatic regimes may contribute to the regeneration patterns of *C. glaucophylla*. In this chapter and throughout the thesis, the focus of the discussion and research is on the northern part of the state, where *C. glaucophylla* is listed as INS.

C. glaucophylla is thought to have become dominant in NW NSW agricultural landscapes following the cessation of Aboriginal fire regimes, a decline in rabbit populations and the introduction of stock, which tend not to graze on seedlings (Lacey 1972; Rolls 1981). However, evidence from the mapping of early pastoral leases and reports from early explorations and surveys of the North-Western Slopes and Plains suggest that there were always tracts of *C. glaucophylla* woodland that were considered 'very dense' (Norris *et al.* 1991).

Colonisation of previously cleared agricultural lands appears to be episodic, and has been linked to a range of climatic and land management events. Two significant regenerative episodes occurred in north-west NSW in the late 1800s and in the 1950s, which were preceded by concurrent years of above-average rainfall and a decrease in burning and grazing on the North-Western Plains (Horne and Robinson 1987; Lacey 1972). The introduction of myxomatosis to control rabbits, which graze on seedlings, in the early 1950s was also thought to be a significant factor in the 1950s regeneration event (Lacey 1972). Since the 1950s, localised germination events have occurred episodically across much of northern NSW (Norris *et al.* 1991). Mass germination and seedling survival is also thought to be related to cooler than average summer seasons and regular rainfall during establishment (Adams 1999).

Following a cool winter and prolonged spring rainfall, prolific seedling establishment is followed by rapid growth of individuals. Often, sites become completely occupied by the rapidly developing stand, and growth of individuals proceeds at an extremely slow rate at somewhere between 2 and 6 m in height (Horne and Robinson 1987). The extremely slowed growth of dense stands [reportedly up to 170,000 stems ha^{-1} (Lacey 1972)] has been referred to as 'lock-up'. The precise causes of 'lock-up' are incompletely understood, but are thought to be the result of intense within-stand competition for nutrients and water (see Chapters Five and Six).

1.2.3. Ecological impacts of C. glaucophylla *regeneration in agricultural landscapes*

Research that has attempted to quantify the precise effects of dense stands on agricultural productivity and ecological diversity is limited, and the most recent studies are reported hereafter. Competitive processes are poorly understood. Presently, there exists a knowledge gap between the present legislative requirements for dense regrowth and an understanding of environmental condition following treatment of dense stands.

1.2.3.1. Tree water use

Although no attempts have been made to link water use with pasture cover or the distribution of other vascular plants, recent research has compared tree-water use with other vegetation types and other tree species. In a comparative study of water use in *C. glaucophylla* woodland and adjacent managed grassland, it was found that total water use did not differ between land uses, although the rate of soil water withdrawal was much more rapid for the woodland (Eberbach 1995). The response of *C. glaucophylla* woodland to vapour pressure deficit in drought was similar to that of another co-occurring *Eucalypt* species (Zeppel *et al.* 2006) and water use did not differ between the two species even though the sapwood area: DBH relationship was substantially greater for the Eucalypt (Zeppel and Eamus 2008).

1.2.3.2. Groundcover

The effect of *C. glaucophylla* on ground-storey vegetation cover has received recent attention, because it is perceived to be a production issue. A lack of vascular plant cover has been reported for dense stands in Northern NSW (Andrews 2003; McHenry *et al.* 2006) and was clearly associated with a rainfall gradient in southern NSW (Thompson and Eldridge 2005a). Increased tree cover is positively correlated with an increase in the abundance of biological soil crusts that become more diverse as vascular plant cover declines (Thompson and Eldridge 2005a). Large amounts of litter are produced in dense stands (Harris *et al.* 2003; Hart 1995), however, this litter does not inhibit the growth of other vascular plant species and may instead enhance the water holding capacity of the soil (Harris *et al.* 2003) and provide micro-sites for vascular plant establishment (Thompson and Eldridge 2005b).

1.2.3.3. Soil condition

Soil loss beneath dense *C. glaucophylla* stands is not thought to result from wind erosion, due to the density of tree cover (Eldridge *et al.* 2003). According to Thompson and Eldridge

(2005b) soil loss resulting from water erosion is likely due to a combination of slope, paucity of vascular plant cover and weakly coherent surface soils on which the species is often prevalent (Eldridge *et al.* 2003). Although Andrews (2003) noted enhanced erosion associated with a decrease in vascular plant cover in dense stands, it is uncertain whether this is a direct consequence of groundcover inhibition or of the interaction between grazing management and rainfall.

Few studies have assessed soil chemical status associated with stands of *C. glaucophylla* (but see McHenry 2007), which was identified as a key knowledge gap when conducting preliminary research (see Chapter Two – McHenry *et al.* 2006). At six grazed sites on the NWS and plains of NSW, it was found that dense *C. glaucophylla* stands had significantly higher levels of C, N, S, extractable P and higher pH in the mineral soil than adjacent un-colonised pasture. The impacts of *C. glaucophylla* trees on surrounding soil chemistry are not well understood however, nor has there been detailed study that accounts for soil nutrient changes under various grazing regimes (Chapter Seven).

In summary, whilst there are studies which demonstrate the effects of dense stands on environmental condition, it is still unclear if these effects result from the tree itself or if they are instead related to a combination of factors such as land management and site characteristics. It is also unclear if these effects are restricted only to dense stands, or if indeed they are associated with trees at any age or density. Perhaps as a consequence of the paucity of published data pertaining to the effects of *C. glaucophylla* in the agricultural landscape, management of the species has become an emotive issue in the community.

1.2.4. Community perceptions of prolific regeneration and establishment

Callitris glaucophylla regeneration and/or colonisation events are a recurrent management issue for landholders (See Plate 4). Dense regrowth *C. glaucophylla* stands are perceived to be problematic by landholders but opinions regarding appropriate management vary widely across the community. Many believe that dense stands decrease agricultural productivity (Cameron 2003; Eldridge et al. 2003; Harris et al. 2003; McHenry 2007; McHenry et al. 2006; Thompson and Eldridge 2005b). Whilst some landholders believe that clearing regrowth is the only option to maximise agricultural productivity (Cobar Vegetation Management Committee 2006), others believe that maintenance of stands by thinning to produce merchantable timber is a more viable option (Andrews 2003). To date, there has been considerable attention directed at the benefits of thinning for farm or commercial forestry purposes (Andrews 2003; Forestry Commission of New South Wales 1988; Horne 1990; Horne and Robinson 1987; Johnston 1975; Knott 1995; Lacey 1972; Lacey 1973), but less consideration has been given to the effects of *C. glaucophylla* regrowth and its management on environmental condition (McHenry 2007; Thompson and Eldridge 2005b).

The rationale for the research presented in this thesis is to address some of the present knowledge gaps with respect to the ecology and management of *C. glaucophylla.* The role of trees in the landscape with respect to groundcover and soil health at various spatial and temporal scales will be examined. The impact that trees can have on the various components of the ecosystem such as soils and ground cover, and the effects that are imposed by different densities of trees is another focus of this investigation. I will refer to the recent legislation where relevant in order to contextualise the effects of management within the '*improve or maintain*' framework.



1935



1955



1985



2005

Plate 4. The distribution and abundance of *Callitris glaucophylla* on a south-facing slope at a property near Mingoola, 66km west of Tenterfield, over a 70-year period. Most other timber species (such as Narrow-Leaved Ironbark, *Eucalyptus melanophloia*) were ring-barked prior to 1935, at which time *C. glaucophylla* was a sub-canopy component of sclerophyll forest according to photographic records of the area. Source (P. Hynes).

1.3. Knowledge Gaps and Aims of the Thesis

Sections 1.1 and 1.2 outlined the literature pertaining to the ecological role of dense *C. glaucophylla* regeneration in agricultural landscapes of NSW. Section 1.2 highlighted some of the issues relevant to the ecology and management of the species, set in the context of other *Invasive Native Scrub* management issues in NSW. From these sections, two key knowledge gaps can be identified with respect to *C. glaucophylla*:

1. There is little understanding of the intra- and inter-specific competitive interactions in *C. glaucophylla* stands, how these vary with different spatial and temporal scales, and what effects the species has on the surrounding landscape; and,

2. There is a paucity of information describing the ecological impacts of managing dense *C. glaucophylla* stands in agricultural landscapes, especially within the '*improve or maintain*' framework of the Act.

Therefore, more information should be sought which attempts to quantify the effects the species (and its management) have on environmental condition in agricultural landscapes.

Chapter Two provides insight into some of the likely environmental variables which might be important indicators of site condition on private lands where *C. glaucophylla* regrowth is a significant component of the vegetative cover. Following on from this preliminary research, and taking into consideration the knowledge gaps outlined above, five specific aims have been generated, which will be examined in a series of sequential investigations throughout the body of this thesis. The unifying theme of the research presented in this thesis is *'Individuals to Landscapes'*, which will set the context for the interpretation of results.

Specifically, the aims of the research presented in this thesis are:

1. To investigate the effects of individual *C. glaucophylla* trees of different ages on environmental condition (soil carbon/organic matter, nutrient status, litter quantity and nutrient status and the cover and diversity of understorey vegetation) on farms on the Northwest Slopes of NSW (Chapter Four);
2. To determine whether the patterns of litter, nutrient and vegetation distribution under regrowth stands on farms are similar to those patterns observed under individual trees (Chapter Five);
3. To determine the effects of intra-specific competition among *C. glaucophylla* seedlings on plant growth and environmental condition (Chapter Six);
4. To investigate the effects of managing *C. glaucophylla* regrowth on environmental condition (Chapter Seven), and;
5. To synthesise the results from investigations at aims 1-4 to devise an optimum management strategy (or strategies) for White Cypress Pine regrowth on private lands in North West NSW (Chapter Eight).

The chapters contained within this thesis have been written in the journal-article style. The status of submitted articles (Chapters Two, Four and Seven) is indicated at the beginning of each chapter. Non-submitted articles (Chapters Five and Six) are preceded by a 'background' section *in lieu* of an abstract, which links the rationale of the chapter to results in previous sections.

Chapter 2. Preliminary Research

Soil and vegetation response to thinning White Cypress Pine (*Callitris glaucophylla*) on the North Western Slopes of New South Wales, Australia

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Modified formatting and original text from the article published in Plant and Soil (2006) 285:245-255.

2.1. Abstract

Dense White Cypress Pine (*Callitris glaucophylla* J. Thompson & L.A.S. Johnson) regrowth occurs frequently across previously cleared landscapes in New South Wales (NSW), and is thought to adversely affect agricultural production and to cause land degradation. The NSW Native Vegetation Act (2003) requires that management of native vegetation including pre-1990 regrowth must 'improve or maintain' site condition, yet there is currently limited information regarding techniques for the optimum management of *C. glaucophylla* in this regard. We conducted a preliminary study to examine floristic composition, soil condition (to 50 cm) and carbon storage under 'Dense' (dense regrowth), 'Thinned' (dense regrowth thinned in 2000/2001) and 'Un-Colonised' (pasture not yet recolonised by *C. glaucophylla*) plots on private lands in NSW. Reduced tree density from thinning resulted in increased biomass of the remaining individual trees. Un-colonised plots had significantly more groundcover than thinned plots, which had significantly more groundcover than dense plots. Differences in plant diversity however, were explained by site factors rather than land use.

Soils in the dense plots were the most acid but soil pH was significantly higher in thinned plots and pH was highest in soil of the un-colonised plots. Mean values for carbon, nitrogen, sulfur and extractable phosphorus varied among sites, although each were significantly more abundant in the mineral soil of dense and thinned plots compared with un-colonised plots, suggesting that thinning had had a minimal effect on the soil parameters assessed. Accounting for all site components, site carbon storage was significantly higher in dense and thinned plots compared with un-colonised plots due to elevated levels of soil and litter carbon as well as the presence of trees. The results indicate that thinning dense *C. glaucophylla* can maintain and (by some measures) improve site condition. However, given the variability in some of the parameters assessed, further study across a wider range of soil types and rainfall is proposed.

2.2. Introduction

Prior to European settlement of Australia, most woodland in central and western NSW had a multiple-age structure where existing large trees would limit the regeneration and growth of other trees and shrubs beneath them. Natural disturbance such as fire or tree fall probably created relatively small gaps in these woodlands that were filled by patches of dense regenerating trees and shrubs, which eventually self-thinned as they grew larger (Eldridge *et al.* 2003). During the past two centuries however, native vegetation communities have been cleared or substantially altered over extensive areas of the state and subsequent agricultural land management has produced relatively large areas where conditions are suitable for seedling establishment. As a consequence, large stands of single-age regrowth are now more common in the landscape (Thompson and Eldridge 2005b).

Many indigenous tree species regenerate on previously cleared land, but one of the most common and widespread in NSW is *Callitris glaucophylla*, which often forms mono-specific stands, with tree densities in excess of 1500 stems ha^{-1}. From a management perspective, dense regrowth is considered problematic and there is a widely held belief in the community

that regrowth causes land degradation and soil erosion (Cameron 2003; Curby *et al.* 2001; Eldridge *et al.* 2003; Thompson and Eldridge 2005b). For this reason, clearing of *C. glaucophylla* is often considered by landholders to be the most appropriate management strategy despite alternative management strategies such as thinning dense stands. Despite the prevalence and commercial value of the species in NSW however, significant knowledge gaps exist with respect to the management and value of this form of regrowth in the rural landscape.

The growth response of *C. glaucophylla* to thinning has received comprehensive review in the forestry literature (Horne 1990; Horne and Robinson 1987; Johnston 1975; Johnston 1979; Lacey 1973). However, the effect of thinning on other components of the ecosystem such as ground-storey vegetation cover and diversity, soil condition, soil organic matter status and nutrient cycling and the response of these components to management have received less attention (Thompson and Eldridge 2005a; b).

Optimum management of *C. glaucophylla* with respect to carbon storage has also attained significance in the context of Greenhouse Gas accounting (Burrows *et al.* 2001) and might offer an additional income source to landholders, assuming that proposed trading of carbon takes place. There is a paucity of information in the literature however, by which to predict increases or losses of carbon storage potential under different management regimes in *C. glaucophylla* stands.

In NSW, The Native Vegetation Act 2003 was intended to end broad-scale clearing of native vegetation, particularly that which existed in the landscape prior to 1990 (or 1983 in the Western Division of NSW). Native vegetation management will be permitted under the new legislation but will now be regulated by an 'environmental test', which determines if a management activity will 'improve or maintain' environmental outcomes, such as soil quality

or biodiversity. Therefore, strategies by which vegetation can be managed to maximise both agricultural production and environmental outcomes will now be required across NSW agricultural landscapes.

The aim of this study was to determine if there were changes in i) the cover and diversity of ground-storey vegetation, ii) soil condition and iii) the allometry and carbon storage in plant biomass, litter and soil across a management gradient in *C. glaucophylla* regrowth on private lands in northern New South Wales, with a view to evaluate the potential of thinning management to achieve multiple outcomes.

2.3. Methods

2.3.1. Site Descriptions

Five sites were selected across the North Western Slopes of NSW (Figure 2). During the study period (January-February 2005) average maximum daily temperatures ranged from 33.9˚ C in Tamworth to 36.5˚ C in Warialda (Australian Bureau of Meteorology 2008). Each site had previously been a component of a larger study of the farm-forestry potential of *C. glaucophylla* (Andrews 2003) and had been randomly assigned two types of treatment plots or 'land-uses', which included a 'dense' plot of dense, un-thinned regrowth *C. glaucophylla*, and a 'thinned' plot in which the tree density had been reduced in 2000-2001 to approximately 6 x 6 m spacing. The vegetative composition, tree density and DBH of *C. glaucophylla* were determined for the original study, and were deemed not to differ significantly between plots prior to treatment (Shane Andrews 2005 pers. comm.).

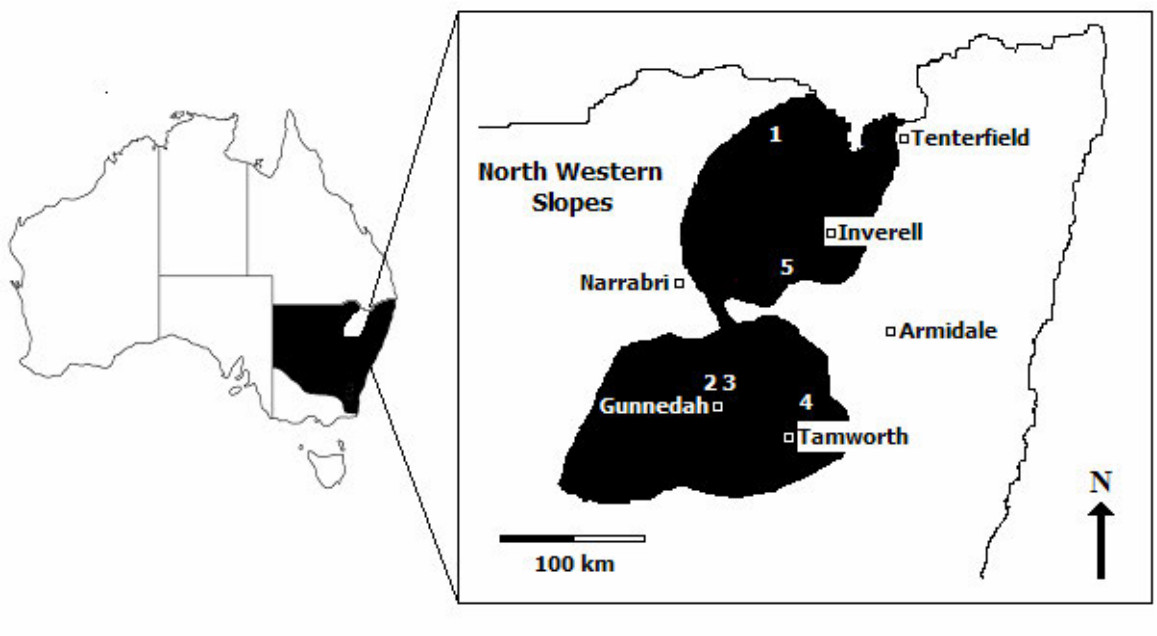


Figure 2. Location of study sites on the North Western Slopes of New South Wales (shaded), Australia, where 1 represents 'Warialda', 2 represents 'Gunnedah 1', 3 represents 'Gunnedah 2', 4 represents 'Tamworth' and 5 represents 'Bingara'.

A third 'un-colonised' treatment was included in the present study, which was comprised of an adjacent cleared plot upon which *C. glaucophylla* had not regrown. All of the sample plots were selected on the basis of similar slope, aspect and elevation as well as soil type (as per Murphy *et al.* 2003). All plots were open to cattle grazing (sites 4 and 5 were heavily grazed) and the additional impact of feral and native animals. The canopies of dense plots at all sites were mono-specific, whilst thinned plots consisted of a few scattered Silver-Leaved Ironbark (*E. melanophloia*) or White Gums (*E. albens*), although approximately 99% of all trees were *C. glaucophylla.* The characteristics of each site are presented in Table 1.

2.3.2. Sampling

Within each treatment plot a sample area of 25m x 25m was established following the method of Mackenzie *et al*. (2002). Nine (0-50 cm) soil profiles were collected in each plot in a regular grid pattern using a steel coring device with 5 cm diameter. Each profile was sub-divided into depth increments of 0-5, 5-10, 10-15, 15-30 and 30-50 cm and increments were

Table 1. Characteristics of the five sites selected for this study, all of which were located on the North Western Slopes of NSW.

Site	Location	Altitude (m)	Rainfall (mm/y)	Geology	Soil Type	Slope
'Warialda'	Yallaroi	273	450	Basalt	Vertosol	Dense (+3°) Thinned (+4°) Un-colonised (+1°)
'Gunnedah 1'	Emerald Hill	312	550	Meta-sediments	Chromosol	Dense (0°) Thinned (+4°) Un-colonised (0°)
'Gunnedah 2'	Emerald Hill	297	550	Alluvial Sand	Kandosol	Dense (0°) Thinned (0°) Un-colonised (0°)
'Tamworth'	Upper Moore Creek	435	650	Granite	Chromosol	Dense (+18°) Thinned (+20°) Un-colonised (+15°)
'Bingara'	Upper Bingara	633	700	Serpentenite	Chromosol	Dense (+16°) Thinned (+14°) Un-colonised (+11°)

treated as separate samples. In one instance, solid rock was reached at 30 cm, and no sample was obtained below this depth. Five 0.25m^2 litter samples were also collected from the corners and middle of each plot using a brush and spatula.

2.3.3. Ground-storey cover and vegetation

Ground-storey vegetation cover and the diversity of vegetation growth forms were recorded for each plot. Vegetation cover was assessed in 10 successive 1m^2 quadrats along 3 randomly-aligned belt transects, 10 m in length. Ground-storey vegetation was classified into four types - grasses, shrubs, forbs and ferns. The presence of each vegetation type was recorded for each quadrat and the data were used to obtain average frequency (i.e. the number of quadrats in a transect containing a specific vegetation type) and 'richness' (i.e. the number of different vegetation types present in a quadrat) along each transect. The biomass of the ground-storey vegetation in each plot was also estimated visually for carbon accounting (MacKenzie *et al.* 2000). Litter samples were dried at 70 degrees to a constant weight. Litter dry weights were converted to t ha^{-1}, and were multiplied by 0.5 to obtain the C content (Snowdon et al. 2001; March 2001).

2.3.4. Soil condition

Soil samples were oven dried at 40 °C for 48 hours and then crushed and sieved to < 2 mm and finally weighed in order to assess bulk density. Samples were analysed for C, N and S by LECO combustion, pH in 0.01 M $CaCl_2$ suspension and ext. P by Olsen method using RobotPrep. All analyses were conducted at the DNR Gunnedah Resources Centre Soils Laboratory, NSW (National Association of Testing Authorities no. 737/15525).

2.3.5. Biomass and C content of C. glaucophylla

The height and DBHOB of ten randomly selected *C. glaucophylla* trees was recorded in dense and thinned plots. Only individuals over 1.6m in height were recorded (after Knott 1995). The density of trees (per hectare) in each plot was estimated by counting the number of trees in four 5 x 5 m (for dense) or 10x10 m (for thinned) plots. Density and DBHOB were used to estimate the basal area (B_A) of each plot occupied by *C. glaucophylla,* which was then used to obtain the C content in tree biomass (B_T) (Equation 1).

Equation 1 $$B_T = B_A * 4.341$$

which was derived from allometric equations for *C. glaucophylla* (Burrows *et al*. 2001) on similar soil types and in similar rainfall zones, community assemblages and topographies as the sites in this study. Root biomass was estimated to be 0.25 of above ground biomass (after (Burrows et al. 2001).

The volume and biomass of coarse woody debris (CWD) was estimated by measuring the height and DBHOB of ten randomly-selected trees in thinned plots. No CWD was present in dense or un-colonised plots at any site. All CWD was classified as ‘sound’ according to (MacKenzie et al. 2000). CWD density was estimated by multiplying the average tree volume by the number of felled trees in the plot (estimated by the subtraction of the thinned density from the dense density). The CWD C content was assumed to be 0.5 of the total tree biomass.

2.3.6. Statistical analysis

In order to determine if there were differences between sites or land use plots for vegetation cover, frequency and diversity, tree height and DBHOB and litter dry weights, a two-way ANOVA was performed, where site and land use were fixed factors. A one-way ANOVA was used to test the differences in tree density between treatments. Tree DBHOB, litter dry weights and tree density were $\log_{10}$ transformed to correct for left-skewed data.

In order to determine if there was a difference between soil C, N, S, ext. P and pH and site, land use or depth, a three-way ANCOVA was performed. The covariate depth was fitted in the ANCOVA as a second order polynomial. Data for C, N, P and S were $\log_{10}$ transformed.

2.4. Results

2.4.1. Ground-storey cover and vegetation

There was a strong and significant interaction between 'site' and 'land use' for groundcover in this study ($f_{(8,135)} = 4.12$, $p = 0.000$), although ground cover was consistently lower in dense plots than thinned plots and was highest in un-colonised plots (Figure 3). Differences in the richness of groundstorey vegetation were mainly attributed to site effects, although the interaction between sites and land use was highly significant due to increased richness in thinned plots at two sites ($f_{(8,149)} = 3.89$, $p = 0.000$) (Table 2). Grasses were more frequent than all other vegetation types across all sites and plots, whilst shrubs were rare and found only on the Bingara site. Litter dry weights differed significantly due to the interaction between site and land use ($f_{(8,74)} = 2.54$, $p = 0.019$), although litter was generally more abundant in dense plots (mean 1006.56 ± 128.75 g) than thinned plots (mean 637.92 ± 91.62 g), with the least litter deposited in un-colonised plots (mean 343.63 ± 36.00 g).

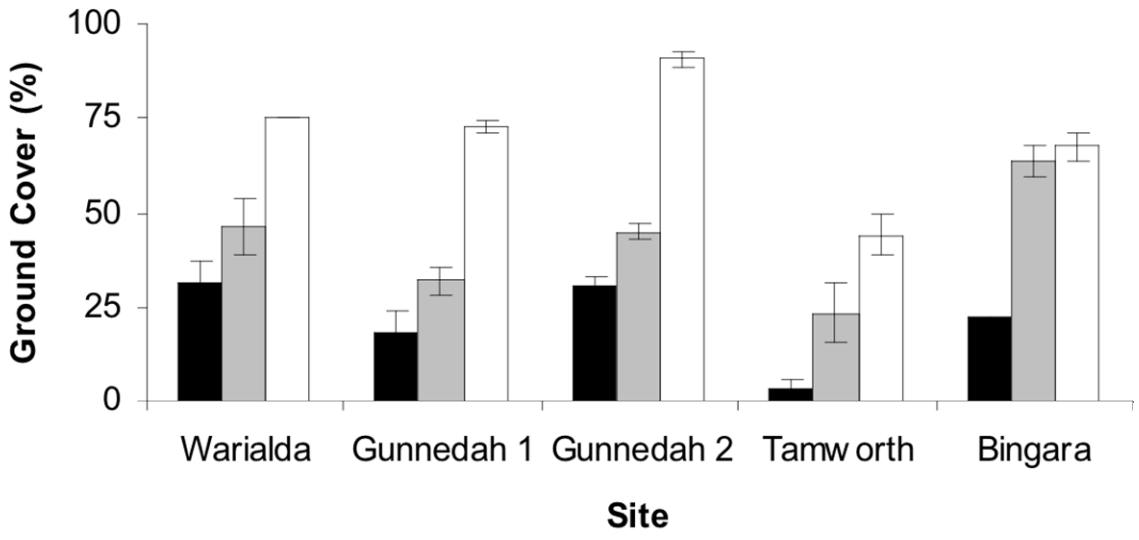


Figure 3. Mean ground-storey vegetation cover under *C. glaucophylla* land use plots across all sites (± S. E.). Cover was least under dense *C. glaucophylla* plots (dense plots – black), and most abundant in un-colonised plots (White). Grey sections represent thinned plots.

Table 2. Two-Way ANOVA testing the effects of site, land use and their interaction on the diversity of vegetative groups under *C. glaucophylla* stands. Most differences were site, rather than treatment related.

	df	**SS**	**MS**	***f***	***p***
Site	4	9.000	2.250	5.52	0.000
Land Use	2	0.653	0.326	0.80	0.451
Interaction	8	12.68	1.585	3.89	0.000
Error	135	55.00	0.407		
Total	149	77.33			

2.4.2. Allometry of C. glaucophylla

Mean tree density was reduced significantly by thinning ($f_{(1,9)} = 22.68$, $p = 0.001$) from 7740 ± 1662 stems ha^{-1} to 494 ± 69 stems ha^{-1}. Height and DBHOB were positively and significantly correlated across all sites and land uses (control - $f_{(1,48)} = 129.68$, $p = 0.000$, Adjusted R^2 = 72.4%; thinned - $f_{(1,48)} = 185.33$, $p = 0.000$, Adjusted R^2 = 79.0%) (Figure 4). Trees had a larger DBHOB for the equivalent height in thinned plots relative to dense plots. Although the interaction between sites and land use was significant for height ($f_{(4,90)} = 3.53$, $p = 0.010$), the mean tree height of trees in thinned plots (8.58 ± 0.32) was greater than that of trees in control plots (6.40 ± 0.28).

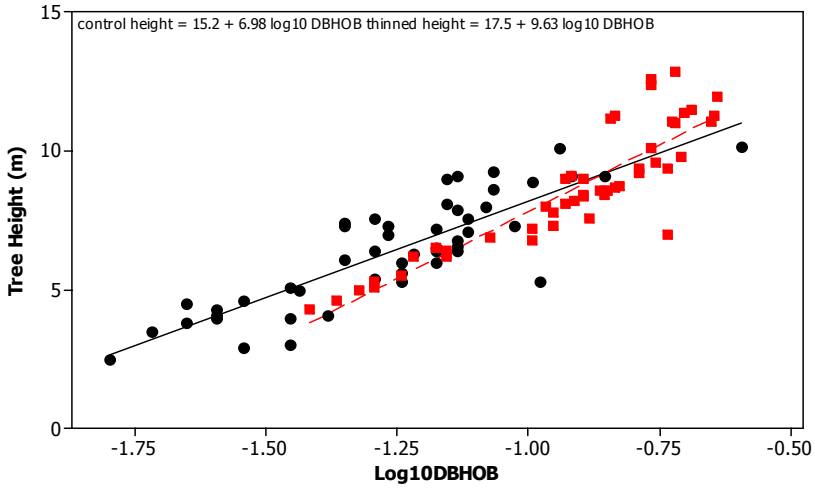


Figure 4. Allometric relationships of trees in dense (circle) and thinned (square) plots across all sites.

2.4.3. Soil condition

The depth profiles for C, N and ext. P were significantly different between land uses, with each parameter less abundant in the upper profile of the un-colonised plots than dense and thinned plots (Table 3, Figure 5). Soil C, ext. P, N and S profiles were also significantly different between sites, although mean values for each element were always lower in un-colonised plots than thinned and dense plots. pH followed the same pattern with depth across all land uses, decreasing with depth to 5-10 cm and increasing with subsequent increases in depth. Profiles differed significantly between land uses across all sites, with a progressively and consistently higher pH from dense, through thinned to un-colonised plots. C:N ratios increased significantly with depth across sites and land uses ($f_{(8,629)} = 3.75$, $p = 0.000$ and $f_{(4,629)} = 6.17$, $p = 0.000$ respectively), but all were between 14 and 17 across the entire dataset.

2.4.1. Site and treatment C storage

Trees and/or (0-30 cm) soil accounted for the majority of total C storage for each land use (Table 4). When CWD was excluded from the dataset for total site C, storage in dense plots was significantly higher than both thinned and un-colonised plots. However, when CWD was included as a component of site C storage, the total was higher in thinned and dense plots compared with un-colonised plots, but thinned and dense plots had similar C values.

Table 3. *F* values from a Three-Way Analysis of Co-Variance (ANCOVA) testing the effects of site, land use, depth and their interactions on soil condition under *C. glaucophylla* stands. Asterisks denote levels of significance (*** = P < 0.001; ** = P < 0.01; * = P < 0.05).

Factor	C	N	Phosphorus	Sulfur	pH
Site	406***	264***	25***	130***	105***
Land use	8***	19***	4***	32***	45***
Depth	1326***	736***	225***	190***	189***
Site * Land use	14***	19***	4***	12***	7***
Site * Depth	13***	7***	10***	10***	10***
Land use * Depth	9***	7***	4**	2 ns	1 ns
Site * Land use * Depth	4***	4***	2**	2 ***	2*

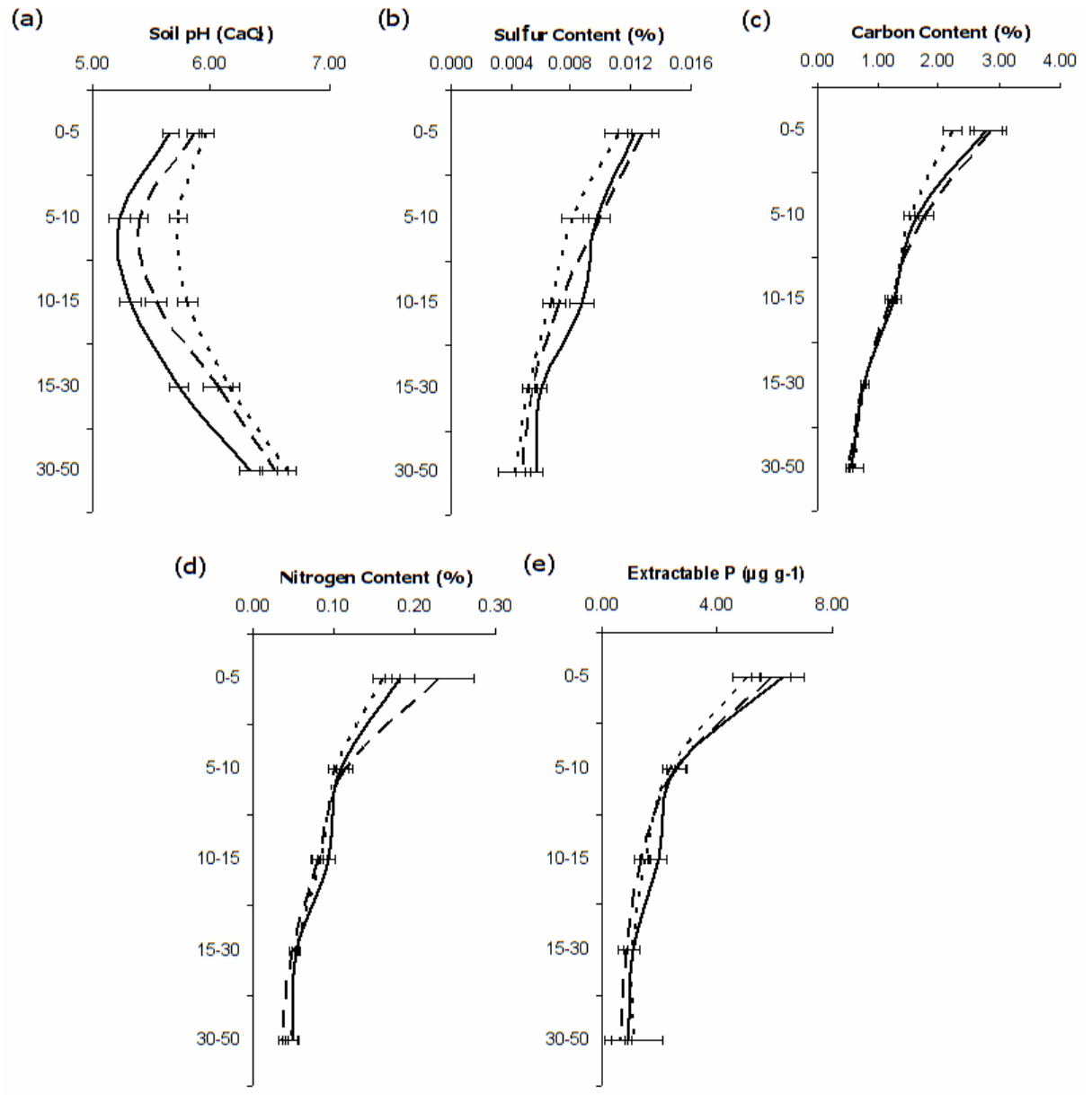


Figure 5. The distribution of (a) pH, (b) sulfur, (c) C, (d) N and (e) extractable phosphorus with depth (± S.E.) in three different land uses (solid line = dense, broken line = thinned, dotted line = un-colonised) across all sites.

Table 4. Total C storage (t ha^{-1}) in different *C. glaucophylla* land uses. Asterisks denote estimates from Burrows *et al.* (2001).

	Dense	**Thinned**	**Un-Colonised**
Trees (above-ground)	47.53	15.56	2.75
Trees (roots)*	1.88	3.89	0.73
Soil (0 – 30 cm)	56.46	57.39	51.59
Ground cover*	1.40	2.00	3.20
Litter	5.03	3.19	1.72
Coarse woody debris	0.00	43.89	0.00
Total (t ha^{-1})	**122.31**	**125.92**	**59.56**

2.5 Discussion

A common perception among the public, which has been expressed anecdotally in the literature, is that dense *C. glaucophylla* regrowth suppresses the growth and cover of ground-storey plants (Andrews 2003; Boland et al. 1984; Clayton-Greene and Ashton 1990; Harris et al. 2003; Nowland 1997). The results of this study lend support to such observations – at each site vegetative cover was lowest in dense plots (dense *C. glaucophylla* regrowth), despite the heavy grazing in the un-colonised plots of some sites. Much of the ground cover component of dense stands consisted of *C. glaucophylla* litter.

Our results suggest that the richness of plant types was not related to management of *C. glaucophylla* but that variation was instead explained by site factors, albeit that the functional group approach adopted in this study may have masked the true diversity of plots. Some limited studies targeted at forestry and farm forestry management on the NWS and Plains of NSW have indicated that unlike vegetative cover, diversity appears to be unaffected by the density of *C. glaucophylla* (Andrews 2003; McHenry 2007). Local rainfall has instead been demonstrated to be an important factor in regulating diversity and composition under *C. glaucophylla* regrowth, irrespective of the management regime (Thompson and Eldridge 2005a). Certainly, our results appear to support such assertions, with a greater diversity of vegetation observed at Bingara (highest rainfall zone) compared with Warialda (lowest rainfall zone). Our results therefore suggest that thinning had no adverse affect on ground-

storey vegetation cover and richness of vegetation types, and, using these parameters, site condition would appear to be at least maintained by thinning management.

Thinning resulted in an increase in height, DBHOB and biomass of trees relative to dense stands across all sites, regardless of geology, soil type and/or management history. The growth response of dense *C. glaucophylla* stands to thinning has been well documented in the forestry literature for the north-western plains of NSW (Forestry Commission of New South Wales 1988; Horne 1990; Horne and Robinson 1987; Johnston 1975; Knott 1995; Lacey 1972). Although no published data exist for the higher rainfall areas of NSW where our study was based, our results suggest that thinning induces a similar response. Thinning of mono-specific *C. glaucophylla* stands is thought to be beneficial from a forestry perspective due to the reduced competition from regenerating seedlings and juveniles (Horne 1990; Horne and Robinson 1987; Johnston 1975; Lacey 1972). A small study conducted by Johnston (1979) in south-western Queensland noted however, that an increase in tree growth in response to thinning diminished rapidly two years after treatment due to prolific regeneration of *C. glaucophylla* and another forestry species in the under-storey. Therefore, the effects and potential benefits of thinning dense *C. glaucophylla* regrowth might be limited over time. Further investigation is required in order to assess the long-term effect of such management with respect to these factors.

Thinning of *C. glaucophylla* had a limited effect on soil condition for the parameters examined in this study. Soil C: N ratios differed significantly with depth across sites and treatments, but all were below the critical value of 20, at which it is presumed that mineralisation and nitrification cease in forest soils (Attiwill and May 2001; Attiwill et al. 1996). Thinning stands either maintained, or improved, soil C, N, S, and extractable P relative to dense or un-colonised plots. Across a range of environments, soil nutrients have been found in higher concentrations in the zone around trees relative to adjacent pasture or ground-storey

vegetation (Belsky et al. 1993a; Belsky et al. 1993b; Dean et al. 1999; Graham et al. 2004; Ryan and McGarity 1983; Wilson 2002) and our results suggest that this is so even for stands of *C. glaucophylla*. Therefore, the retention of this species in the landscape can create local 'environmental improvements' (Ozolins et al. 2001).

Significantly lower soil pH at all soil depths were observed under *C. glaucophylla* stands, which, given the nature of the experimental design, suggests that *C. glaucophylla* had had a significant acidifying effect on the soils studied. This acidity under *C. glaucophylla* conforms to similar effects identified under a range of coniferous tree species in other environments (Anderson et al. 1993; Barton et al. 1999; Belton et al. 1996; Davis 1995; Giddens et al. 1997; Groenendijk et al. 2002; Hawke and O'Connor 1993; Moffat and Boswell 1990; Parfitt et al. 1997). However, few examples of such induced acidification have been observed *in situ* across agricultural landscapes in Australia and especially not associated with native species (but see(Lockwood et al. 2003; Wilson and Lemon 2004). A number of processes might explain such soil acidification. For example, (Noble and Randall 1998; 1999) proposed that the relocation of anions from depth in the soil through a 'biological pumping' process by the trees themselves and indeed this phenomenon has been observed under some eucalypts in Australia (Wilson and Lemon 2004). Alternatively, root exudate production by tree roots may also contribute to decreases in rhizosphere pH (Dakora and Phillips 2002; Hinsinger et al. 2003), which may significantly influence the surrounding soil, particularly in a high-density stand. These processes themselves however would be insufficient to explain the surface acidification that was also observed under *C. glaucophylla*. Graham et. al. (1996) suggested that the effects of plant litter on surface soils might depend on the ash alkalinity of the litter. The *C. glaucophylla* litter might therefore have quality such that it causes surface acidification in a similar fashion to that observed for *Eucalyptus caliginosa* Blakely & McKie on the Tablelands of NSW (Graham et al. 2004).

Our results suggest that the soil acidification apparently induced by *C. glaucophylla* can be ameliorated by management actions and thinning of *C. glaucophylla* resulted in an increase in soil pH through the whole soil profile. This was possibly due to the liberation of organic anions from soil organic matter as the canopy opened and soil organic matter decomposition commenced, and perhaps also due to a reduction in anion removal from depth as tree density was reduced. These processes are however currently conjectural and worthy of further study. Nevertheless, such rapid change in soil pH through the whole soil profile might be viewed as a soil improvement resulting from management action.

The results of this study suggest that C storage was higher under *C. glaucophylla* regrowth compared with un-colonised sites. Total site C was only marginally affected by thinning and the CWD retained in the understorey, combined with the growth increase of the standing trees, resulted in larger total site C storage relative to dense stands. Therefore, should financial incentives for the retention of C stocks become available, management of *C. glaucophylla* regrowth might have significance from a C storage perspective.

The results of this preliminary study have addressed a number of community and legislative concerns with dense *C. glaucophylla* regrowth. The retained trees in thinned plots had grown taller and had greater DBHOB, suggesting that thinning resulted in an increase in the growth rate of *C. glaucophylla.* The cover of ground-storey plants increased in response to thinning but there was little change in the diversity of life forms (shrubs, grasses etc.) of this plant cover. Thinning dense regrowth maintained or improved soil condition and pH. Total site C storage was larger under *C. glaucophylla* than under adjacent un-colonised pasture, but thinning had little effect on total site C storage.

Given the results of this study, we suggest that thinning dense *C. glaucophylla* stands can be undertaken whilst maintaining, and by some measures improving site environmental

condition. The wide variation in some parameters across sites highlights the preliminary nature of the results and suggests that further investigations into regrowth management are warranted, in order to account for other management effects (e.g. grazing), soil, rainfall and topographic variation and other aspects of community concern pertaining to dense regrowth on private lands. As a result, this study has now been expanded to include a wider range of environmental and land-management variables.

2.5. Statement of Originality

Journal-Article Format for PhD Theses at the University of New England

STATEMENT OF ORIGINALITY

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Chapter Two	
"Plant and Soil"	
paper	

} 100% McHenry with contributions from Supervisors, statistical advice and technical advice.

Name of Candidate: Melinda McHenry

Name/title of Principal Supervisor: Dr. Brian Wilson

[redacted]
Candidate

17/12/08
Date

[redacted]
Principal Supervisor

14/12/08
Date

2.6. Statement of Authors Contributions

Journal-Article Format for PhD Theses at the University of New England

STATEMENT OF AUTHORS' CONTRIBUTION

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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Date

Chapter 3. Study Area

3.1. General Description – North-Western Slopes, NSW

Study sites were located within the area bounded by the North-Western Slopes botanical division in northern New South Wales, Australia (Figure 6). These slopes lie directly adjacent to, and west of, the Nandewar, Moonbi and Great Dividing Ranges, and span an area from the Queensland border in the north to Gilgandra and Binnaway (north of Dubbo) in the south. The topography is hilly to gently undulating, and includes extensive plains country to the northwest (Harden 1992; 1993; 2000; 2002).

The region has an estimated population of 98,428 residents (Bureau of Statistics estimate 2007), although most of the land area is occupied by farming enterprises. Principal land uses of the district include sheep and cattle grazing, as well as cropping - primarily wheat, sorghum, cotton and canola.

Although the original native vegetation of the region has been extensively cleared, many tracts of remnant woodland and forest can still be found on sloping country, particularly to the east. The typical native vegetation cover is comprised of woodlands with limited structural diversity, most commonly dominated by White Box (*Eucalyptus albens* Benth.) or Narrow-Leaved Ironbark (*E. melanophloia* F. Muell.) on soils of low fertility. Occasionally grassy woodlands occurring on basalt-derived soils can be found, especially in the Bingara-Narrabri and west Tenterfield regions, although these areas have largely been cleared for their high agricultural value. Areas of dry rainforest occur along the Liverpool and Nandewar Ranges, and further north, endangered Vine Thickets occur in sparse patches of non-arable land, especially between Bingara and Yallaroi (Keith 2006).

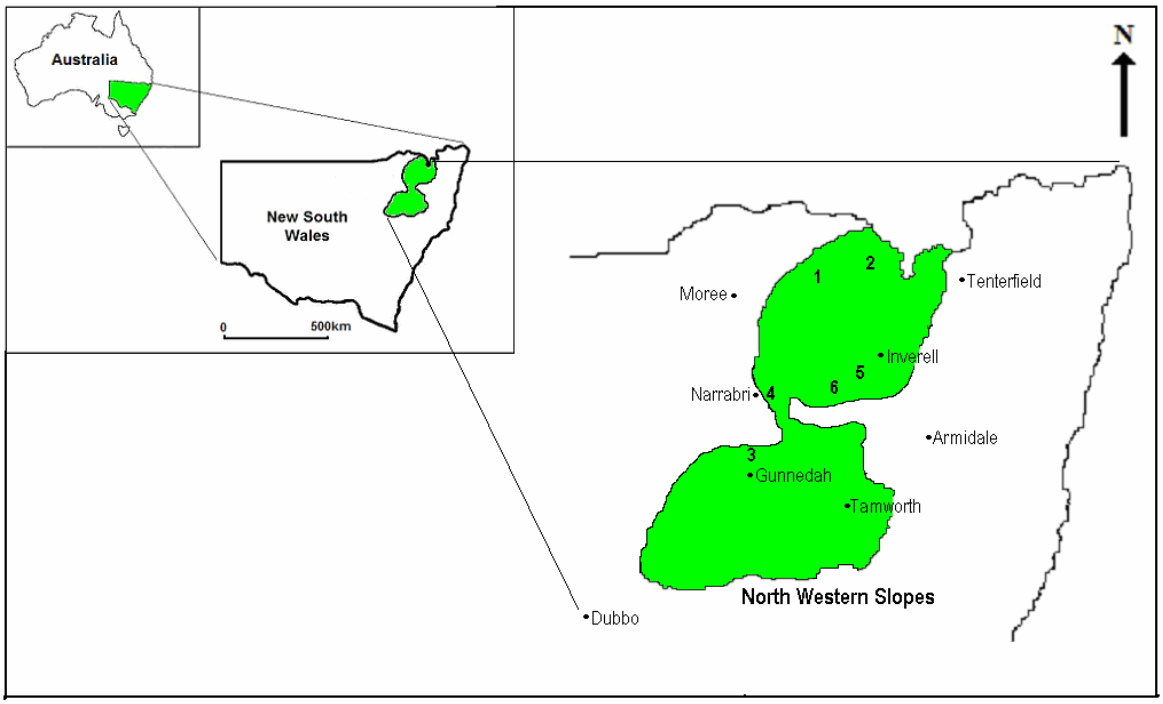


Figure 6. Approximate location of sites (1 = Yallaroi, 2 = Mingoola, 3 = Emerald Hill, 4 = Narrabri, 5 = Myall Creek and 6 = Bingara) on the North-Western Slopes (denoted by shaded section) of NSW, Australia.

Callitris glaucophylla is distributed across the entire NWS region of NSW. Historically, the species occurred in association with eucalypt species as a component of forests and woodlands. A range of disturbance events and long-term management actions have resulted in a significant increase in populations, especially in agricultural landscapes (See section 1.1). On many farms, a series of regeneration episodes has resulted in almost the complete replacement of the original canopy vegetation with dense mono-specific stands of *C. glaucophylla.* In such areas, the cover of ground storey vegetation is also inhibited, although there is little evidence to suggest that dense regrowth adversely impacts upon ground storey diversity, except at extremely high tree density (Andrews 2003; Thompson and Eldridge 2005a; b). Each of the three Catchment Management Authorities responsible for property vegetation plans across the NWS (Border-Rivers Gwydir, Namoi and Central West) list *C. glaucophylla* as INS.

Climate in the region is sub-humid. Temperatures in the region range from warm to hot summers with maximum temperatures over 30 degrees Celsius, and cool to mild winters with

infrequent moderate to mild frosts (Figure 7). Average annual rainfall varies from 850 mm at Inverell in the east to 625 mm at Gunnedah in the south-west, although a drought in the region from 2002 – 2007 (including the first two years of the study period for this thesis) resulted in rainfall much lower than the long-term average across most of the study region (Figure 8). Rainfall is slightly more abundant in late summer.

3.2. General Site Descriptions

Following the preliminary research (Chapter Two), a number of sites across the North-Western slopes were selected for further study (See Figure 2 and Plates 5-10). Each site was characterised by areas of dense, post-1990 *C. glaucophylla* regrowth, which to some extent was also associated with a degree of land degradation such as soil loss or weed invasion. At each site, tracts of remnant vegetation that contain 'old' (stem DBHOB greater than 60 cm) *C. glaucophylla* (I. Lunt, 2008 pers. comm.) indicate that the species was always present, at least as a sub-canopy component of woodland. For the purposes of this study 'dense' *C. glaucophylla* regrowth indicates stands with stems in excess of 2000 per hectare. Though precise measurements are reported in preceding and subsequent chapters, it is worth noting here that some of the properties included in this study have areas in which the density of *C. glaucophylla* exceeds 100 000 stems per hectare.

A description of each of the six study sites follows[2]. Nomenclature designated for the properties in this chapter will be used throughout the remainder of the thesis.

[2] Exact location information of each site has been withheld due to the interest of privacy. More specific information can be gained from the author subject to approval from the individual landholders.

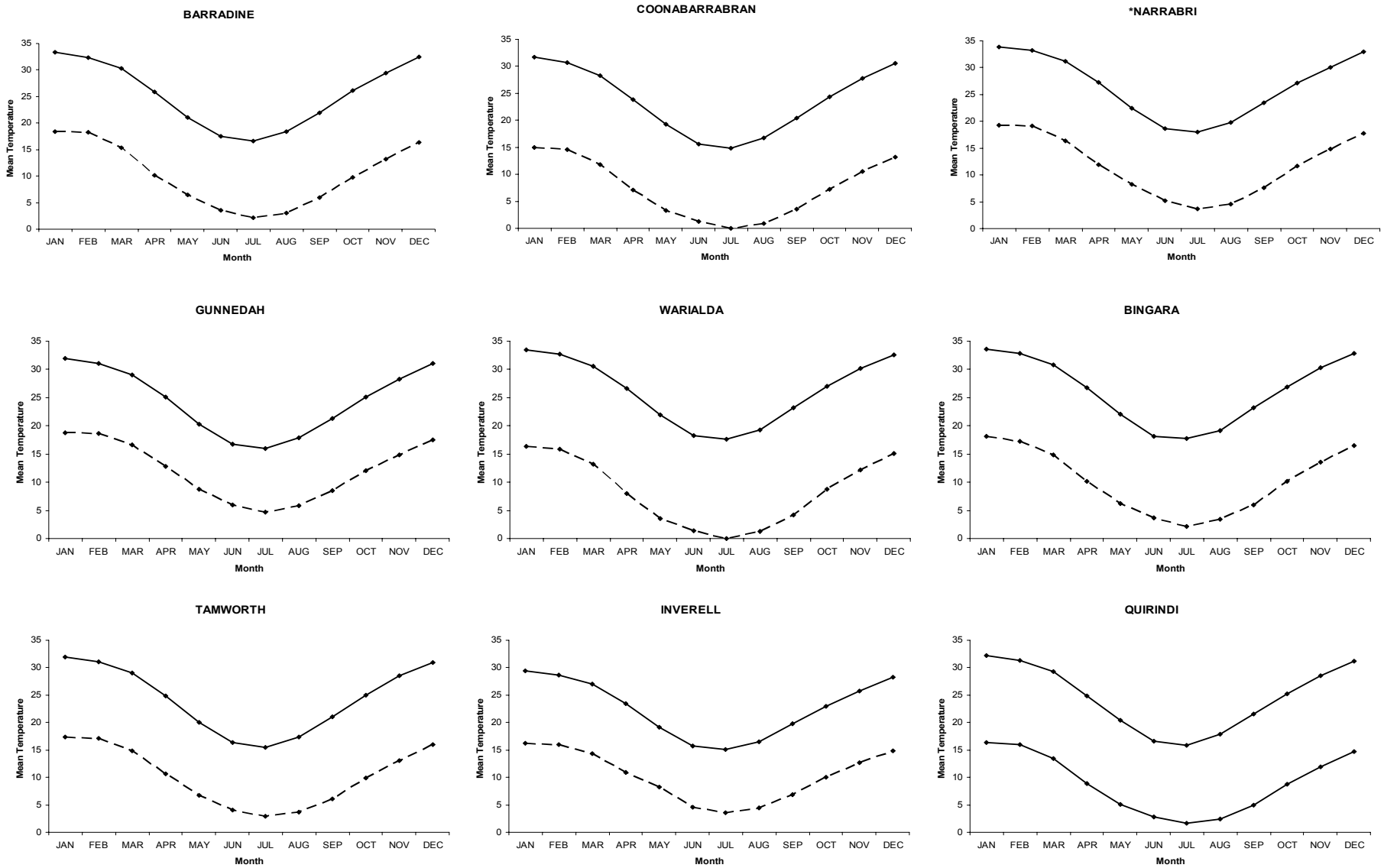


Figure 7 Mean maximum (solid line) and minimum (broken line) temperatures in NW Slopes towns from 1977 – 2007 (Bureau of Meteorology 2008). * = Adjacent to NW Slopes.

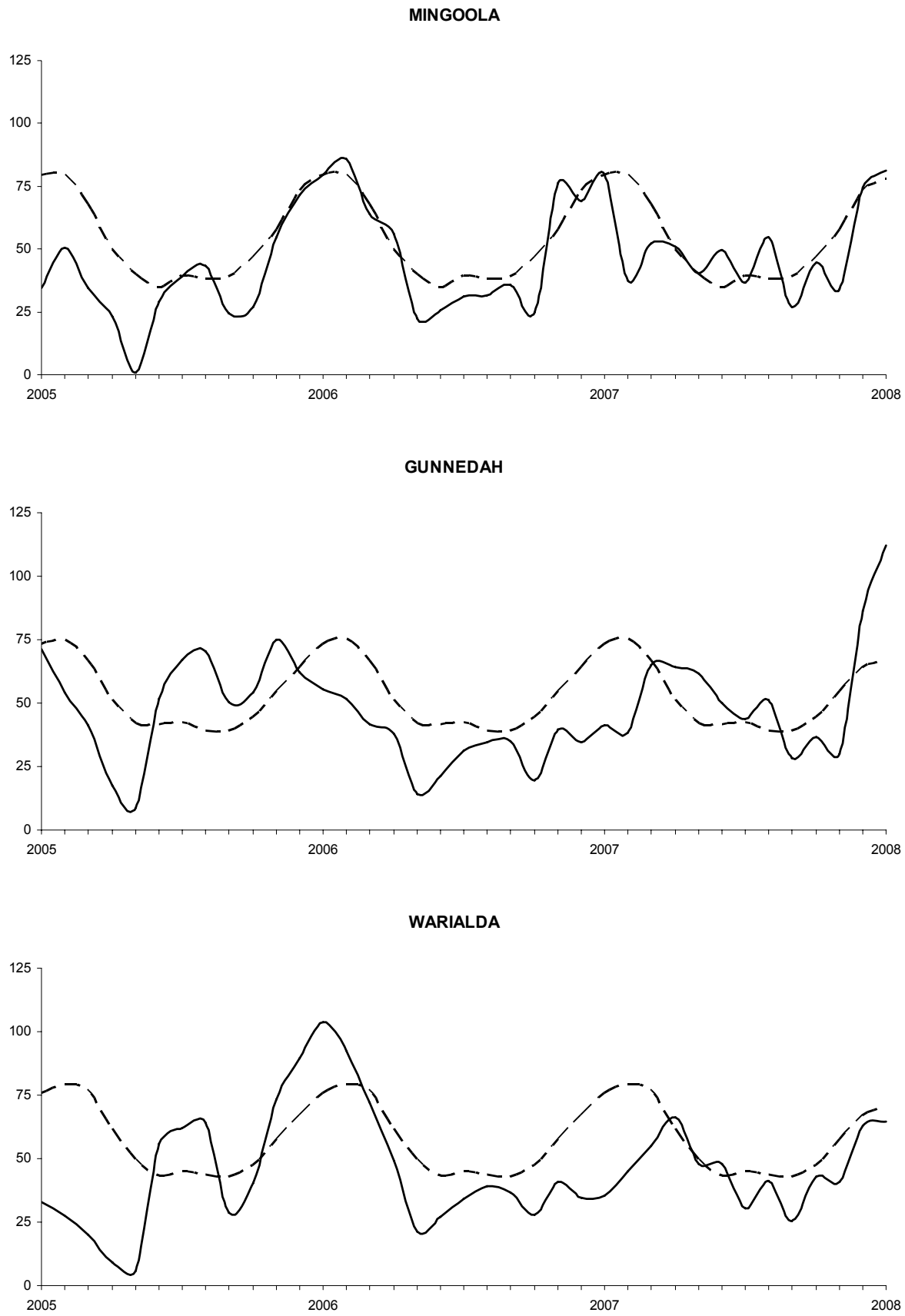


Figure 8. Three-monthly averages of rainfall from long-term data (1977-2007 – broken line) and for each of the study years (solid line) for selected townships on the NW Slopes. Mole River is not represented in Figure 3.2 because there were no temperature data available (Bureau of Meteorology 2008).

3.2.1. Site 1 – Mingoola

151˚ 57’ E, 29˚ 2’ S, 333 m above sea level. Plate 5.

The Mingoola property is a 2000-hectare mixed farming enterprise located approximately 60 km west of Tenterfield. The principal land use is sheep, and the property has been grazed intensively over large areas. Set stocking at rates of 3 DSE ha^{-1} have occurred for at least the past 50 years (P. Hynes, personal communication 2007). Soils on the property are predominantly Kurosols and Sodosols (Isbell 2002) with sandstone geology. Pasture improvement (superphosphate) is widespread across the property and applied annually.

Small tracts of remnant vegetation suggest that the original communities may have consisted of *E. melanophloia* open woodlands, as well as denser sclerophyll forest with *E. albens* as the dominant canopy species. Scattered rainforest elements also remain in patches on the property, such as a grove of *Cadellia pentastylis* F. Muell. (Ooline trees) located near the study site. *Allocasuarina* sp. is common bordering the Mole River. Extensive areas of the Mingoola property are subject to significant soil loss, exposed sub-soil and sodicity. Very dense regrowth affects approximately half of the Mingoola property.

3.2.2. Site 2 – Yallaroi

150˚ 40’ E, 29˚ 27’ S, 316 m above sea level. Plate 6.

The Yallaroi property is the Douglas McMaster Research Station, owned by the University of New England, located approximately 37 km north-west of Warialda. Since its donation to the University of New England in 1967, the 1000-hectare station has been maintained as a research farm and has subsequently been exposed to a number of variable land management regimes. Presently, the principal land uses are cropping (Lucerne and Triticale) and grazing (cattle). Pasture improvements and amendments such as superphosphate application and the sowing of legumes are routine but vary across the property.

There are three soil types on the property ranging from Vertosols and Dermosols over basalt on gently undulating plains to red Chromosols with sandstone geology on hillsides still covered with a variety of native species. Whilst much of the station has been cleared for various management trials and experiments, some remnant vegetation remains. Unique western semi-evergreen vine thickets can be found on the outer edges of the property, as well as *E. albens* open woodland and sclerophyll forest. Native grasslands populated by *Bothriochloa macra* (Stued.) S.T.Blake are contracting, primarily due to a serious infestation of *Hyparrhenia hirta* (L.) Stapf. (Coolatai grass), which is widespread. Dense *C. glaucophylla* regrowth does not occupy a large proportion of the station, but is a significant issue for some of the adjacent landholders. Soil loss is most serious beneath *C. glaucophylla* stands where groundcover is sparse, but is negligible in comparison to the degree of erosion at the *Mingoola, Myall Creek* and *Bingara* properties.

3.2.3. Site 3 – Myall Creek

150˚ 79’ E, 29˚ 74’ S, 347 m above sea level. Plate 7.

Myall creek is located approximately 18 km south of Delungra. The 1100 hectare property changed ownership in 2002, and the previous regime of intensive sheep grazing ceased. Since 2002 paddocks severely afflicted by gully erosion and soil loss associated with product removal and exposed surfaces have been left to regenerate, and in some areas, water has been diverted in an attempt to remediate soil wash. The present land management strategy incorporates only a few sheep and cattle, which are rotationally grazed. Superphosphate has been applied to small areas four times over the last 25 years (B. Newton, pers. comm. 2007). Soil types vary from Dermosols over basalt on flat plains to red Chromosols on metasediments near the creeks and on sloping country.

Myall Creek has extensive riparian vegetation zones that border Myall and Staggy Creek and are comprised of *Leptospermum brevipes* F. Muell. and *Allocasuarina* spp. Steep country bordering the property has never been cleared and is comprised of *E. albens* woodlands with a well developed understorey. Approximately one third of the property is affected by very dense *C. glaucophylla* regrowth, which is mainly restricted to moderate slopes.

3.2.4. Site 4 – Bingara

150˚ 54’ E, 29˚ 76’ S, 410 m above sea level. Plate 8.

The property is located approximately 10 km north-west of the township of Bingara, and has been owned by one family for 50 years and managed primarily for sheep and some cattle grazing. The grazing intensity has decreased in the past ten years, and some stock rotation occurs. Superphosphate application was an annual management activity prior to its cessation in 2002. Soil types are Chromosols and Dermosols over some basaltic and primarily serpentine parent materials.

Much of the flora on the property is adapted to ultra-mafic parent material. On slopes surrounding managed paddocks, remnant tracts of dry rainforest and semi-evergreen vine thickets remain. *Eucalyptus serpentinicola* L.A.S. Johnson & Blaxwell and *Angophora floribunda* (Sm.) Sweet are the dominant tree species other than *C. glaucophylla*. *Triodia scariosa* N.T.Burb. subsp. *scariosa* was also a component of open woodland areas. Approximately one quarter of the property is occupied by dense stands of *C. glaucophylla*, and soil erosion is also common. The property also supports large mono-specific tracts of *H. hirta.*

3.2.5. Site 5 – Narrabri

150˚ 26’ E, 30˚ 01’ S, 317 m above sea level. Plate 9.

The 5000 hectare property is located approximately 70 kms north-east of Narrabri and changed ownership in 2003, prior to which it was grazed intensively by sheep and cattle. The property is now grazed on a rotational basis at a reduced stocking rate for both animals. Soils range from Vertosols on the flats near the creek, to Dermosols overlaying basalt on the slopes. Fertiliser application to the property has been minimal and restricted to a few small areas since 2003; the previous regime is unknown.

Most of the Narrabri property was cleared extensively prior to its acquisition by the present landholders. Only scattered *E. albens* remain, along with remnant *C. glaucophylla*, which have been retained as paddock trees. The shrub layer is mostly absent, however, well-developed (managed) native grassland covers much of the property, and at the time of sampling many ephemeral herbs such as *Wurmbea* sp., *Bulbine* sp. and a number of orchids were represented in the groundcover. Dense stands of *C. glaucophylla* occupy only a small proportion of the Narrabri property, and the soil condition and integrity of the groundcover are high.

3.2.6. Site 6 – Emerald Hill

150˚ 06’ E, 30˚ 92’ S, 297 m above sea level. Plate 10.

The property is located approximately 26 km north of Gunnedah. The 40-acre farm was once part of a larger sheep grazing enterprise, but has been maintained since 2001 as a ‘lifestyle block’. Grazing on the property is restricted to two sheep confined to a small area near the main residence. The soil type at the Emerald Hill property is a Kandosol over metasediments.

There is no application of fertiliser on the property, but the management history prior to the 2001 change of ownership is unknown.

Scattered *E. albens* and *Geijera parviflora* Lindl. are the only tree species other than *C. glaucophylla* that have been retained at the site. The groundstorey is almost entirely dominated by *H. hirta* and scattered chenopods such as *Einadia* sp. Dense regrowth occupies approximately half of the Emerald Hill property, and soil loss is negligible.

3.3. Study area overview

Sites were selected for a range of different studies, including observations of *individual trees* (Chapter Four), *regrowth trees* (Chapter Five) and for a *regrowth management trial* (Chapters Seven and Eight). All six sites were involved in the study reported in Chapter Four. Only *Yallaroi, Mingoola* and *Myall Creek* sites were selected for further study, as set out in Chapters Five to Seven. Specific references to sites and their characteristics henceforth will be modified from the full descriptions provided in journal articles presented as chapters in this thesis for the purposes of brevity. Except where the 'site descriptions' section of each paper (chapter) provides new information not already set out in sections 3.1 and 3.2, only a brief reference to the sites involved in each study will be provided.





Plate 5. (above) *Callitris glaucophylla* as a scattered paddock tree at the McMaster Research Station, Yallaroi, and below, a dense stand.





Plate 6. Managed pasture at Mingoola (above), and a view of the property showing extensive areas of dense *C. glaucophylla* regrowth.





Plate 7. View of the farming landscape at Myall Creek (above) and (below) dense regrowth on a slope with some soil loss beneath the canopy.





Plate 8. (above) A rested paddock at Bingara invaded by Coolatai grass (*H. hirta*) and a scattered pine landscape (below).





Plate 9. Diverse groundcover was common at Narrabri, including species such as *Wurmbea dioeca* (R.Br.) F.Muell. (above) although *C. glaucophylla* was the most common tree species (below).





Plate 10. Stands of dense *C. glaucophylla* occupy almost half of the Emerald Hill site (above), and most appear to have regrown after one germination event (below).

Chapter 4. Individual Trees

The impact of individual *Callitris glaucophylla* trees on agricultural soils and pastures of the North-Western Slopes of NSW, Australia

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Modified formatting and original text from the article published in *The Rangeland Journal, 31 (3): 1-21*.

4.1. Abstract

Woody vegetation thickening occurs in agri-ecosystems worldwide, often with negative consequences for production. Dense *Callitris glaucophylla* stands affect landscapes across NW NSW, Australia, and strategies to reduce tree density to levels, which maintain biodiversity values alongside agricultural production, are currently being sought. We investigated soil chemical and groundcover patterns associated with individual small and large *Callitris glaucophylla* trees at 6 sites of variable management history and lithology in North West NSW, Australia. We posed two questions: (1) do individual *C. glaucophylla* trees impose patterns on soil and groundcover (soil extractable P, C, N, S and pH, litter biomass, litter P and pasture cover), and, (2) if patterns exist, do they differ between tree sizes?

Extractable P, C and pH declined away from trees of both sizes but significantly higher values were recorded adjacent to the stem of large trees. Litter biomass exhibited a strong site-related trend independent of soil variables. Positive correlations between litter and soil variables existed for some sites and not others, indicative of processes such as grazing which contribute

to the transport of litter away from the tree. Irrespective of tree size ground-storey vegetation cover increased significantly away from the stem, presumably as a consequence of competition for soil water.

The results indicate that single *C. glaucophylla* trees enrich soils in patterns analogous to other species in similar environments worldwide. However localised soil improvements must be weighed up against the negative effects of decreased groundcover associated with trees, and the potential for the species to re-seed prolifically into managed paddocks. Future research will discern the impact of individual *C. glaucophylla* trees at higher densities, where soil patterning may be modified by intense within-stand competition.

4.2. Introduction

Woody vegetation thickening has occurred in many ecosystems around the world, as a consequence of altered grazing regimes and changes in the populations of introduced and native herbivores (Attiwill and Clayton-Greene 1984; Eldridge and Simpson 2002; Walker et al. 1981; Williams and Ashton 1987), the exclusion of fire (Boer and Stafford Smith 2003; Harrington 1991) and climate change (Johnson et al. 1993). Management changes that adversely affect surface soil condition also favour the establishment of woody vegetation over pasture (Walker and Noy-Meir 1982). On the North-Western Slopes of NSW, Australia, *Callitris glaucophylla* (Joy Thomps. and L.A.S. Johnson – White Cypress Pine) is an indigenous conifer which has responded to a series of agriculturally-imposed conditions (e.g. exposure of bare soil, removal of other vegetation types) by regenerating prolifically at densities of up to 30 000 stems ha^{-1} (McHenry et al. 2006). The species is considered to impact negatively on the productive capacity of agri-ecosystems due to the occupation of managed land by dense stands.

There is a community perception that dense *C. glaucophylla* stands should be actively managed or cleared because they contribute to land degradation through soil nutrient depletion, soil loss and groundcover inhibition (Cobar Vegetation Management Committee 2006; Harris et al. 2003), and there is some evidence to suggest that the removal of woody vegetation from managed landscapes will result in soil nutrient release and short-term gains in forage production (Walker et al. 1986). In NSW, the Act (2003) has been used to regulate the management of dense stands in agri-ecosystems whilst allowing for treatments of *C. glaucophylla* which '*improve or maintain'* environmental outcomes. The most appropriate methods for managing the species in order to maximise ecological and productive outcomes are still unclear, however, because there is a paucity of published information that describes the roles and functions of the species at any spatial scale in the agricultural landscape.

Numerous Australian and international studies suggest, that unlike high-density stands of trees, there are localised enhancements associated with single trees in agri-ecosystems. Scattered trees maximise faunal diversity and habitat (Dean et al. 1999; Law et al. 2000; Oliver et al. 2006). The tree canopy zone is often associated with an accumulation of soil nutrients and organic matter (Dahlgren et al. 2003; Eldridge and Wong 2005b; Graham et al. 2004), reduced bulk density and enhanced soil structure (Chilcott et al. 1997; Degans 1997) and modifications to vegetation composition and increased diversity (Murphy 1999; Spooner et al. 2002). To date, little research has described the environmental impacts of *C. glaucophylla* trees at any spatial scale or density, and this has hindered attempts to develop appropriate management strategies for the species.

In this study, we examined the influence of isolated *C. glaucophylla* trees on surface soil and groundcover properties in farming landscapes of the NWS of NSW, Australia. We conducted this research as part of a series of investigations pertaining to the roles and functions of *C.*

glaucophylla in agri-ecosystems at a variety of spatial scales, in order to inform the debate with respect to the optimum management of the species. Prior to conducting this study, we expected that juvenile trees colonising partially cleared landscapes might impose different effects on soil and groundcover than established mature trees due to the requirement of establishing vegetation to draw upon soil nutrients for early growth (Grove et al. 1996). Therefore, we also compared soil and groundcover patterns associated with both juvenile and mature trees.

Specifically, we posed the questions:

1. Do individual *C. glaucophylla* trees impose patterns on soils and groundcover; and,

2. If patterns exist, do they differ between juvenile (small) and mature (large) trees?

4.3. Methods

4.3.1. Regional and site descriptions

The six study sites were located on the NWS of NSW, Australia (See Chapter Three, Figure 6) and were sampled in October 2006. Altitude across the region varies from approximately 270 m at Gunnedah to over 800 m near Inverell. The climate of the region is sub-humid with summer temperatures over 35 ˚C common in January and February and mild winters with occasional frosts. Average annual rainfall is 400-700 mm (Bureau of Meteorology 2006); although a drought from 2002 to 2008 resulted in much lower than average rainfall (c. 60% of the annual mean) across the region. Most native vegetation on the North-Western Slopes, which included *E. albens* or *E. melanophloia* with *C. glaucophylla* as a sub-dominant species, was cleared for agriculture prior to 1950 and now only small remnants remain. Scattered trees with a managed (grazed) grassy understorey, including both native and introduced species (notably the invasive grass *H. hirta*) and dense stands of *C. glaucophylla* are now common in agricultural landscapes of the NWS (Plate 11).



Plate 11. An individual small tree in a paddock near Narrabri, NSW, with managed mature *C. glaucophylla* forest in the background.

Across this region, we selected six sites of variable management history and lithology. Three of the sites were stocked with sheep and cattle at various intensities, whilst the other three sites had not been grazed for the last five years (Table 5).

4.3.1. Sampling design

At each study site, five small trees (juveniles which have not yet set seed - between 1.6 m and 3.5 m tall, canopy radius < 1.1 m) and five large trees (established fecund individuals - over 5 m tall and > 1.6 m canopy radius) were selected and the DBHOB, tree height and canopy radius (r) were determined. The large trees are believed to be from the period prior to a substantial 1950s regeneration event across the region, and from landholder photos we are of the opinion that most of the large trees surveyed were 65 -100 years old. We did not

Table 5. Characteristics of sites on the North-Western Slopes of NSW, Australia. Soil types follow Isbell (2002). Grazing history is defined by frequency and intensity of stocking.

Site	Location	Geology	Soil Type	Grazing History (post-2001)
1. Mingoola	29.07˚ S 151.57˚ E 390 m a.s.l.	Black silicified mud/siltstones	Kurosol	Stocked. Set-stocked, high intensity (sheep)
2. Yallaroi	29.27˚ S 150.40˚ E 416 m a.s.l.	Basalt	Vertosol	De-stocked. Previously low-intensity, infrequent (cattle)
3. Myall Creek	29.74˚ S 150.79˚ E 377 m a.s.l.	Basalt	Dermosol	De-stocked. Previously set-stocked, high intensity (sheep)
4. Bingara	29.76˚ S 150.54˚ E 410 m a.s.l.	Serpentenite	Chromosol	Stocked. Periodically stocked, high intensity (sheep)
5. Narrabri	30.01˚ S 150.26˚ E 417 m a.s.l.	Basalt	Vertosol	Stocked. Set-stocked until 2000, periodically stocked, low intensity 2002-2006 (cattle)
6. Emerald Hill	30.92˚ S 150.06˚ E 297 m a.s.l.	Quaternary alluvial sand	Kandosol	De-Stocked. Previously periodically stocked, high intensity.

sample trees around which there were obvious signs of stock camping. *Callitris glaucophylla* were the only trees present in the sampling area. Beneath each tree, soil and litter were sampled along a transect aligned to magnetic north at five intervals: adjacent to the stem, half the canopy radius (0.5 r), at the edge of the canopy (r), 1.5 canopy radii (1.5 r), and an adjacent sample at 3 canopy radii (3 r) beyond the influence of the tree. Trees were a bare minimum of 10 canopy radii away from each other in order to be classified as 'individuals'.

4.3.1. Method details

(Soil profiles (0-50 cm) were collected at each of the five sampling points along the transect, using a 45 mm diameter steel coring device, but only mineral soil results (0-5cm) are presented in this chapter, with the remainder presented in Chapter Five). At each point along the transect, 10 cm x 10 cm litter samples were collected and the depth of the litter layer determined. Due to the difficulty in ascertaining percentage vascular plant cover directly adjacent to the tree, cover was recorded in a 1 m^2 quadrat centred *between* each sampling

point. If sampling points were < 1m apart (which occurred in small tree transects), we recorded groundcover in a centred between adjacent pairs of sampling points. Although this resulted in groundcover sampling points which did not align with the position of soil and litter samples, this method minimised the potential error in attempting to average groundcover between sampling points that were a considerable distance apart.

Soil samples were oven dried at 40° C for 48 hours, crushed and sieved to < 2 mm. We assessed soil parameters which have been demonstrated to respond to the presence of trees in the study region (Wilson *et al.* 2007). Samples were analysed for total C, N and S by LECO combustion at 900 º C and Olsen-extractable phosphorus (ext. P) (Olsen *et al.* 1954). Soil pH was determined in a 1:5 0.01 M $CaCl_2$ soil suspension. Dried litter samples (80˚ C for 24 hours) were ground to < 2 mm and were pooled to create one sample per distance for each tree size per property. Litter samples were analysed for P following a sealed container digest (Anderson and Henderson 1986) using an inductively coupled plasma-optical emission spectrometer.

4.3.2. Statistical analyses

We expected that mean values for soil chemical parameters would differ between sites due to variable management history and soil type across this study. Therefore, we employed statistical techniques to describe similar trends along transects which were evident at all sites. In order to determine whether small and large trees imposed similar soil chemical patterns irrespective of site, we used multivariate exploratory Multi-Dimensional Scaling (MDS) with tree size as a potential grouping variable using Primer version 6. Multi-Dimensional Scaling was a preferred option over other clustering methods such as Principle Components Analysis (PCA) because it compares non-parametric data when there are a number of variables with different distributions (non-normal). In addition, a Euclidean distance matrix was constructed for S, C, N, extractable P and pH, for MDS computation to account for environmental

parameters with different units of measure (e.g. μg g^{-1}, pH). The main effect of distance along transects was assessed using two-way crossed analysis of similarities (ANOSIM) which described differences between levels of factor A (distance) when it was known that factor B (site) would vary. Finally, the variables that contributed most to each significant group (distance) were determined using the SIMPER function. Once the MDS for soil parameters was established, all analyses were re-run to include the variable LDW in order to determine if patterns imposed on soils by trees were also reflected in the distribution of litter.

In order to quantify the patterns imposed by trees on soils and litter, and whether these patterns varied between tree sizes, we conducted a three-way analysis of covariance (ANCOVA) with the fixed factors 'site', 'tree size' and the covariate 'distance' on the largest contributing variables (extractable P, C and pH) to the MDS previously revealed by the SIMPER analysis. Data were transformed where necessary to satisfy normality assumptions. Due to pooling of samples and loss of replication we omitted litter P and groundcover from the initial multivariate analyses. These parameters were also analysed by three-way ANCOVA. Where there appeared to be a consistent trend with distance for all variables irrespective of site ($\alpha = 0.05$), we performed post-hoc tests (Fishers protected LSD) on two-way ANCOVA (factors 'size' and 'distance'). To determine if litter and soil characteristics were related, spearman correlations were performed for soil ext. P and litter P, litter biomass and soil C as well as litter biomass and soil extractable P from the pooled data across all sites. Univariate analyses were performed in S-Plus™ version 7.0 (Insightful Corporation 2005).

4.4. Results

4.4.1. Do C. glaucophylla *trees impose patterns on soil and groundcover?*

The stress values for the MDS representing soil variables for small or large trees were low, at 0.1 and 0.08 respectively (Figure 9) indicating a good and reliable representation of the data in multivariate space. Clarke and Warwick (2001) suggest interpretations of MDS can be

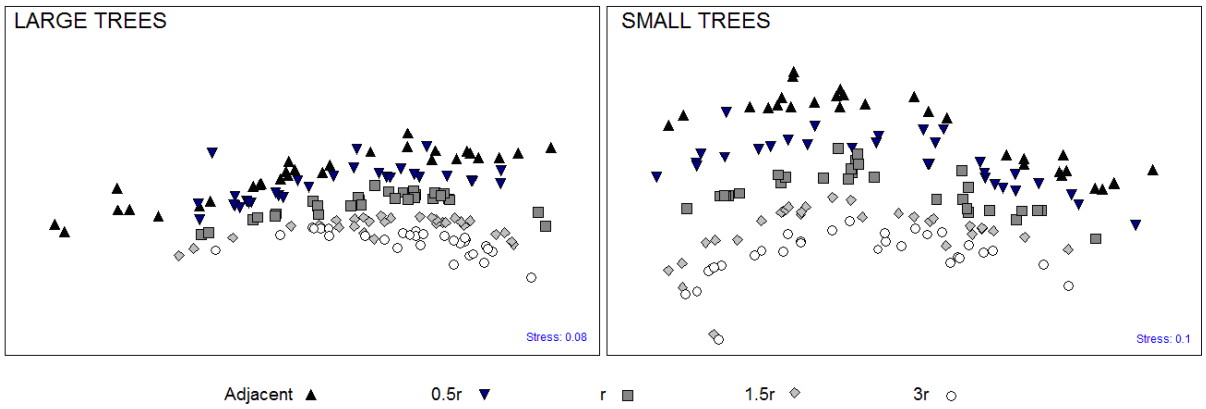


Figure 9. Multi-Dimensional Scaling (MDS) plots of soil variables assessed across six sites for small and large trees, clustered by distance from tree. The first dimension represents variation associated with sites and the second dimension represents variation associated with distance from tree. Images are to scale.

made until a stress value of 0.22 is reached). A similar pattern was evident for both small and large trees in the MDS, with a broad scatter across the 'x' axis reflecting the substantial variation in mean soil parameters due to site. Irrespective of this site variation, five groups, each containing one distance from the tree, were ordered consecutively from adjacent through to 3 r along the 'y' axis. The ANOSIM revealed significant differences between each distance group ($p < 0.02$) for both tree types, with the exception of 1.5 r and 3 r for small trees.

From the SIMPER analyses for small trees, ext. P contributed most to distance groupings adjacent to the tree (48%), followed by pH (37%) and C (14%). At 1.5 r pH became most dominant variable (44% contribution compared to ext. P = 40% and C = 14%). The variables ext. P (76% - 81% contribution), C (11-16%) and pH (6-9%) contributed to dissimilarity between distance groups for small trees. For large trees, ext. P, pH and C again contributed to the similarity within the adjacent distance group (54%, 33% and 13% respectively) and changed to 42%, 41% and 16% respectively at the 3 r distance. Extractable P and C contributed most to dissimilarity between each distance group, with a minor contributing effect of pH (5 – 8% of dissimilarity explained) at distances further from the tree (1 r to 3 r). Levels of similarity within each distance group ranged from 75-79% across transects for both

small and large trees. Therefore, there was a trend in soil parameters associated with distance from the tree stem for small and large trees, and the most important contributing soil variables were ext. P, C and pH.

Including the variable litter biomass resulted in different clusters in the MDS for both small and large trees, with slightly higher stress values (0.14 and 0.11 respectively – still indicating good data representations). Unlike the analysis without litter, not all distance groupings were significantly different from each other when pooled across sites, and these varied for each tree size (adjacent, 0.5r and r were significantly different from each other for large trees and adjacent was different from all other distances for small trees). Levels of similarity *within* groups were lower (50 – 59%) for both tree sizes than in the soil variable analysis, indicating that litter introduced much more variation into the analysis. Litter biomass also contributed 40 to 60% of the dissimilarity between distance groupings, followed by extractable P, C and sometimes pH. Thus, litter introduced more variation into the analysis, making groups more variable but also making the differences between distances closest to the tree more pronounced.

4.4.2. If patterns exist, do they differ between tree sizes?

Soil S and N did not appear to be good indicators of tree-soil patterns in the MDS and hence only ext. P, C and pH were further explored by univariate analyses. For ext. P, there was a highly significant interaction between sites, size and distance ($F_{(5,276)} = 3.24$; $P = 0.007$) which was indicative of between-site variability, and a trend of decreasing values with each distance away from the tree. All distances were significantly different from each other along the transect. Mean values for ext. P were significantly lower along small tree transects than large tree transects. Comparisons between tree-adjacent and 3 r values revealed a 240% increase in ext. P beneath large trees when averaged across all sites whilst the increase for small trees was 130% (Figure 10*a*).

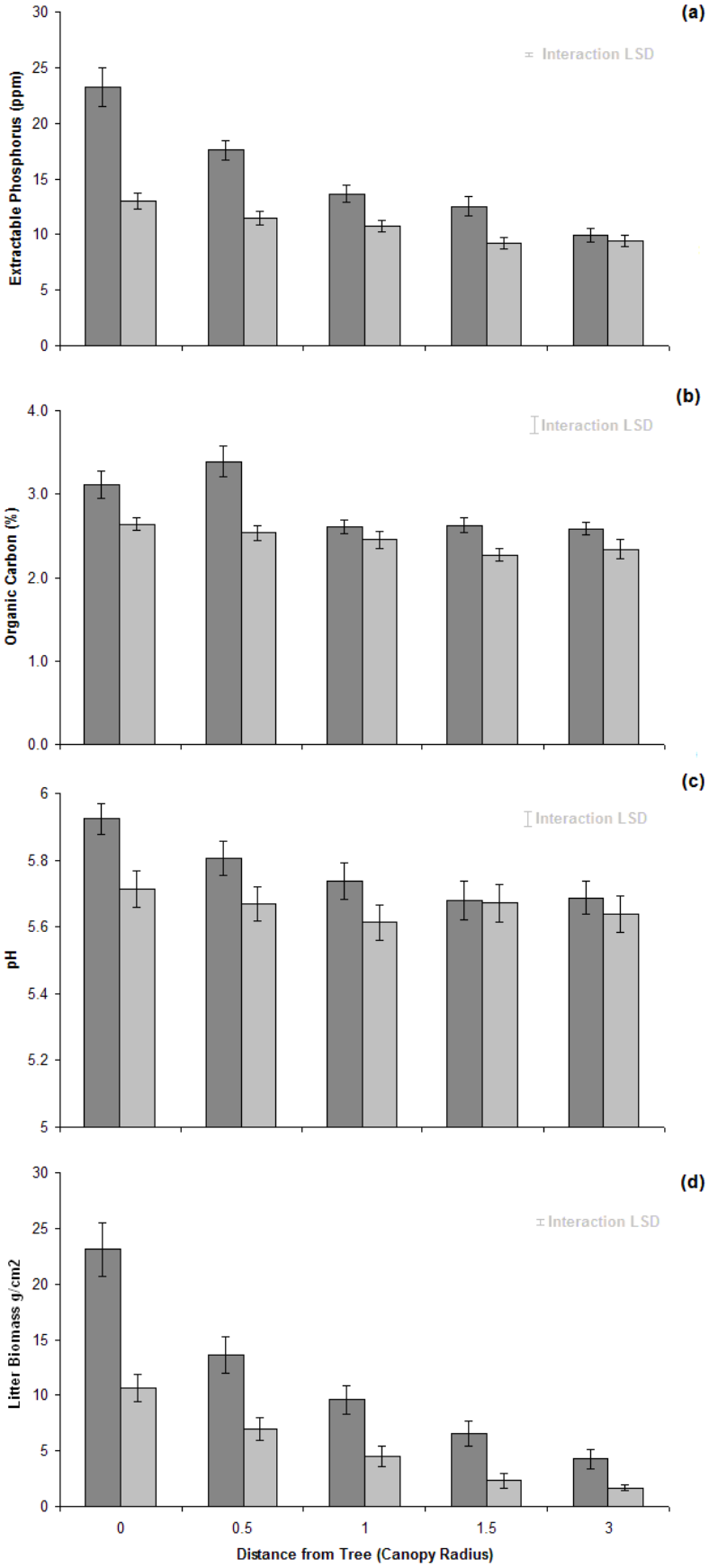


Figure 10. The distribution of parameters (*a*) soil extractable P, (*b*) organic carbon and (*c*) pH, as well as (*d*) litter biomass with distance from small (light shaded) and large (dark shaded) trees across all sites. Interaction LSDs were calculated using two-way ANOVA (size*distance).

Soil C distribution varied significantly by the factors site ($F_{(5,276)}$ = 69.18, P = 0.0001), size ($F_{(1,276)}$ = 12.01, P = 0.0001) and distance ($F_{(1,276)}$ = 8.05, P = 0.0040). For large trees, all distances except 1.5 r and 3 r were significantly different from each other (Figure 10*b*). Mean C peaked at 0.5 r, which was 130% higher than at 3 r. Carbon values exhibited a 3% decline along transects from small trees, although only the values closest to trees (0 and 0.5 r) and around the canopy (1 r and 1.5 r) were significantly different from each other. Carbon associated with large tree transects had significantly higher values than small tree transects, except at 1 r. Two way interactions were significant for soil pH (site×size: $F_{(5,276)}$ = 2.27, P = 0.047; site×distance: $F_{(5,276)}$ = 3.01, P = 0.011; size×distance: $F_{(1,276)}$ = 4.13, P = 0.42).

There was significant decrease in pH between the adjacent value and 3 r for large trees, although this represented a decline of only 0.3 of a pH unit across the entire transect when averaged across all sites (Figure 10*c*). pH declined significantly with distance from large and small trees, with the exception of 1.5 r and 3 r for large trees. pH values were only 0.1 unit higher adjacent to the stem compared with 3 r for small trees. Therefore, soil C and pH were both significantly higher beneath the canopy of trees, although mean values were lower and the pattern was restricted to a lesser area beneath small trees.

The distribution of litter varied significantly with site and distance ($F_{(5,276)}$ = 3.00, P = 0.011) as well as size and distance ($F_{(1,276)}$ = 4.13, P = 0.040). Litter declined significantly with each distance from large trees, and at each distance from the tree stem to 1.5 r for small trees (Figure 10*d*). Litter biomass was significantly higher at every distance along large tree transects than small tree transects. The interaction between sites, size and distance was significant for litter P ($F_{(5,36)}$ = 2.69, P = 0.036). Litter P declined with increasing distance from small and large trees, although values were not significantly different from each other between tree size except at the greatest distance from trees (3 r).

Vascular plant cover varied significantly with site and size ($F_{(5,216)}$ = 12.73, P = 0.0001), and distance ($F_{(1,216)}$ = 14.01, P = 0.0001) (Figure 11). Between-site variation in cover was high and made statistical trends difficult to determine but vegetation cover increased away from trees of both sizes at all but one site (Myall Creek). Both the Emerald Hill and Bingara sites were invaded by *H. hirta*, especially around small trees, resulting in significantly higher and more uniform values across transects in these sites compared with other sites.

Moderate positive correlations were demonstrated for large trees across all sites and distances between soil ext. and litter P (r = 0.70), litter biomass and soil C (r = 0.63), and soil P (r = 0.90). Litter P and soil ext. P were positively correlated for small trees (r = 0.90).

4.5. Discussion

Our results can be summarised in two key points pertaining to the roles and functions of individual *C. glaucophylla* trees in agricultural landscapes. Firstly, irrespective of site characteristics, a distinct spatial pattern was imposed upon soil chemical parameters and groundcover by *C. glaucophylla* trees. This pattern is analogous to patterns observed for other tree species worldwide with respect to the distribution of litter and soil properties; although in this study we recorded a decrease in vegetation cover associated with trees. Secondly, these patterns were present for both small and large trees, which has significant implications for the way in which recolonising juvenile trees should be viewed.

4.5.1. Do individual C. glaucophylla trees impose patterns on soils and groundcover?

There was a significant decline in the soil parameters measured with distance from trees. This spatial arrangement conforms to other literature describing scattered trees in managed landscapes as ‘islands of fertility’ (Ozolins et al. 2001) and is consistent with numerous other

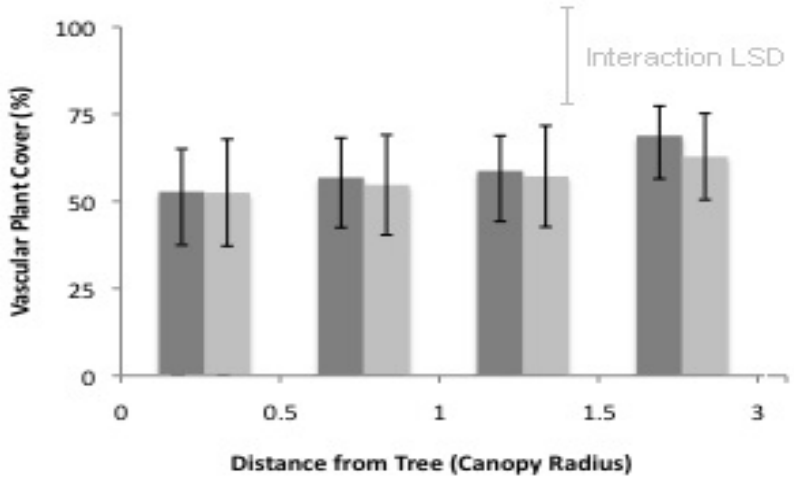


Figure 11. Variation in vascular plant cover with increasing distance from individual small (light shaded) and large (dark shaded) trees across all sites. Interaction LSDs were calculated using two-way ANOVA (size*distance).

studies, both in Australia and worldwide (e.g. (Belsky et al. 1993a; Belsky et al. 1993b; Dahlgren et al. 2003; Prober et al. 2002; Schlesinger and Pilmanis 1998; Wilson 2002). Nutrient accumulation associated with tree canopies has been attributed to litterfall, canopy nutrient interception and transport via stem flow and throughflow and concentration of nutrients in extensive root systems (Belsky et al. 1989; Prober et al. 2002). Biological pumping, whereby cations withdrawn by the roots deep in the soil profile are counterbalanced by organic anions in the plant deposited as litter, has been proposed as a cause of elevated surface pH close to tree stems in Australian *Eucalyptus* species (Noble and Randall 1999; Wilson et al. 2007). The elevated pH associated with trees in this study is a finding discordant with international literature from temperate environments, which indicates that conifers acidify soil (Boettcher and Kalisz 1990; Crampton 1982; Wilson and Campbell 1996).

The difference between ext. P, C and pH at adjacent and 3 r positions was lower at sites with more intense grazing regimes (Mingoola and Bingara), which might indicate lateral redistribution of nutrients from beneath the tree to the paddock during grazing. Belsky *et al.* (1993b) reported contrasts in soil nutrient patterning across a grazing gradient in Kenya and found that patterns of nutrient accumulation beneath trees diminished proportionally with the

level of grazing. The distribution of litter, although decreasing away from trees in a similar pattern to soil parameters when averaged across all sites, varied significantly at each distance due to the effects of site, especially for large trees. In this study, litter distributions were related to site, and correlations between litter biomass and soil properties were generally weak, which might also indicate limitations to localised soil enrichment by trees where litter has been removed, scattered or incorporated into the mineral soil by domestic livestock. On this basis, we suggest future research should be focused upon the assessment of tree-induced soil patterning across a wider range of land uses, especially where various grazing regimes can be compared and contrasted.

4.5.2. If patterns exist, do they vary with tree size?

Soil and litter parameters differed significantly between tree sizes, with more substantial accumulations in the canopy zone beneath large trees for all soil parameters studied. Since tree age is related to the magnitude of influence on soil properties (Scholes and Archer 1997), the spatially restricted, less intense enrichments surrounding small trees will presumably increase over time. A lack of temporal accumulation of resources may also have been reflected in the weak correlations between litter and soil parameters beneath small trees.

The results of this study contradict popular opinion regarding the effects of recolonising woody vegetation. In this study, we assumed tree size to be an approximate indicator of tree age, therefore that small trees were juveniles recently re-established on previously cleared pastures. There is much debate on the impacts of vegetation thickening in NSW that has been expressed primarily in community-orientated literature. In NSW, there is a particular concern that individual, regenerating *C. glaucophylla* trees pose specific threats to soil condition, vegetation cover and productivity (e.g. Cobar Vegetation Management Committee 2006). The Act now permits management of the species providing that doing so '*improves or maintains*'

environmental condition. For the soil and litter parameters reported here, we have demonstrated that single *C. glaucophylla* trees do not diminish fertility or condition. Despite the observation that the small trees in this study were still growing, soil fertility enhancements still occurred at the base of individual trees.

Conversely, individual *C. glaucophylla* trees appeared to have an adverse effect on vascular plant cover in this study, which was lowest adjacent to the stems of trees of both sizes. Although this pattern was spatially restricted around small trees, mean values were similar for both tree sizes and obscured only by extensive populations of *H. hirta* associated with two sites. The limited effects of tree size on cover in this study would suggest that a relationship with soil fertility, which differed between sizes, is unlikely. Although litter chemistry has been suggested as a cause of groundcover inhibition beneath dense stands, mean plant cover along the transect was similar regardless of tree size yet litter biomass was significantly lower beneath small trees. Harris *et al.* (2003) found that *C. glaucophylla* litter from a similar environment actually facilitated the growth of other species *ex situ* due to its effect on enhancing the water holding capacity of the soil. Given the limited projection and density and hence shading capability of the canopy, we postulate that the negative impact of *C. glaucophylla* trees on vascular plant cover is probably the result of below-ground processes, such as competition for water during drought.

4.5.3. Implications for future management

Our research highlights the important role of trees in influencing soil properties in managed landscapes, even for this 'problematic' woody species. Whilst these effects are consistent with other local and international literature, the benefits must be weighed against the potentially negative impacts imposed by the presence of *C. glaucophylla* trees. The consequences of retaining these trees include a reduction in vascular plant cover beneath the canopy and the

prolific re-seeding of mature trees into otherwise cleared landscapes. Grazing might also have resulted in lower litter biomass and impacted upon vegetation cover, which has potentially serious implications for soil loss beneath tree canopies, especially when the dense cover of litter adjacent to the stem is scattered or removed by livestock. Our future research will investigate management strategies for the species through a series of studies encapsulating soil condition, silvicultural management, pasture diversity and tree demography at a variety of spatial and temporal scales.

4.6. Statement of Originality

Journal-Article Format for PhD Theses at the University of New England

STATEMENT OF ORIGINALITY

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Chapter Four	
"Rangeland Journal"	
paper	

} 100% McHenry with contributions from supervisors, statistical advice and technical advice.

Name of Candidate: Melinda McHenry

Name/title of Principal Supervisor: Dr. Brian Wilson

[redacted]

17/12/08
Date

[redacted]
Principal Supervisor

17/12/08
Date

4.7. Authors Contributions

Journal-Article Format for PhD Theses at the University of New England

STATEMENT OF AUTHORS' CONTRIBUTION

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name (please print clearly)	**% of contribution**
Candidate	MELINDA MCHENRY	~~80~~ 70.
Other Authors	BRIAN WILSON	5%.
	PETER LOCKWOOD	5%.
	CHRIS GUPPY	3%.
	BRIAN SINDEL	2%.
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Date

Chapter 5. Regrowth Trees

Do dense plant populations influence soil nutrient and groundcover distribution?

5.1. Background

In Chapter Four, I presented the results of a study of nutrient and groundcover distributions surrounding individual *C. glaucophylla* trees of different sizes; size being used as a surrogate for tree age. There was a clear association between the presence of trees and elevated soil C, pH and ext. P, similar to other tree species in similar environments worldwide. For the groundcover parameters litter biomass and vascular plant cover however, spatially dependent patterns associated with single trees varied greatly between sites. It was concluded that the factors influencing this site-specific variation were most likely weed incursions and the effects of grazing livestock.

In this chapter, I examine tree-mediated soil chemical patterns and groundcover distributions within dense, mono-specific *C. glaucophylla* stands at three study sites on the north-western slopes of NSW. Given the results of Chapter Four, the following question is posed, 'Does tree size and location influence soil condition and groundcover distribution in dense stands?' In this chapter I also build on the results of the preliminary research presented in Chapter Two, in which I compared dense stands with adjacent un-colonised pasture. Furthermore, incorporating the results from Chapter Four, I compare and contrast the net accumulation of resources beneath single trees and adjacent paddocks with dense stands, in order to determine the role of dense *C. glaucophylla* stands in these agricultural landscapes.

5.2. Introduction

Spatial heterogeneity of soil properties in grazed, open woodlands can arise from interactive soil-plant relationships which result in the net accumulation of soil nutrients and soil C beneath the tree canopy (Belsky et al. 1989; Graham et al. 2004; Zinke 1962 and see Chapter Four). The accumulation of soil nutrients and C beneath the canopy usually represents a substantial increase in soil nutrient concentrations, especially in resource-poor environments (Li et al. 2008; Schlesinger and Pilmanis 1998).

Due to the complex interdependence of trees, soils and groundcover, accounting for the processes that lead to spatial heterogeneity within fragmented vegetation populations and communities in managed landscapes is fraught with difficulty (Mora and Iverson 2002). Most studies describing plant-soil interactions in woodlands worldwide are concerned with changes in the growth and composition of plant *communities* (Puignaire et al. 1996; Tilman and Pacala 1993; Tongway and Ludwig 1990) or the relative performance of individuals in *populations* (Chapin et al. 1994) in response to soil heterogeneity. At the population level, the relative contributions of individuals to soil and groundcover patterning through processes such as nutrient cycling are poorly understood.

Most plant populations consist of individuals that differ in age, size and distribution. This asymmetry leads to variable resource competition, and often, different degrees of competitive advantage based on plant size (Caldwell et al. 1996; Chapin et al. 1994; Pacala and Weiner 1991). Larger plants have both the ability to capture more resources (Casper and Cahill 1996), and can also potentially re-distribute more mineral resources through the processes of litterfall and fine-root turnover. In plant populations that exhibit asymmetric nutrient turnover, some soil chemical parameters will show strong spatial dependence on individuals within the population, even if the stand is from one recruitment event and is evenly spaced and hence plant size is the only variable (Riha et al. 1986).

Many studies have likened the cumulative effects of woody vegetation in agri-ecosystems to the 'islands of fertility' effect of individual trees, but these studies have compared woodland *communities* to adjacent open pasture (Eldridge and Wong 2005a; Mathers et al. 2006; Wilson et al. 2008; Yates et al. 2000). Comparative studies between woody plant *populations* and adjacent agricultural land commonly describe the effects of forestry plantation establishment (Brunet 2007; Davis and Condron 2002; Groenendijk et al. 2002), which typically results in favourable outcomes for soil fertility, understorey vascular plant re-establishment and increases in farm profit. In contrast, invasive native scrub populations in NSW such as dense *C. glaucophylla* stands, do not enhance farm productivity or profitability, and there has been little research, which describes the effects of these species at any spatial scale on environmental condition.

In the previous chapter I described zones of elevated soil C, ext. P and higher pH associated with the canopy of individual trees growing in a semi-isolated configuration on farms. In this chapter, I investigate fine scale patterns of the same soil and groundcover parameters, and their association with individuals in dense, mono-specific *C. glaucophylla* stands at three grazing properties in North-West New South Wales, Australia. The following questions were posed:

1. Is there a relationship between tree size and/or distribution and the spatial pattern of soil chemical parameters (C, N, ext. P, S, pH) and groundcover (litter biomass and vascular plant cover) in dense stands?
2. Do dense stands perform the same 'ecosystem services' (e.g. increased soil ext. P, litter, C) as individual trees or does the cumulative effect of trees produce different environmental outcomes?

5.3. Methods

5.3.1. Site Descriptions

Three study sites were selected from the six in the previous chapter – Mingoola, Yallaroi and Myall Creek, each of which are located on the North-Western Slopes of NSW. The original vegetation of the region was typically woodland dominated by *Eucalyptus albens* (White Box) or *E. melanophloia* (Ironbark), which grew in association with *C. glaucophylla.* Tree clearing for agriculture across the North-Western Slopes has resulted in conditions suitable for the prolific regeneration of native shrubs and trees at very high population densities. Each site was characterised by the presence of dense mono-specific *C. glaucophylla* stands*,* which had repopulated previously cleared land after 1990 and no other tree species were present within the sampling zones. Other site characteristics are listed in Table 6.

5.3.2. Sampling procedure

Sampling took place in November 2006. Three 25 m^2 (5 x 5 m) replicate plots were established no more than 20 m apart from each other at each site, and were selected on the basis that they were of similar slope, soil type and density of *C. glaucophylla* within each site, but were not necessarily exactly the same aspect. Plots were subdivided by ropes and pegs into 25, 1 m^2 squares. One 0-5 cm soil sample (taken with a 45 mm diameter steel coring device) and a 10 cm x 10 cm litter sample were taken at a random location in each 1m^2 square. The depth of the litter layer was also recorded for each sample. Each 1m^2 square was further subdivided by four into 0.25m^2 zones in which the percent cover of vegetation and micro-topography (using a GPS) were recorded.

The position of all *C. glaucophylla* trees (over 1.6 m in height) was recorded across the 25 m^2 plot. Seedlings under 1.6 m tall, and other shrub species were rarely encountered in any plot. The height, DBHOB and canopy radius were recorded for each tree.

Table 6. Characteristics of three sites on the North-Western Slopes dominated by dense *C. glaucophylla* regrowth. * Denotes average of three, 25 m^2 sub-plots. Adjacent paddock values are the mean of 3 r samples from small and large trees reported in Chapter Four, superscript letters denote significantly different groups.

Site	Location	Soil Type	Geology	Slope and Aspect	Tree Density (Stems ha^{-1})*	Mean adjacent paddock value (n = 10)				
						C (%)	N (%)	S (%)	Ext. P (mg/kg)	pH
Mingoola	29.0˚ S 151.5˚ E 390 m a.s.l.	Kurosol	Black Silicified Mudstones and Siltstones	1. – 9 º NE 2. – 9 º NE 3. – 10 º NE	10933	2.50^{b}	0.19^{b}	0.010^{b}	4.5^{c}	5.12^{b}
Yallaroi	29.2˚ S 150.4˚ E 416 m a.s.l.	Chromosol	Permian Warialda Sandstone	1. - 3 º S 2. - 3 º W 3. – 3 º W	7330	4.32^{a}	0.38^{a}	0.017^{a}	10.8^{b}	6.81^{a}
Myall Creek	29.7˚ S 150.7˚ E 377 m a.s.l.	Dermosol	Myall Creek Conglomerate	1. – 7 º NE 2. – 5 º NE 3. – 8 º NW	12400	1.94^{c}	0.15^{b}	0.007^{b}	15.5^{a}	5.57^{b}

5.3.3. Laboratory methods

Soil samples were dried at 40 °C for 48 hr, crushed and sieved to < 2 mm. Soil parameters were assessed that have been demonstrated previously to respond to the presence of trees in the study region (Wilson et al. 2007) and see Chapter Four). Samples were analysed for total C, N and S by LECO combustion and ext. P by the Olsen method (Olsen et al. 1954). Soil pH was determined in a 1:5 0.01 M $CaCl_2$ suspension containing 8 g of soil. Dried litter samples (80˚ C for 24 hours) were weighed in order to determine litter biomass.

5.3.4. Statistical analyses

5.3.4.1. Tree-groundcover-soil relationships in dense stands

Nested two-way ANOVA was used to determine if there was variation between the effects of plot (random) nested within site (fixed) for soil and groundcover parameters (Table 7). Where plots within sites were not significantly different from each other, parameters were pooled across sites. Conversely, if the plot effect was significant, then plots within sites were treated as separate entities in subsequent analyses (e.g. for ext. P and groundcover parameters).

Table 7. *F* – values from a nested, two-way ANOVA assessing variation in soil and vegetation parameters between the factors site (fixed; n = 3) and plot (random; n = 3). Asterisks denote levels of significance: *** $p < 0.001$, ** $0.001 > p < 0.01$.

Factor	DBH	Ext. P	pH	C	Litter	Cover	S	N
Site	n.s.	493.85 ***	226.63 ***	67.51 ***	7.92***	8.04 ***	35.34 ***	130.83 ***
Plot(Site)	n.s.	10.32 ***	n.s.	n.s.	7.03 **	7.91 ***	n.s.	n.s.

In order to determine if there was a relationship between tree size and soil parameters, I used exploratory multiple-regression analyses with the factors 'cell DBHOB' (the sum of the DBHOB of all trees in each 1 m^2 square), 'litter biomass' and 'vascular plant cover (averaged across sub-plots to give one value in each 1 m^2 square)'. For groundcover parameters, the factors were 'cell DBHOB' and either 'litter biomass' for the cover analyses and vice versa. Cell DBHOB was chosen as the most appropriate tree characteristic to regress soil parameters against, because of its significant positive relationship with canopy radius ($F_{(3,229)} = 3006$, $P = 0.000$) and height ($F_{(3,229)} = 872$, $P = 0.001$), whereas canopy radius and height did not have a significant relationship. Further, spatial mapping of tree canopy radii indicated that tree canopies intersected in some sections of each plot (Figure 12) which would make it difficult to interpret tree-soil-groundcover relationships.

Regression analyses were performed for a second time to include only the significant factors or combinations of factors. Separate regression equations were generated for each site, except for extractable P, litter and cover, where regression equations were generated for each plot within site. Outliers that appeared to skew the results of individual regressions were excluded after visual inspection of the data. Another statistical approach to assessing the relationships between spatially distributed data in different layers (e.g. soil C and trees) is co-kriging. This approach could not be used in a manner that would allow for efficient interpretation for these data because trees and soil samples had different spatial points of origin, and the analysis is also sensitive to isotropic factors such as slope.

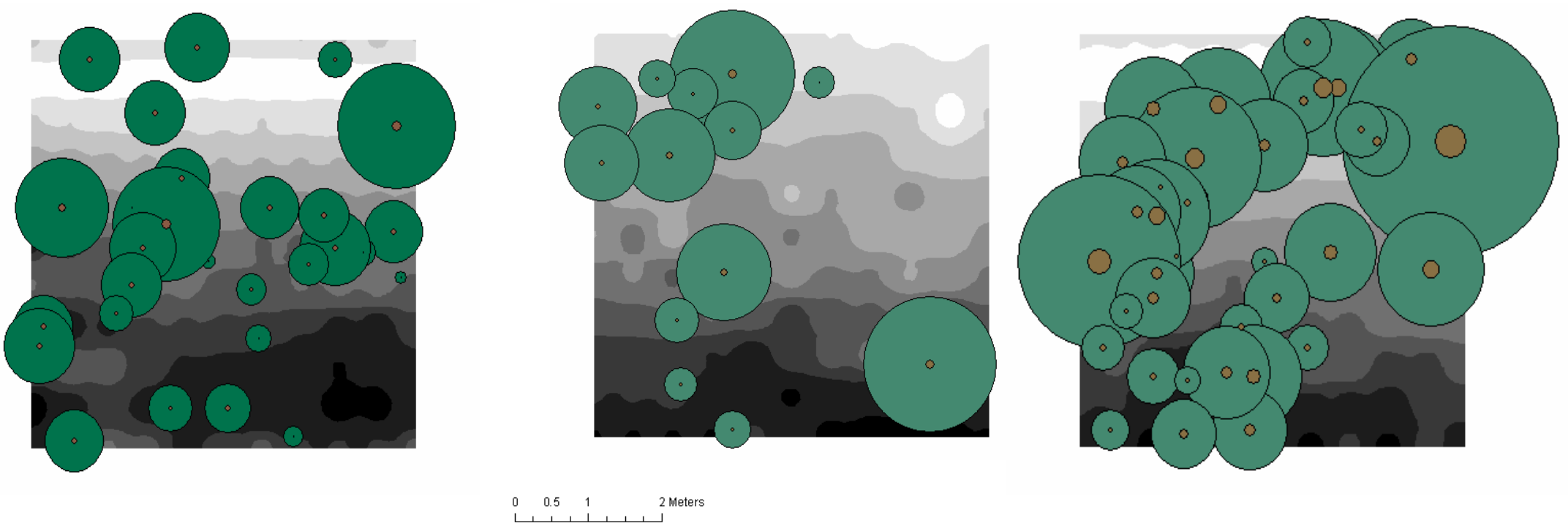


Figure 12. An example of intersecting canopies and their underlying DBHOB and micro-topography (black – lowest point, white highest point) for plot 1, Mingoola (left), plot 1, Yallaroi (middle) and plot 1, Myall Creek (right). All images here are presented with a northern orientation to the top of the page. Slopes at each site were 7, 3 and 9 degrees (L-R) respectively.

5.3.4.1. Comparisons between dense stands, individual trees and paddocks

Mean values for soils and groundcover were compared between the groups of trees studied in this chapter with adjacent paddock values (3 r; n = 10 per site) and values under individual small and large trees (adjacent and 0.5 r; n = 10 per tree size per site) reported in Chapter Four using unbalanced ANOVA with the factors 'site' (fixed) and 'zone' (random). A comparison between C:N ratios is provided, which was omitted from 5.3.4.1 because it provided no further information on spatial relationships than C or N alone. The close proximity of dense stands to the individual trees sampled (less than 200 m and on the same soil type) and the limited temporal separation of sampling excursions (3 weeks, same season, no rainfall) supports the comparison of these data.

5.4. Results

5.4.1. Tree-Groundcover-Soil relationships in dense stands

Extractable P, groundcover and litter biomass differed significantly between sites and plots (Table 7), however all other variables differed between sites only. Higher soil pH and levels of extractable P, total N and C were found at the Myall Creek site (Figure 13a). There was substantial within-plot variation in groundcover and litter biomass (Figure 13b), which contributed to low R^2 (i.e. < 0.55) values in the ANOVA. Within plots, variation in soil parameters was not as substantial as for groundcover parameters. For instance, extractable P varied between 5 – 10 μg g^{-1} in Mingoola plot one, whilst groundcover at the same location varied between 0 – 55 % across the same area.

Visual inspection of the data using ArcGis indicated few spatial correlations between trees and soil and vegetation parameters, which was confirmed by the results of the multiple regression analyses (Table 8). At Mingoola, marginally significant positive relationships were evident between cell DBHOB and C, as well as N. At plot one, Mingoola,

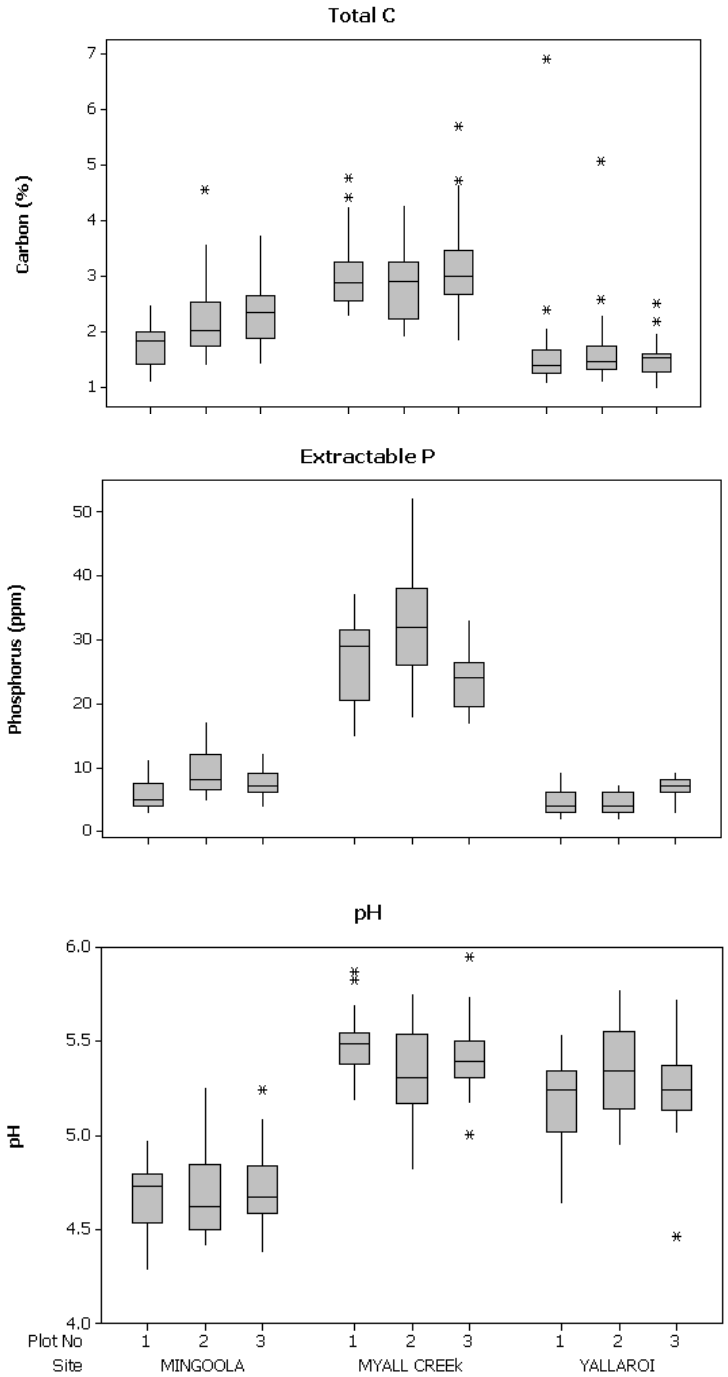


Figure 13-a. Box-plots representing the variation in soil parameters within plots (1-3) at the Mingoola, Myall Creek and Yallaroi sites. Asterisks denote outliers.

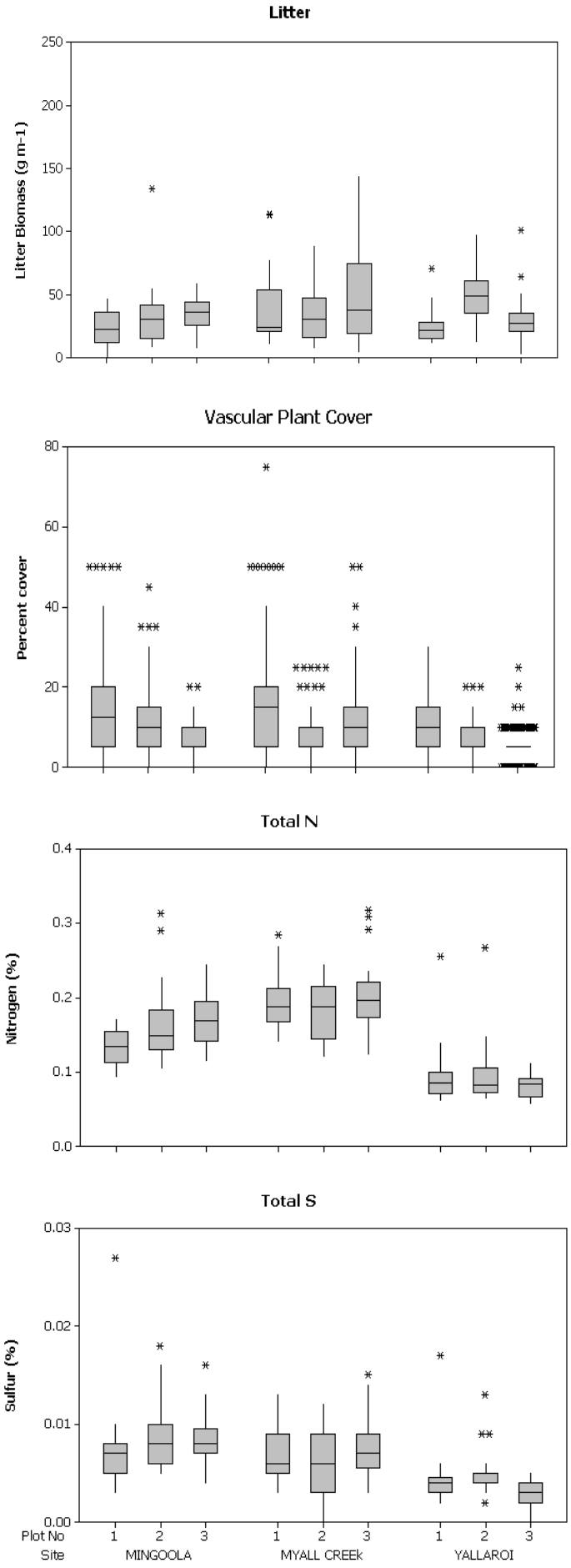


Figure 13-b. Box-plots (continued) of groundcover and soil parameters.

Table 8. The results of regression analyses, which investigated the relationship between soil and groundcover parameters (left column) and the variables Cell DBHOB, Litter Biomass and Groundcover at three sites: Mingoola, Yallaroi and Myall Creek. Variables that exhibited a significant relationship with each soil and groundcover parameter are indicated for each site and the nature of the relationship is indicated with *t* – values and levels of significance (*** $P < 0.001$, ** $0.001 > P < 0.01$, * $0.01 > P < 0.05$). Degrees of freedom, *F*, *P* and R^2 values for the regression are indicated in parenthesis below each significant parameter.

	Mingoola	Yallaroi	Myall Creek
Carbon	Cell DBHOB 1.25 * ($F_{(1,74)} = 2.07$, $P = 0.046$. $R^2 = 25\%$)	n.s.	n.s.
Nitrogen	Cell DBHOB 1.29 * ($F_{(1,74)} = 2.18$, $P = 0.042$. $R^2 = 27.5\%$)	n.s.	n.s.
Sulfur	n.s.	n.s.	n.s.
Extractable P	(Plot 1) Cell DBHOB 3.22 ** ($F_{(1,23)} = 10.35$, $P = 0.004$. $R^2 = 29.9\%$)	n.s.	n.s.
pH	n.s.	Cell DBHOB 2.03 *; Litter Biomass 2.02 * ($F_{(2,73)} = 7.69$, $P = 0.001$. $R^2 = 55\%$)	n.s.
Litter Biomass	n.s.	n.s.	n.s.
Plant Cover	(Plot 2) Cell DBHOB 6.53*** ($F_{(1,24)} = 7.59$, $P = 0.011$. $R^2 = 21.5\%$)	n.s.	n.s.

Table 9. *F* values for a general linear model describing variation in soil parameters between the factors site and zone (individual small tree canopy, individual large tree canopy, dense stand, paddock). Asterisks denote levels of significance (*** $P < 0.001$, ** $0.001 > P < 0.01$, * $0.01 > P < 0.05$).

Factor	Ext. P	C	pH	N	S	C/N
Site	121.22***	28.30***	59.62***	55.09***	33.82***	n.s.
Zone	13.46***	n.s.	66.92***	4.95**	n.s.	53.43***
Interaction	5.85***	2.94**	5.91***	2.20*	n.s.	20.83***

there was a significant positive relationship between cell DBHOB and extractable P, and between cell DBHOB and cover at plot 2. Both cell DBHOB and litter biomass exhibited a significant positive relationship with soil pH at Yallaroi (Figure 14), but there were no relationships between any parameters/factors studied at Myall Creek.

5.4.2 Comparisons between dense stands and individual trees

The interaction between site and zone (under small or large tree canopy, paddock or dense stand) was significant for all soil variables except S (Table 9, above), which differed significantly only between sites (Table 9 and Figure 15). C was significantly higher beneath dense stands than in the paddock at the Yallaroi and Myall Creek sites, but was lowest beneath dense stands at Mingoola. Soil N was significantly higher in association with trees than the paddock at Myall Creek, but was comparable to paddock values and lower than under single-tree canopies at Yallaroi and Mingoola. C:N ratios were similar at all zones at the Mingoola site, but were significantly higher under dense stands at Yallaroi and Myall Creek. Extractable P declined marginally with tree density at Mingoola, but was significantly higher beneath large tree canopies at the other sites, whilst extractable P concentrations in dense stands were much higher than paddock values at Myall Creek, but only marginally so at Yallaroi. Soil pH was always 0.5 of a pH unit lower beneath dense stands than large trees at all sites, and was significantly lower than paddock values at the Mingoola and Yallaroi sites.

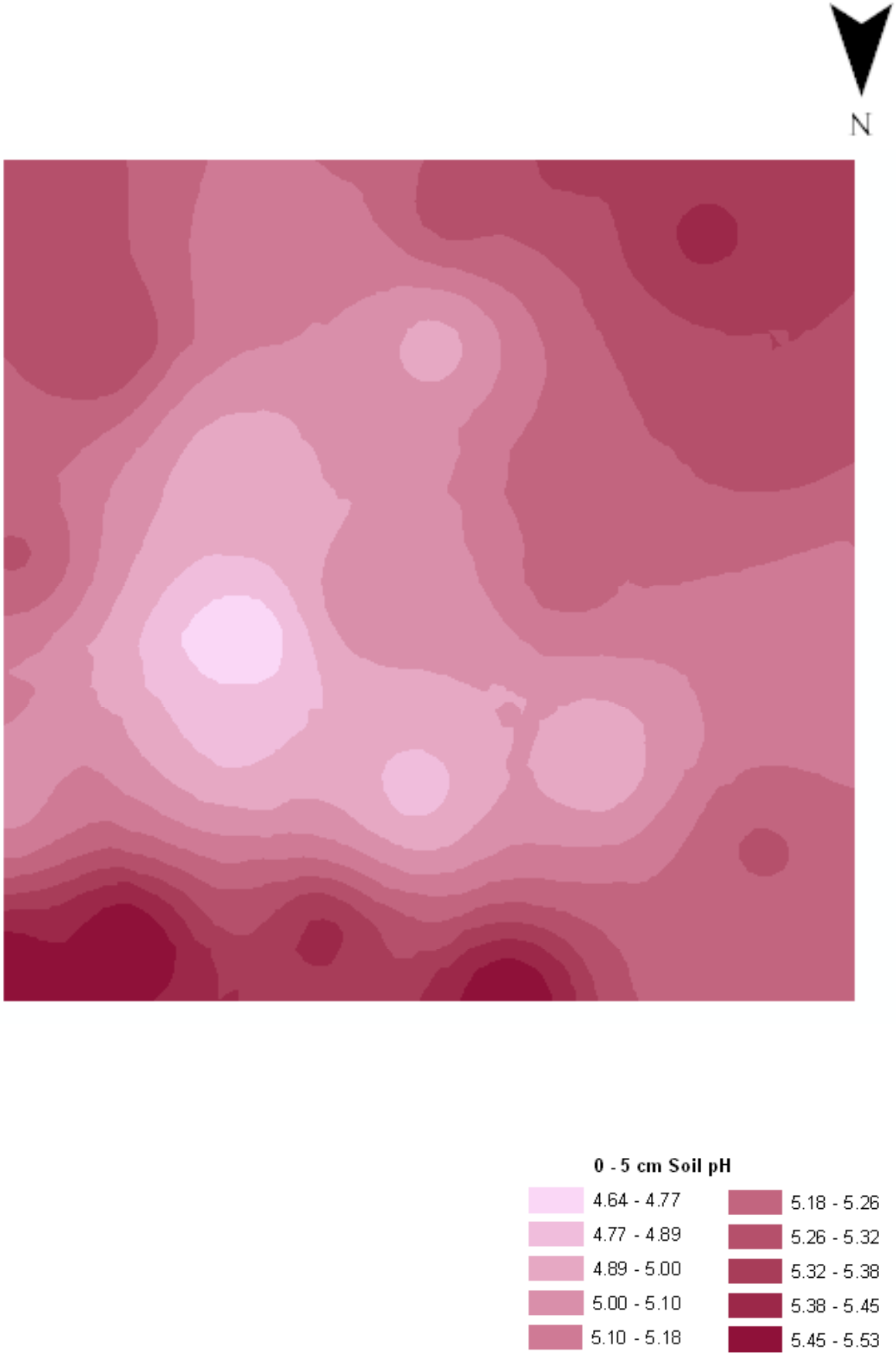


Figure 14. Variation in soil pH (bottom sheet) and its significant relationship with litter biomass (g m^{-2}) (middle sheet) and cell DBHOB (actual DBHOB is shown here – top sheet) in plot 1, Yallaroi. Unshaded circles denote canopy radii.

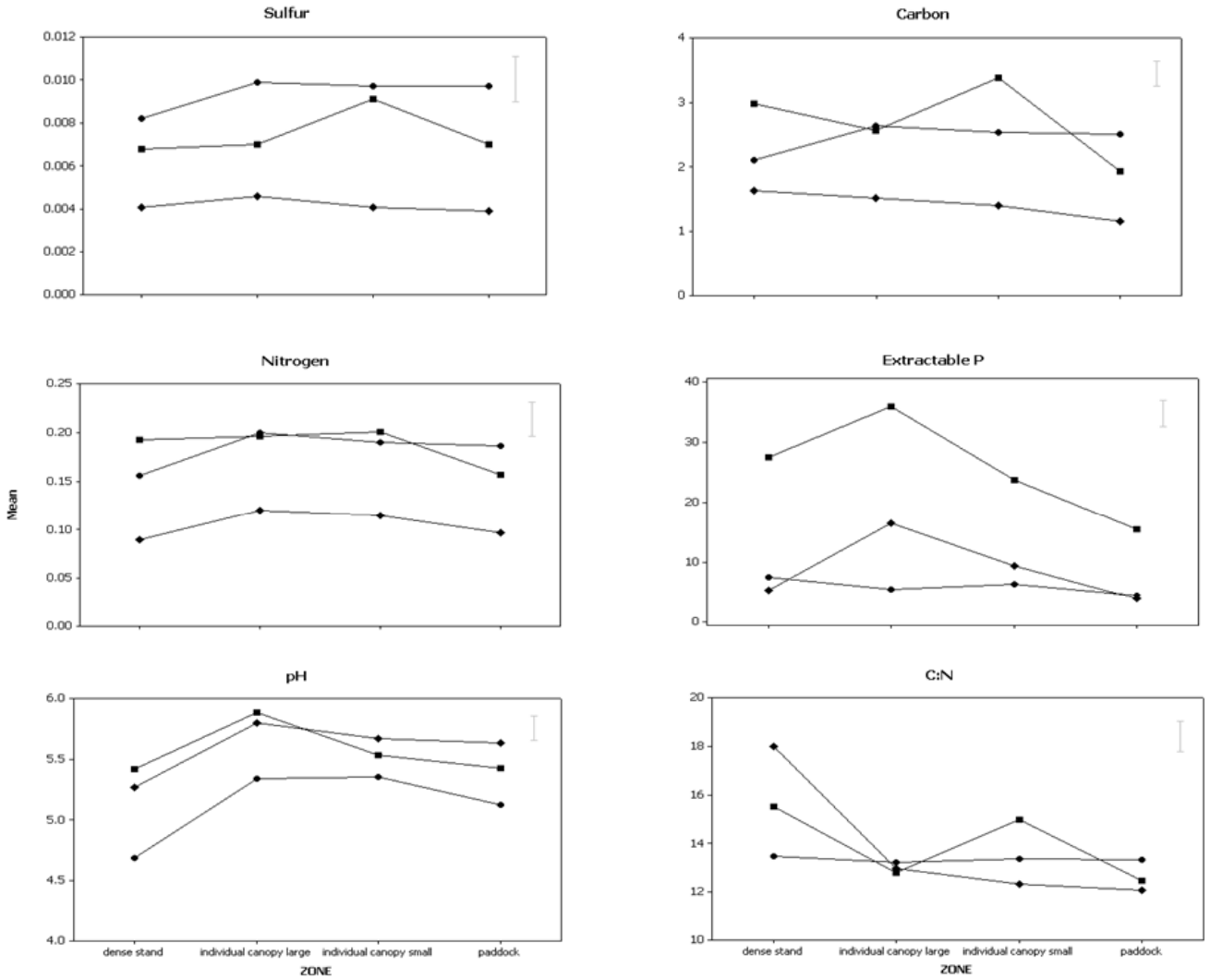


Figure 15. Factor plots for selected soil parameters demonstrating variation in the data by site (circles = Mingoola, diamonds = Yallaroi, squares = Myall Creek) and by zone (beneath tree canopy for small or large trees, paddock and dense stand). Grey panel bars indicate interaction LSDs.

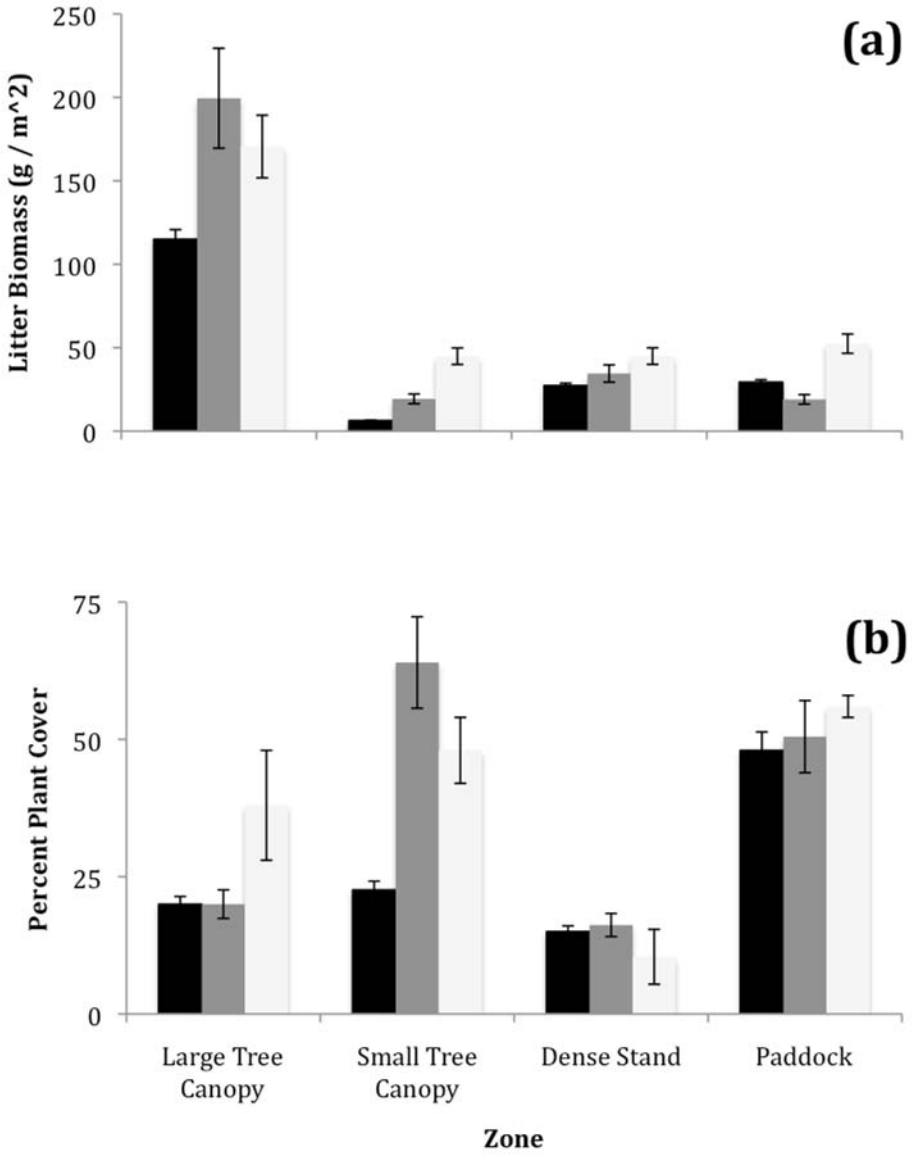


Figure 16. Variation in (a) litter biomass and (b) vascular plant cover (± S.E.) by site (black = Mingoola, grey = Yallaroi, White = Myall Creek) and zone (beneath tree canopy for small or large trees, paddock and dense stand).

There was no significant site or interaction effect for the groundcover parameters. Litter biomass beneath large tree canopies was three times higher ($F_{(3,313)} = 27.62$, $P = 0.000$) at 150 g m^{-2} than all other zones (Figure 16a above). For vascular plant cover, significant between zone variation ($F_{(3,283)} = 34.85$, $P = 0.001$) was due to higher groundcover beneath small tree canopies and in the paddock (c. 50 %) than under large trees (c. 25%) and then dense stands (mean = 15%) (Figure 16b above).

5.5. Discussion

There were some, albeit weak, relationships between tree size and location and soil parameters at the sites studied, for instance a correlation between soil pH, litter distribution and trees was observed at Yallaroi. However, the lack of consistent patterns across the various sites suggests that other processes influence spatial variation in soil and vegetation in dense *C. glaucophylla* stands. The cumulative effect of trees in a dense stand, whilst generally having higher levels of soil C, N and ext. P than the adjacent cleared paddock, were not analogous to the effects of individual trees. From this study it can therefore be postulated that nutrient cycling processes in dense stands are presumably modified either directly or indirectly by the effects of competition between individuals. The possible effects of intra-specific competition on tree growth and nutrient turnover will now be discussed within the context of this study.

There are a number of reasons why only one moderate correlation was observed between trees, soils and groundcover in this study, all of which are interrelated and are presumably mediated by the strong competition in dense *C. glaucophylla* stands. Firstly in this study, as in previous observations of the species (Andrews 2003; Thompson and Eldridge 2005a), it was noted that vascular plant cover was significantly reduced in high-density stands (see also Plate 12). This lack of vascular plant cover is postulated to be the result of intense inter-specific competition between trees and groundcover species in the stand, for belowground resources such as soil water and nutrients (e.g. Harris et al. 2003), or for light (e.g. Thompson and Eldridge 2005a). Secondly, all of the plots studied in the NWS region supported dense stands and were located on slopes ranging from three to eleven degrees. Thirdly, despite there being many more trees (of an equivalent size to the 'small' individual trees studied in Chapter Four) per unit area in dense stands than in paddocks scattered with individual trees, litter biomass in dense stands equated to no more than levels of the cleared paddock. These factors, when combined, describe a system in which plant litter, which is a significant source of nutrients to the soil could be readily lost during rainfall events.

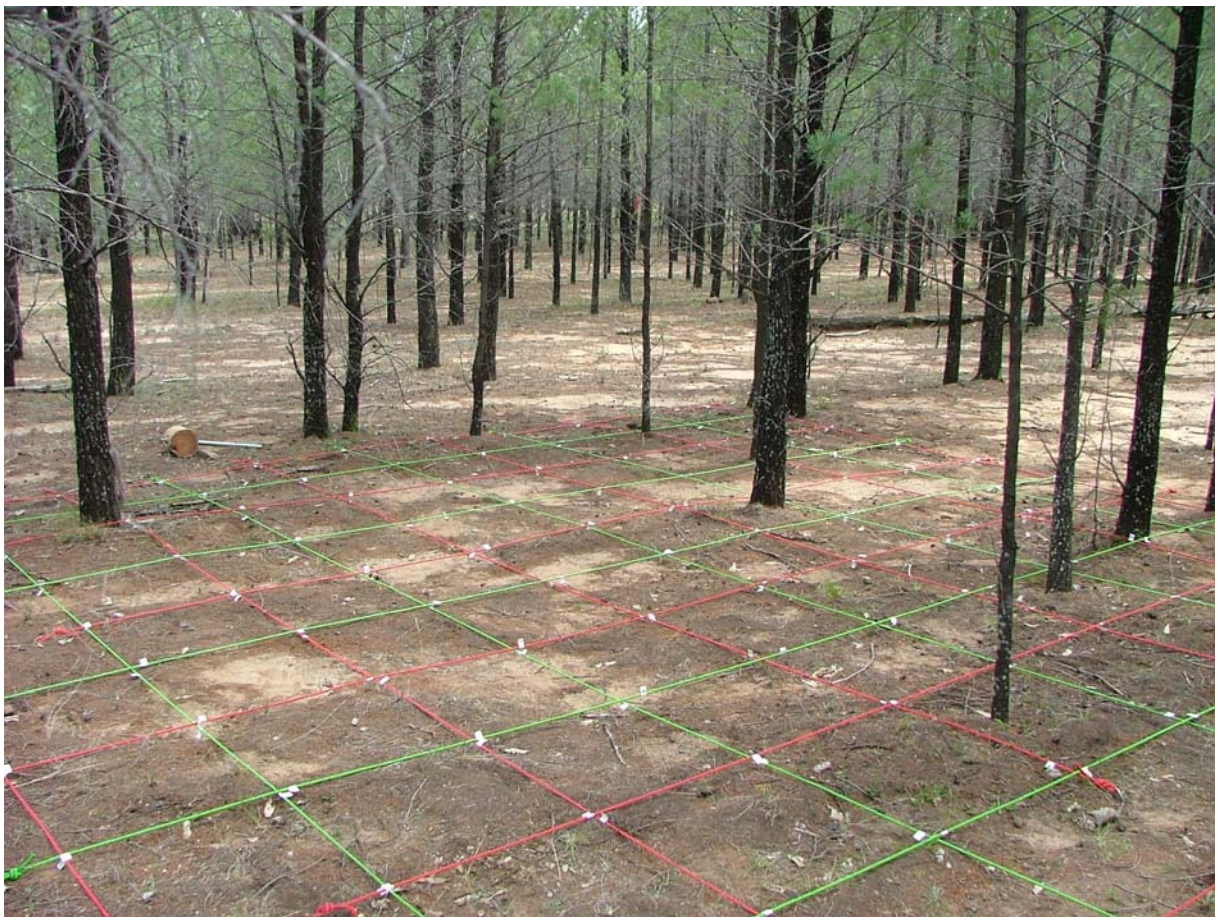


Plate 12. Part of a sampling plot beneath a lower density stand at Yallaroi occurring on gently sloping country. The Yallaroi site had a high degree of litter deposition relative to the other sites, however, the absence of vascular plant cover in the understorey was characteristic of all sites.

Evidence for litter-driven soil nutrient patterning has been demonstrated previously by Tongway and Ludwig (1990) in semi-arid regions of NSW dominated by Mulga (*Acacia aenura*), whereby 'run-on' zones associated with rainfall-mediated litter transport had higher soil nutrient status than 'run-off' zones. In this study, soil C, N and ext. P were barely higher per unit area on average in dense stands than the canopy zone of individual trees, despite there being many more trees in the immediate vicinity to contribute litter. Therefore, it follows that litter loss or variable litter transport might be a key process driving the lack of spatial variation in dense stands associated with trees as well as a lack of soil nutrient accumulation in dense stands.

At high plant population densities, intra-specific competition for resources such as soil nutrients, water and light intensifies. Often, large plants have the ability to accumulate more

resources, which implies that they contribute more resources to the soil in the form of litter. However, this assumption only holds if the effects of competition do not inhibit production of litter. Further, should stands be nutrient limited, then the quality and quantity of litter might be reduced. Many studies that have focused on nutrient cycling in conifers refer to economically important species (e.g. Monterey Pine – *Pinus radiata* or Loblolly Pine – *Pinus taeda*), which tend to have a high nutrient demand and prefer sites with higher rainfall. Of the studies referring to conifers in low nutrient environments, such as those which might be expected in parts of north-west NSW, it is noted that trees employ strategies to ensure that most N and P required for foliage growth is withdrawn from older phyllodes and re-distributed to the new tissue prior to abscission (Miller et al. 1979). The limited growth of trees in dense *C. glaucophylla* stands would also imply that nutrient replenishment to the soil surface is infrequent at best and that the spasmodic litter fall from dense stands (Hart 1995) is most likely from low-nutrient, senescent foliage.

Competition for resources in dense stands may have altered the composition and quantity of litter deposited on the soil surface. Further, intense inter-specific competition between trees and vascular plants in the understorey adversely affects the distribution of groundcover, which, when combined with the effects of slope, indicates that any litter deposited on the soil surface is susceptible to transport away from the site by rain and perhaps wind. As groundcover appears to be inversely related to plant density in dense *C. glaucophylla* stands, the likelihood of finding a relationship between trees, soils and groundcover is presumably much higher in stands with lower plant density. Indeed, the stands with the lowest plant densities and on the smallest slopes in this study were located at Yallaroi, where the strongest correlation between trees soils and groundcover was observed to occur between soil pH, cell DBHOB and litter biomass.

At the Yallaroi sites, the least acid soils within the stands were associated with the largest trees and the highest litter biomass. This pattern is strongly indicative of the biological pumping process (Noble et al. 1996; Wilson et al. 2007), which was proposed to influence soil pH in the immediate vicinity of individual trees in Chapter Four. However upon canopy closure, there were no spatial relationships between soil acidity and litter deposition and the cumulative effects of trees in these dense stands resulted in soil which was significantly more acidic than the canopy zone of individual trees and even the open paddock.

In this study, images supplied by the landholders indicate that most of the trees at the sites studied have only recently established, because only scattered individuals existed in imagery from 1990. The process of nutrient uptake (which presumably occurred *en masse*) would also result in temporary 'acidification' of the soil. Over time this acidity in the surface soil would progressively be neutralised and the pH may even increase relative to the surrounding paddock as it did for individual trees, because of the deposition of alkaline, anion-rich litter. However, a reduction in the deposition of litter in dense stands due to competitive regulation between trees, and the high potential for litter to be transported away from the site of deposition suggests that this process is interrupted and soil in dense *C. glaucophylla* stands does not become 'alkalinised'. Biological pumping and soil pH patterning in dense stands is therefore a complex issue worthy of further investigation.

The lack of litter produced/retained by dense stands suggests that the high C:N ratios observed beneath dense stands in this study are not so much due to a predominance of C in the soil but may instead be the result of N-limitation. In this study, stand N deficiency is likely to be the result of a paucity of N-fixing vascular plants (e.g. legume species), a rapid uptake of soil N during the first few years of growth, the withdrawal of N from the leaves after rainfall-induced growth (therefore further increasing the C:N ratio – (Attiwill and Adams 1993; Cole 1981) and a lack of rainfall to stimulate mineral N transformations.

Given the nature of the questions posed in this study and the experimental design, it was impossible to separate the effects of trees imposed directly on soils and those processes that are the partial result of soil variability which might drive size variation among individuals in the first instance. Spatial dependence between trees and soils is most likely in populations that exhibit size-asymmetric competition for resources and hence individuals will return nutrients to the soil at different rates according to their size and age. In a review of mechanisms determining the degree to which size asymmetry affects resource-partitioning in plant populations however, Schwinning and Wiener (1998) suggested that competition for resources was not size-asymmetric when populations occurred on very poor soils and or when plants were competing only for below-ground resources. In dense *C. glaucophylla* stands, it is postulated that there is intense below-ground competition due to the species' expansive root morphology (Harris *et al.* 2003). Therefore, it is possible that the soil spatial patterns observed for individual *C. glaucophylla* trees are not replicated in dense stands because the potential for nutrients to be distributed asymmetrically by trees within the population is inherently low. Therefore, future work in this area should be directed at tracking competitive processes over time with tree growth and nutrient uptake.

In summary, soils and groundcover in dense *C. glaucophylla* stands have a variable distribution, and individuals within the stand influence these patterns only in some circumstances and even then the relationship was weak. Dense stands reduce vascular plant cover, and it is likely that this is due to competition for resources, which, when considering the high C:N ratios and low N concentrations observed in this stand, may be driven by rainfall and water availability. Further investigation is required to understand the precise mechanisms by which soil is acidified in dense stands, especially within the context of the extremely slow growth of trees, which is characteristic of the species, and how this might affect temporal processes such as biological pumping. The results of this study have also established that dense *C. glaucophylla* stands do not function as 'islands of fertility' in grazing landscapes on

the North-Western Slopes of NSW, except perhaps in their conservation of soil C. Therefore, management strategies for the species are required that reduce plant density to levels which represent the optimum integration of environmental services (produced by individual trees) and production.

Chapter 6. Demography

Demographic and phenological characteristics limit self-thinning in *Callitris glaucophylla*

6.1. Background

In the previous chapter, the effect of trees in dense stands on soil and vegetation parameters was demonstrated and it was found that, when trees occur in such a configuration, it is difficult to ascribe soil and vegetation patterns to individuals within the stand. This is presumably because competition for resources and hence the re-distribution of these resources through processes such as litter fall do not occur in very dense stands of *C. glaucophylla* as growth and nutrient turnover has been inhibited by the high density of the plants. At the stand level, dense populations have equivocal outcomes for soil nutrient status when compared to the adjacent paddock, but adversely affect soil pH and vegetation cover. Many of these results may again be driven by the spatial (and temporal) distribution of litter, which in turn has been affected by intense within-stand competition.

In this chapter, I have chosen to focus on some of the aspects of the ecology of *C. glaucophylla* that potentially refine the knowledge of competitive processes in dense stands, most of which appear to result in deleterious ecological and productive outcomes. I have used a glasshouse trial to simulate the growth of the species at various densities, measuring plant growth, survival and nutrient partitioning. Some notes on germination of the species, which have not been reported in published literature, are also discussed.

6.2. Introduction

The interaction between individuals driven by a shared requirement for a resource in limited supply is termed competition (Grace and Tilman 1990; Silvertown and Charlesworth 2001). There is a substantial focus on competitive interactions in forestry and agricultural literature because resource-constrained plant populations usually exhibit reductions in survivorship, growth and reproduction (Donald 1951; Grace and Tilman 1990; Parsons et al. 1996; Prioul and Silsbury 1982). Many such studies incorporate the results of both field and glasshouse based experiments; the latter are sometimes preferred methods for investigating the effects of competition because most growth-influencing factors can be controlled (Florentine and Fox 2003, in (Lei 2004).

When the number of individuals in a plant population is high, competitive interactions are usually related to the density of individuals (density-dependent competition). A practical application that utilises the effects of density-dependent competition involves the germination of forest tree species at higher densities than can be sustained over the life of the stand (which is thinned regularly) in order to take advantage of the straight timber produced by trees that produce almost no lateral branches in a search for light at the top of the canopy during early growth (Schönau and Coetzee 1989). Below the soil surface, intense within-stand competition for resources can result in the decreased growth and performance of the species. Hence in most plant populations, there is often a negative correlation between density and performance (White 1980, in Petraitis 1995), and as a result plants grown at very high densities often exhibit substantial mortality rates (Hett 1971; Lei 2004; Packer and Clay 2000).

Self-thinning, or the mortality of some individuals which are usually the smallest or lacking in genetic fitness, ensures the continued allocation of resources to other members of the population. Self-thinning is likely to occur in plant populations where plant size varies greatly as a result of crowding, often resulting in size-asymmetric competition for resources

(Silvertown and Charlesworth 2001, and see Chapter Five). Self-thinning has been observed in many plant populations worldwide such as agricultural species (Carlassare and Karsten 2003; Matthew et al. 1995; Sackville-Hamilton et al. 1995), and in forest plantations (Bi et al. 2000; Jack and Long 1996; Kashian et al. 2005; Zhang et al. 2007). The precise reasons for self-thinning vary with species and habitat, but evolution, genetic fitness, seed mass-plant size relationships and nearest-neighbour interference are all proposed causes for selective mortality within plant populations.

Whilst the general ratio for survival over time after the commencement of density dependent mortality conforms to a -3/2 slope, some plant populations do not self-thin. The reasons for this are thought to be related to plant morphology and the way in which plants which lack extensively branched or spreading shoot systems lack the capacity to interfere with each other spatially (Ellison 1987; 1989; Miyanishi et al. 1979; Westoby 1976), even at very high densities (Weller 1987b; but see Weller 1987a).

On the NWS and Plains *C. glaucophylla* has expanded within its natural range and now invades and colonises cleared managed land previously devoid of the species. This is consistent with literature which links disturbance, whether natural or human-induced, with the success of some plant species over others (Richardson and Richardson 2000). The perceived problem with dense *C. glaucophylla* regrowth is two-fold in that stands are both space occupying in managed rural landscapes and are also thought to consume all available soil resources to sustain plant growth (therefore hindering the growth of other plants) prior to canopy closure. Despite acknowledgement of its status as an invasive native species in the regulations of the Act, very little is known about the ecology of *C. glaucophylla*, and this has hindered attempts to manage the species effectively over the long term. At the population level, it has been noted that self-thinning in dense stands is either negligible or very infrequent, and perhaps as a consequences of this, once plants have reached a certain stage

(presumably when all available resources are exhausted), increases in above-ground biomass are almost negligible (lock-up). The precise causes of 'lock-up' are as yet unknown.

In this chapter, I will investigate some of the effects of competition on a number of plant and growth medium (i.e. soil) characteristics for *C. glaucophylla* using a glasshouse trial. The aims of the experiment are:

1. To determine the effects of plant density on plant phenology – plant height, bark development, lateral branching, shoot and root biomass;
2. To determine the effects of plant density on seedling survival;
3. To determine the effects of plant density on nutrient partitioning (N and P) and soil N and P content; and,
4. To investigate the effects of plant density on soil pH over time.

6.3. Methods

6.3.1. Seed germination techniques

Approximately 10 000 seeds were collected in late 2004 from 30 mature *C. glaucophylla* trees near Baradine (Lat/Long 30.9500,149.0672) on the North-Western Slopes of NSW. Staining with tetrazolium indicator revealed viability of 85% of the seed store. Seeds were stored in a cool room facility until germination trials began in May 2006. Two primary methods of germination were attempted. Seeds planted into a low nutrient sand were watered three times weekly in a climate controlled (26 º C / 14 º C day/night) glasshouse, but no germination was observed and after 6 weeks the trial was discontinued.

Germination was also attempted in a climate-controlled laboratory (STP). Seeds were soaked in 1 L of deionised water and were constantly aerated by a bubbler inserted through a hole in a sealed plastic container (Plate 12). Germination by this method was deemed to be successful after 7-9 days when the radicle emerged from the testa. A small germination trial was set-up

due to observations of a tea-coloured leachate present in the solution within hours of soaking seeds. Six containers were set up containing two replicates or 10, 50 or 100 seeds, which were soaked and bubbled in 1 L of deionised water over a 7-9 day period. In one replicate for each seed density, seeds were decanted from the container and the water was changed up to four times over the course of the trial. In the other replicate, the water was not changed. In order to assess the affect of altering seed number or the concentration of leachate present in each container on germination rate, a two-way ANOVA with the binary fixed effect 'water change' and the fixed effect 'seed number' was used.

6.3.2. Experimental design – plant density experiment

Germinated seeds were planted progressively over a 12-week period between mid-May and mid-August 2005 in thumb-pots containing a 50:50 low nutrient sand / peat moss mixture. Seedlings were transported to a shade-house at the Department of Environment and Climate Change Gunnedah Research Station during September. *Callitris glaucophylla* is common on the research station and forms very dense stands on properties immediately to the west of the town. Seedlings were carefully removed from the low-nutrient medium and the roots were thrice washed with deionised water. Washed seedlings were immediately replanted in a low-nutrient (LECO C = 0.37%, N = 0.03%, S = 0.002%; Olsen-extractable P = 9.4 $\mu g\ g^{-1}$, pH = 6.2) sandy loam soil sieved to less than 2 mm sourced from the Gunnedah region. Of the 996 seedlings planted at the beginning of the trial, there were four losses during the six-week establishment period. These were removed and replaced with spare seedlings of an equivalent age.

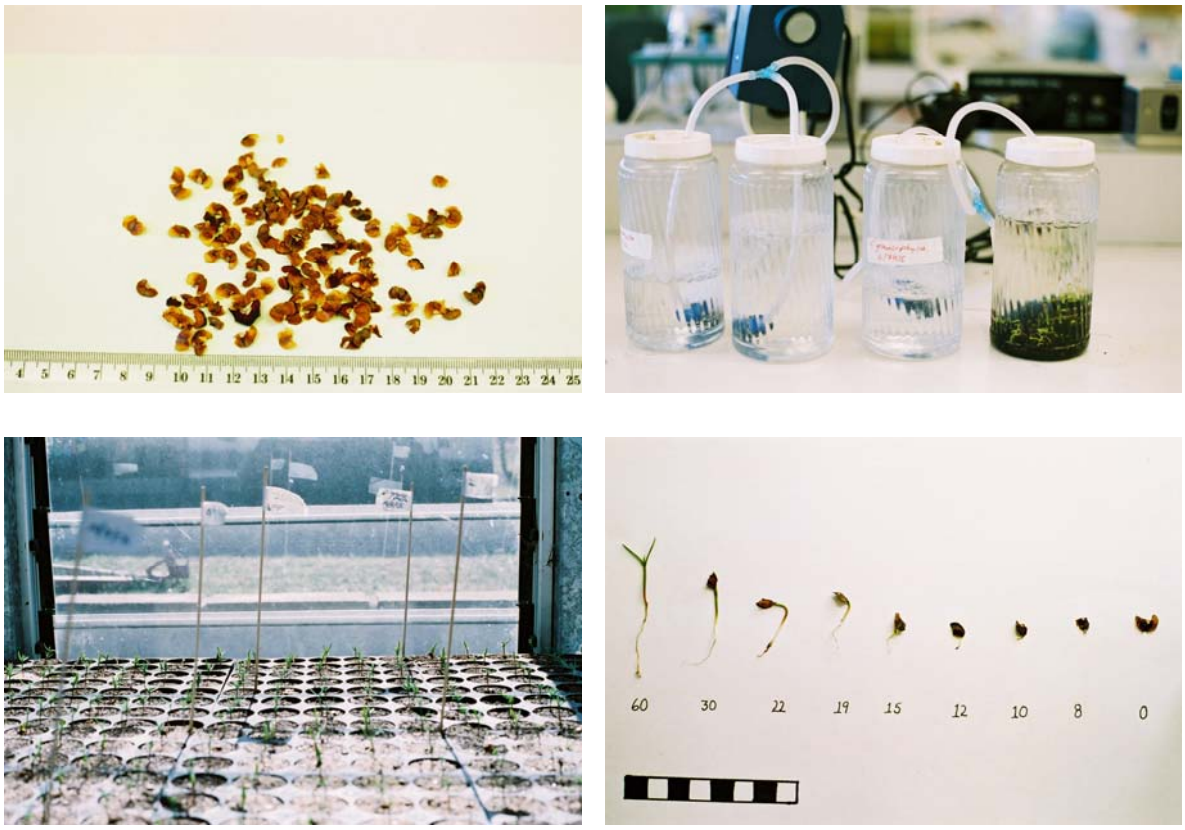


Plate 13. (Clockwise from top left) – 'Mature' C. glaucophylla seeds; an example of the seed-germinating apparatus illustrating a 100-seed, fresh water treatment; seedling development after 60 days: and, early seedling growth in a potting mix: low nutrient sand medium.

Seedlings were planted in 1.1 m tall, 300 mm diameter poly-pipe with a mesh capped bottom to allow root permeation and water flow at densities of 3, 30 and 50 seedlings per pot. There were 12 replicates of each treatment, which were harvested, six-monthly in groups of four. A reference soil treatment, containing soil only, was also destructively sampled every six months. Once established six weeks later, these treatments were thinned to 1, 25 and 40 seedlings per pot respectively (141 471, 3 536 780 and 5 658 847 seedlings ha^{-1}, respectively). Plants were watered on a timed sprinkler system for 5 minutes every 48 hours in the winter months (average daily temperature range in glasshouse = 12 – 24 º C max, -1 – 8 º C min) and 5 minutes per 24 hours in summer (30 – 46 º C max, 15 – 24 º C min). A further six seedlings were replaced within the first 8 weeks of the start date of the experiment due to insect attack which caused two losses and the defoliation of a further four seedlings. Pyrethrum insecticide

was applied to the foliage eight times during the first six months of the trial, but was not required subsequntly for the duration of the experiment.

6.3.3. Sampling techniques and analytical parameters

6.3.3.1. Repeated measures

Seedling height was measured from the bottom of the primary axillary buds to the end of the terminal node for each seedling in every treatment once a month for the entire 18-month trial. The number of lateral branches and their length were also recorded. Seedlings in some treatments developed bark and foliage dieback on the primary stem over the course of the trial, and the length of stem exhibiting these characteristics was determined from the bottom of the primary axillary buds. Seedling mortality was deemed to be the result of competition after herbivore-related injury and losses were replaced and treated in the first few months. Further seedling mortality was recorded as part of the trial.

6.3.3.2. Destructive sampling

Thirteen containers (four each of the 40, 25 and 1 seedling treatments plus one 'reference soil' pot) were destructively sampled at six, twelve and eighteen months. Aerial foliage was clipped below the primary axillary bud and dried to a constant weight at 70 º C (usually 48 hours). Pots were halved and the depth of roots recorded. Soil free of roots was transferred to large foil trays and the remaining soil and root mixture was sieved gently to separate the components. Finally, all roots were washed in deionised water to remove residual soil. Soil and roots were oven dried to a constant weight (up to 7 days for saturated soil and 48 hours for roots) at 40 and 70 º C respectively. Dried root and shoot samples were weighed and then ground to less than 0.5 mm.

Root and shoot samples were analysed for total P using an inductively-coupled atomic emission spectrophotometer and total C and N using LECO combustion at 950 º C. Soil

samples were analysed for Olsen-extractable P (Watanabe and Olsen 1956), C and N using LECO combustion at 950 º C and soil pH was determined in a 1:5 water 0.01 M $CaCl_2$ soil suspension.

6.3.4. Statistical analyses

6.3.4.1. Plant phenology

Plant height was assessed using a two-way repeated measure ANOVA with density and time as fixed factors using just one seedling randomly selected in each pot in the 25 and 40 treatments to enable the most appropriate comparison with the single-seedling treatment. Where treatments differed significantly, regression lines were fitted for each time period between harvests and these slopes were compared using equations described by Zar (1999) (Equation 2).

Equation 2. $$f = (SS_c - SS_p) \ / (k - 1) \ / (SS_p / df_p)$$

Where SS_c is the Residual Sums of Squares for a regression inclusive of all three densities (i.e. height versus time), SS_p is the sum of the Residual Sums of Squares for each of the three regression equations for each density, k is the number of regression slopes to be compared (3), and df_p is the sum of the residual degrees of freedom for the three regressions. A significant f-statistic is used to confirm that the slopes were different (Equation 3) at $\alpha = 0.05$.

Equation 3. $$f_{(k-1,\ dfp)} = x$$

Within-pot variation in plant height was assessed by calculating the co-efficient of variation (Equation 4 – population standard deviation divided by the mean) across 25 and 40 seedlings per pot treatments. These values were converted to a Relative Standard Deviation (RSD –

Equation 5) in order to provide a value by which to compare the observed *within-pot* variance between pots.

Equation 4 $C_o = \partial / \mu$

Equation 5 $RSD = C_o * 100$

Variation in the number of lateral branches (only secondary branching was observed by the end of the trial) and the length of the plant stem which developed into bark over the course of the trial was assessed for 1 representative seedling in each pot using two-way ANOVA with density and harvest as fixed factors. This analytical approach was employed to overcome the lack of replication in single seed pots. Time was not used as a factor for these analyses because the data did not represent repeated measures on the same samples over time, but were instead separate replicates of the same treatment. Variation in root biomass was assessed by a General Linear Model (GLM) using the fixed-factors density, harvest number and the covariate depth. Differences between shoot biomass and root:shoot ratios (i.e. pooled for each pot) were assessed at each harvest by two-way ANOVA where treatment and harvest number were fixed factors.

6.3.4.2. Plant Survival

A theoretical self-thinning slope was constructed for each treatment. The original self-thinning law (Yoda et al. 1963), relates mean plant weight to the -3/2 power of density (Equation 6).

Equation 6 $w = Kp^{-3/2}$

where w is mean plant weight, p is density and K is a constant. However there are a number of limitations to this calculation (e.g. see Miyanishi *et al*. 1979, Weller 1987), and hence Ellison

(1989) suggested the use of survival over time presented in graphical format. Plants that self-thin are expected to self-thin along a -3/2 line of survival over time. Using mortality data from this experiment, plant densities were plotted and the theoretical self-thinning slope was identified for comparison.

6.3.4.3. Plant and Soil Chemistry

Variation in pooled shoot, root and soil N and P was assessed by two-way ANOVA with the fixed factors density and harvest number. The concentration of N and P in shoots harvested at each time period was regressed against soil (for the whole pot) concentrations at the same time. Regression lines were also constructed for soil and root N and P for each depth, at each time period and for each density. Change in soil pH was assessed by GLM with the fixed factors density and harvest number, and the covariate depth.

6.4. Results

Increased germination rates were observed when seeds were supplied with fresh water ($F_{(1,36)}$ = 18.92, P = 0.000); however, rates of germination were similar irrespective of the amount of seeds in the germination trial ($F_{(2,36)}$ = 0.83, P = 0.445) (Figure 17).

Growth characteristics were significantly influenced by plant density at each harvest. Single seedlings were the only individuals to develop lateral branches prior to the first harvest (199 days). At the end of the trial, bark and lateral branch development were significantly higher for single seedling densities than the 25 and 40 seedling densities, with significantly less lateral branch development on 40 seedling pots (Table 10).

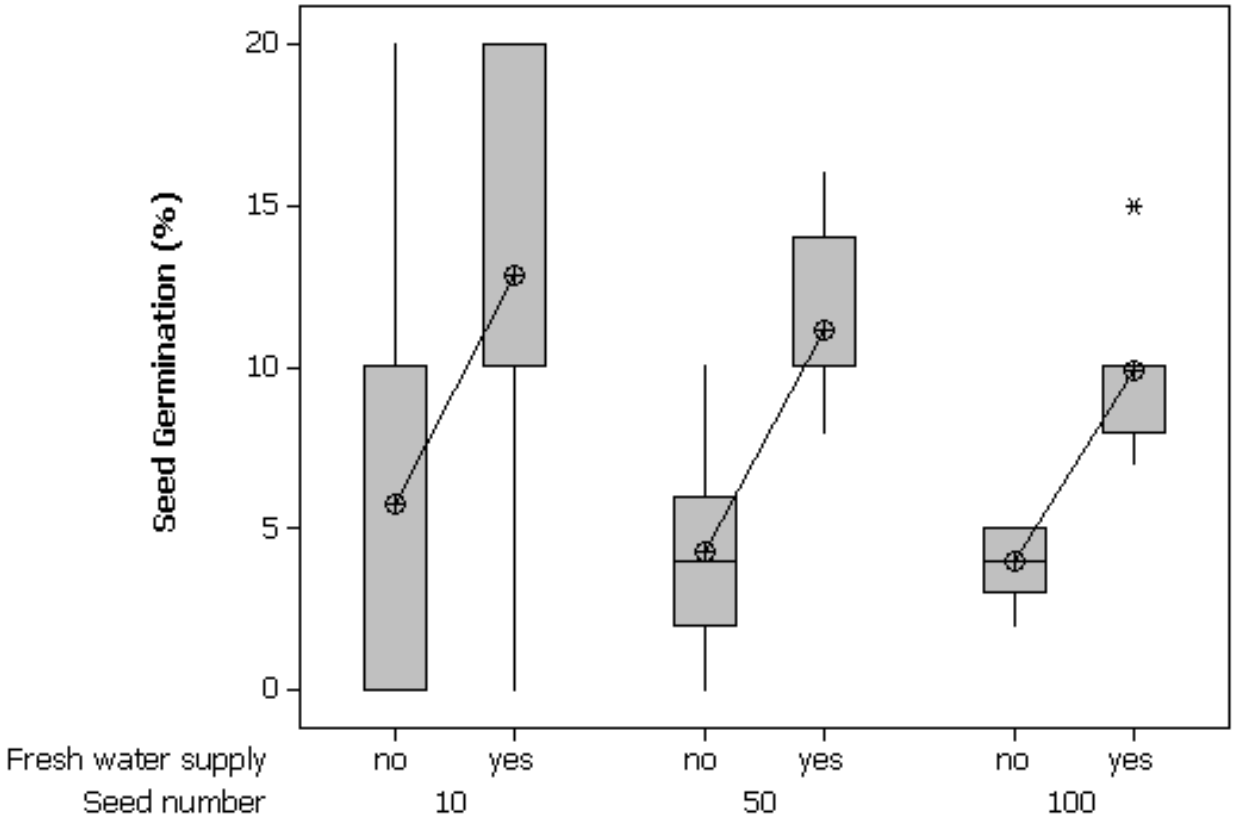


Figure 17. Box-plot of a small germination4 trial for *C. glaucophylla* seeds bubbled in water over a period of 10 days when seed number (10, 50, 100 per container) and a supply of fresh water ('yes' – frequently, 'no' – no change of water) was varied. Circles are means.

Table 10 The bark length along the primary stem and the number of lateral branches determined for *C. glaucophylla* seedlings grown at three planting densities and harvested on approximately a six monthly basis for a period of three harvests. Values in parenthesis indicate the range of values for each entry. Superscripts denote statistically significant groups (Tukeys Multiple Comparison of Means).

Time (days)		Plant Density (seedlings per pot)		
		1	25	40
199	Bark (cm)	-	-	-
	Branch No.	5 (3 -7)	-	-
370	Bark (cm)	10 (7-14) [a]	4 (0 – 6) [b]	-
	Branch No.	18 (13 – 24) [a]	10 (7-14) [a b]	3 (0 – 4) [b]
617	Bark (cm)	22 (15 – 30) [a]	13 (9 – 16) [b]	10 (6 – 12) [b]
	Branch No.	34 (30 – 41) [a]	20 (16 – 22) [b]	8 (6 – 11) [c]

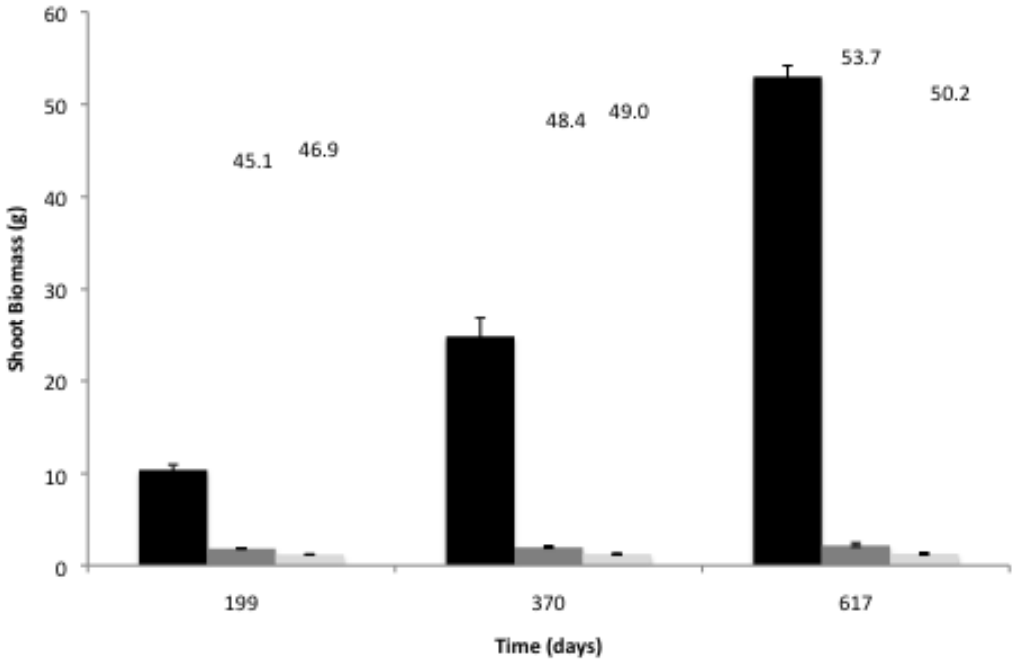


Figure 18. Variation in shoot biomass (per shoot ± S.E.) for *C. glaucophylla* seedlings grown at three densities (one seedling per pot = black, 25 seedlings per pot = dark grey, 40 seedlings per pot = light grey) at three harvests times. Total pot biomass (g) is indicated above 25- and 40-seedling treatments in numerals.

Total pot shoot biomass was significantly lower in the single seedling treatment at 199 days ($f_{(2,11)}$ = 52.21, p = 0.000) and 370 days ($f_{(2,11)}$ = 39.60, p = 0.000), but by 617 days, shoot biomass was significantly higher in the single seedling treatment than any other plant density ($f_{(2,11)}$ = 11.96, p = 0.003). On a per seedling basis, shoots in single seedling treatments always had significantly more biomass than other plant densities (Figure 18).

Root biomass was marginally higher in the top 5 cm of all pots at all three densities at the end of the first harvest (199 days) ($f_{(2,83)}$ = 4.15, p = 0.03) than at any other depth, and the 25 and 40 seedling densities had significantly more root biomass across the whole pot than single seedling treatments ($f_{(2,83)}$ = 10.96, p = 0.000). On a per plant basis, single seedling treatments had higher root biomass at first harvest. By the second harvest, pot and seedling root biomass was significantly higher in the 25 and 40 seedling densities than the single seedling pots, especially in the top 5 cm of the pot. By the completion of the third harvest, root biomass was significantly higher in the 40 seeding pots than any other density ($f_{(2,83)}$ = 24.62, p = 0.000).

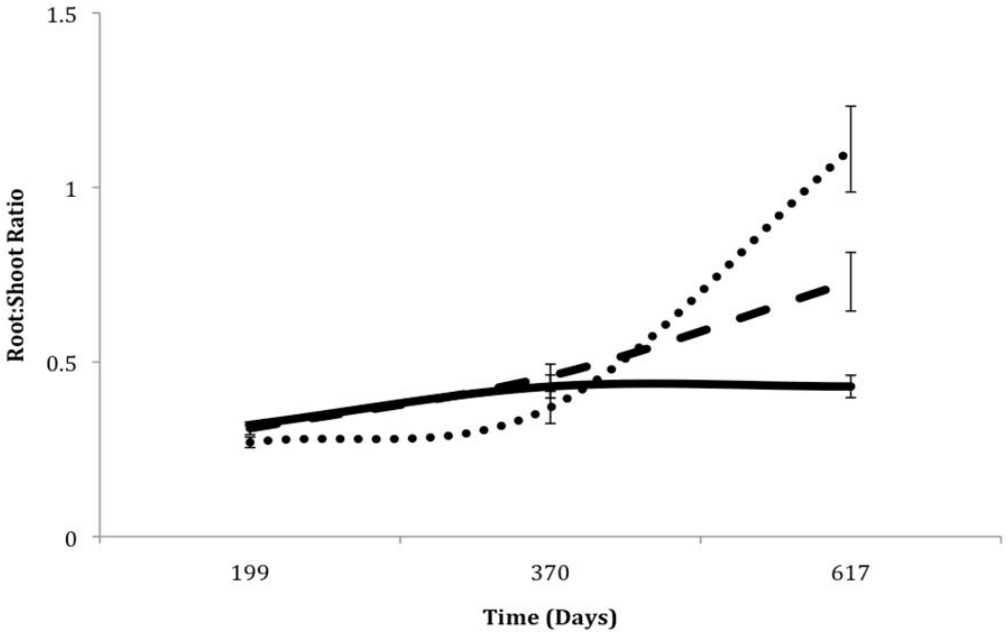


Figure 19. Variation in root:shoot ratios over time for *C. glaucophylla* seedlings grown at three seedling densities per pot (1 = solid line, 25 = broken line and 40 = dotted line).

Plants exhibited significantly different root:shoot ratios between treatments, and with successive harvest (Treatment | Harvest Number $f_{(4,35)} = 13.99$, $p = 0.000$). There was only a marginal increase in root:shoot ratios in single seedling treatments with successive harvest, a significant linear increase for the 25 treatment, and a significant increase at 617 days relative to the first two harvests for the 40 seedling treatment. At the conclusion of the trial root:shoot ratios increased significantly with increasing plant density (Figure 19 above).

The growth rate of seedlings was similar irrespective of density until approximately 341 days (Figure 20). A two-way ANOVA which employed density and time (after 341 days) as categorical variables (i.e. because the same plants were not measured continuously because some were harvested) and Tukey's post-hoc testing identified a significant growth effect between plant densities ($f_{(2,147)} = 35.13$, $p = 0.000$) from time 463 days ($f_{(10,147)} = 41.84$, $p = 0.000$). Therefore regression slopes were constructed from the preceding time period (431 days), where it could be assumed that the lines would have the same intercept. All three slopes were significantly different from each other ($f_{(2,78)} = 36.10$, $p = 0.000$) (Figure 21),

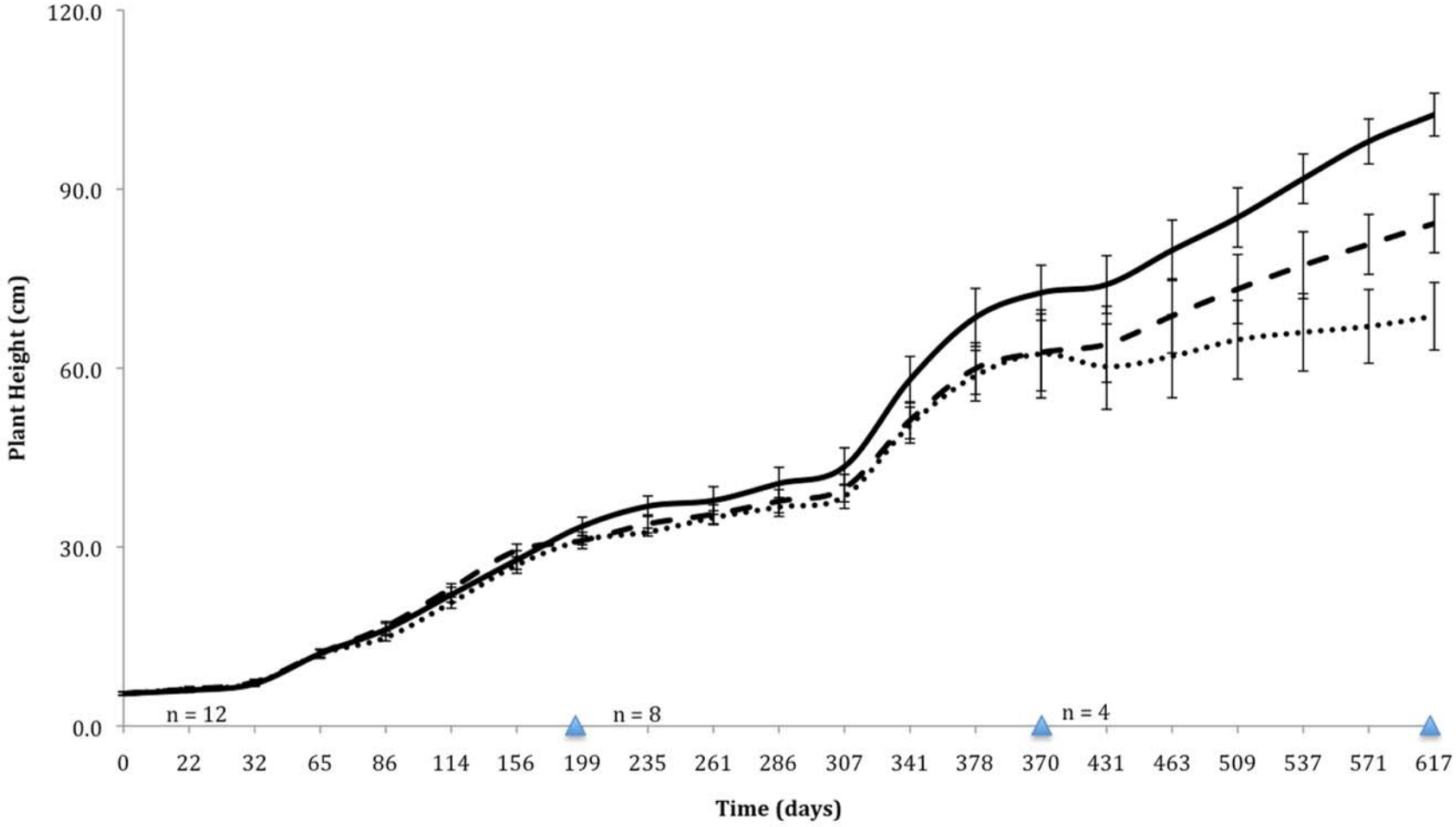
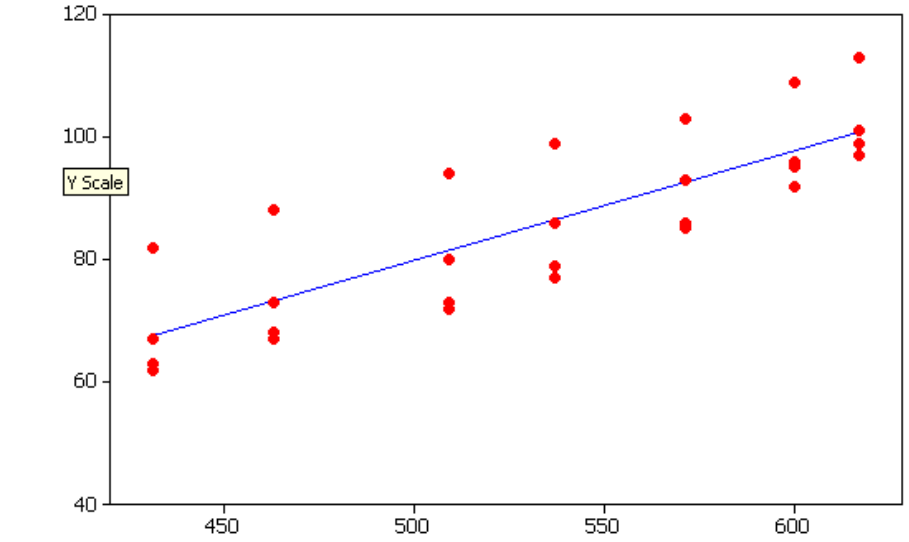


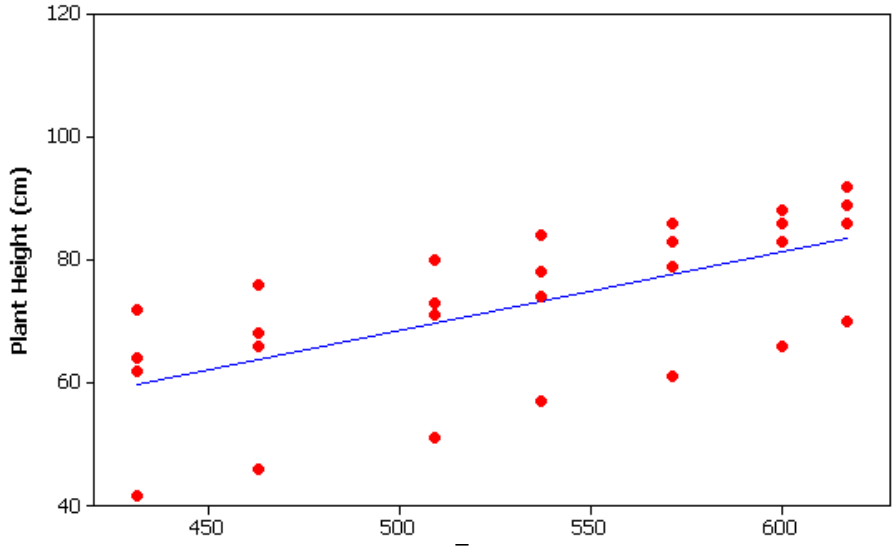
Figure 20. Growth (± S.E.) of *C. glaucophylla* seedlings at different densities (40 = dotted line, 25 = broken line, 1 = solid line). Triangles denote harvest times (*n* for each treatment prior to destructive harvest of some pots indicated on the image). Decreases in height are the artificial results of harvest of some individuals within each density treatment.



Ht = -9.8 + 0.179 time

$F_{(1,27)} = 56.33$, $p = 0.000$

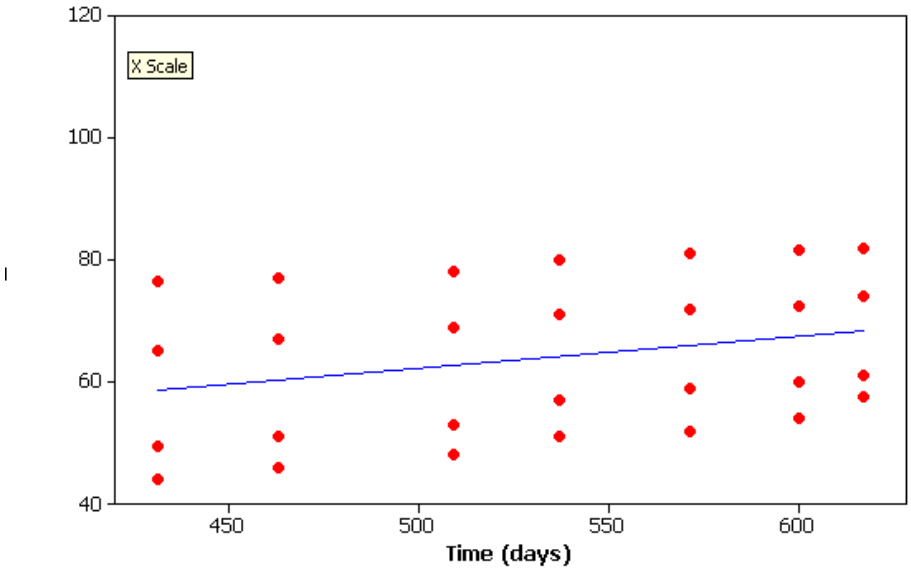
$R^2 = 67.2\%$



Ht = 4.5 + 0.128 time

$F_{(1,27)} = 17.33$, $p = 0.000$

$R^2 = 47.7\%$



Ht = 35.8 + 0.05 time

$F_{(1,27)} = 2.24$, $p = 0.0.146$

$R^2 = 4.4\%$

Figure 21 Regression equations and model fit describing the change in C. glaucophylla seedling height over time at three planting densities (1 – top, 25 – middle, 40 – bottom) from 431 days when the effects of plant density first induced a significant change in height for the seedlings, until completion of the trial at 617 days.

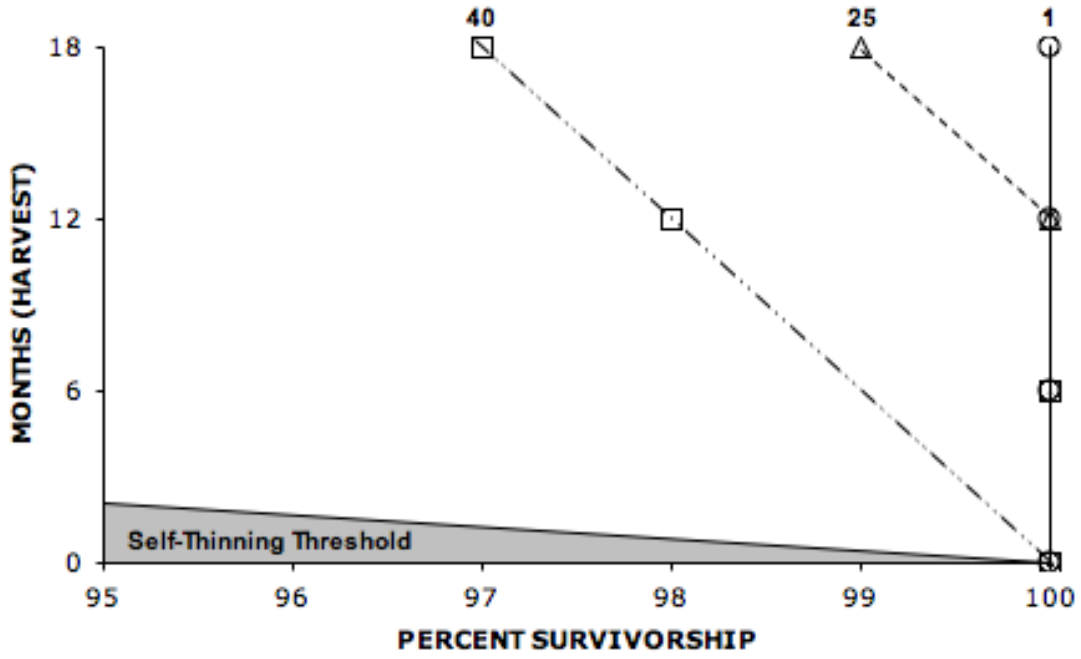


Figure 22. Percent survivorship over time of *C. glaucophylla* seedlings grown at a density of 25 or 40 seedlings per pot, as compared with the theoretical self-thinning slope (-3/2) for trees (after Ellison 1989).

with the regression slope describing change in plant height in the 40 seedling pots almost equivalent to zero. The RSD for height within pots was very small for both the 25 and 40 seedling treatments at only 3% and 5% respectively. In summary, seedlings grew at the same rate, irrespective of density, until 463 days when variation *between* treatments became substantial, however variation between individuals *within* treatments at the end of the trial was minimal.

Plant survivorship in each treatment was high, with the highest average mortality rates at the completion of the trial evident in the 40-seedling density at just 3% (range 0 – 4%). A graphical representation of Yoda's self-thinning law (1963), adapted by Ellison in 1989 to recognise morphological variation in plant geometry was produced to describe the survival of *C. glaucophylla* plants at each treatment density over time (harvest number) (Figure 22 above). The self-thinning slopes for the 25 and 40 densities greatly exceeded the theoretical self-thinning slope for trees.

Table 11. F-values and levels of significance for GLMs comparing the effects of harvest time and plant density on shoot and root biomass N and P, as well as soil N and ext. P. Input values were averaged over each pot, therefore $n = 4$ for each plant density per harvest time.

	Soil N	Soil ext. P	Shoot N	Shoot P	Root N	Root P
Harvest Time	26.66***	32.42 ***	37.23***	6.05*	5.45*	5.50*
Density	n.s.	3.76*	29.45***	12.48***	14.11***	18.92***
Harvest Time | Density	9.66***	3.51*	6.19**	5.48**	7.14**	16.19***

Soil C, N and P differed significantly over time and between density treatments (Table 11 above and Table 12). Soil C decreased over time in each treatment, and for the most part soil C was highest in single-seedling treatments (Table 12). Soil N was highest in single seedling treatments at 199 days, but by 617 days, both single and 25 seedling pots had lower soil N concentrations than the 40 seedling pots. Soil N concentration decreased significantly at 370 days in single seedling pots, whereas significant decreases in soil N did not occur until 617 days in other treatments. Irrespective of treatment, soil N was always at least 0.05 % lower in treatment plots than in 'reference' pots. Soil ext. P was significantly higher than other densities in single seedling pots at 199 days and 617 days, whereas there was no difference in soil ext. P concentration between treatments at 370 days. Soil ex. P decreased over time, irrespective of treatment, and soil concentrations were much lower (c. 3 $\mu g\ g^{-1}$) in seedling pots than in the 'reference' pots by 370 days.

The interaction between harvest time and plant density was significant for shoot N and root N concentration (Table 11 above and see Table 12). Shoot N did not differ between density treatments until 370 days, when shoot N concentrations were significantly higher in single seedling treatments than other densities. By 617 days, shoot N concentration decreased significantly with increasing plant density. Irrespective of treatment, shoot N concentration decreased significantly at each harvest time. Root N concentration increased over time and was significantly higher in single seedling pots but decreased over time in other treatments.

Table 12. The concentration of C, N and ext. P in soils, and N and P in roots and shoots, of *C. glaucophylla* seedlings grown for 617 days at three planting densities – 1, 25 and 40 seedlings per pot. There were four replicates of each plant density 'treatment' at each of the three harvest times, with the exception of a 'reference' soil (Density = 0) consisting of a single pot at each time period containing soil only. First superscript letters denote statistically significant groups (Tukeys) *between* different density treatments *within* the same harvest. Second superscript letters denote statistically significant groups *within* the same density treatment *between* harvests. *a* = lowest, *c* = highest value.

Time	Density	Soil C (%)	Soil N (%)	Soil ext. P (µg g^{-1})	Shoot N (%)	Root N (%)	Shoot P (µg g^{-1})	Root P (µg g^{-1})
199	0	0.52	0.038	7.6				
	1	0.41 (0.018) $^{a\,a}$	0.033 (0.0018) $^{a\,a}$	8.02 (0.291) $^{a\,a}$	1.508 (0.395) $^{a\,a}$	0.442 (0.016) $^{a\,c}$	3548 (287) $^{a\,a}$	6346.8 (342) $^{a\,a}$
	25	0.37 (0.025) $^{b\,a}$	0.027 (0.0014) $^{b\,a}$	6.82 (0.388) $^{b\,a}$	1.448 (0.206) $^{a\,a}$	0.449 (0.028) $^{a\,a}$	2612 (188) $^{b\,a}$	5207 (401) $^{b\,a}$
	40	0.44 (0.033) $^{a\,a}$	0.026 (0.0021) $^{b\,a}$	7.10 (0.292) $^{b\,a}$	1.410 (0.128) $^{a\,a}$	0.491 (0.035) $^{a\,a}$	2031 (31) $^{c\,a}$	3169 (539) $^{c\,a}$
370	0	0.51	0.031	8.1				
	1	0.31 (0.006) $^{b\,b}$	0.014 (0.0003) $^{b\,b}$	5.50 (0.108) $^{a\,b}$	0.807 (0.059) $^{a\,b}$	0.497 (0.042) $^{a\,b}$	2317 (263) $^{a\,b}$	2092 (475) $^{a\,b}$
	25	0.39 (0.010) $^{a\,a}$	0.025 (0.0021) $^{a\,a}$	5.73 (0.144) $^{a\,b}$	0.532 (0.027) $^{b\,b}$	0.432 (0.021) $^{b\,a}$	1917 (101) $^{b\,b}$	2841 (242) $^{a\,b}$
	40	0.34 (0.028) $^{b\,b}$	0.027 (0.0032) $^{a\,a}$	5.85 (0.405) $^{a\,b}$	0.51 (0.049) $^{b\,b}$	0.421 (0.041) $^{b\,a}$	1918 (114) $^{b\,a}$	2068 (93) $^{a\,b}$
617	0	0.50	0.028	8.0				
	1	0.32 (0.002) $^{a\,b}$	0.017 (0.0006) $^{b\,b}$	6.35 (0.222) $^{a\,c}$	0.485 (0.110) $^{a\,c}$	0.565 (0.015) $^{a\,a}$	1515 (354) $^{b\,c}$	1239 (120) $^{b\,b}$
	25	0.28 (0.006) $^{b\,b}$	0.016 (0.0010) $^{b\,b}$	5.97 (0.085) $^{b\,b}$	0.347 (0.019) $^{b\,c}$	0.399 (0.034) $^{b,\,a}$	1895 (173) $^{a\,b}$	2029 (120) $^{a\,c}$
	40	0.29 (0.011) $^{b\,c}$	0.021 (0.0021) $^{a\,b}$	5.15 (0.357) $^{c\,c}$	0.292 (0.008) $^{c\,c}$	0.293 (0.015) $^{b\,b}$	2032 (108) $^{a\,a}$	1887 (38) $^{a\,c}$

The interaction between harvest time and plant density was significant for shoot and root P concentration (Tables 11 and 12). At 199 days, shoot P concentrations increased significantly with increasing plant density. At 370 days, shoot P was significantly higher in single seedling treatments than in other treatments. At the conclusion of the trial shoot P concentration was significantly lower in the single seedling concentration than higher density pots. Shoot P concentrations decreased significantly over time in single seedling treatments, decreased between 199 and 370 days for 25 seedling treatments, but did not decrease significantly at all in 40 seedling treatments. Root P concentrations decreased significantly between treatments with increasing plant density at 199 days, did not differ between treatments at 370 days, and were lowest in single seedling pots at 617 days. Root P concentration decreased significantly and substantially between 199 and 370 days in single and 25 seedling pots, to almost a third of the 199-day value (Table 12). In forty seedling pots, root P concentrations decreased significantly at each time period, albeit not at the same rate as the other treatments.

Total N uptake differed significantly between time | density ($f_{(5,588)}$ = 92.51, p = 0.000) (Figure 23a). At 199 days, the daily N withdrawal rate differed significantly between all treatments, with the least N withdrawal occurring in single seedlings and the most occurring in 40 seedling treatments. By 370 days this pattern had reversed however, with daily N withdrawal rates becoming significantly higher in single seedling treatments and decreasing significantly with increased plant density. By 617 days, the daily N withdrawal rate was almost 2.5 times greater in single seedling pots than forty seedling pots (Table 13).

Total P uptake differed significantly between time ($f_{(2,588)}$ = 217.4, p = 0.000) and density ($f_{(2,588)}$ = 198.6, p = 0.000) (Figure 23b). Daily P withdrawal rates increased significantly with increased plant density, and over time, irrespective of treatment (Table 13).

Table 13 Shoot and root N and P uptake at each time period, and cumulative total N and P uptake and withdrawal over a 617 day trial of *C. glaucophylla* seedlings grown at different planting densities of 1, 25 and 40 seedlings per pot. First superscript letters denote statistically significant groups (Tukeys) *between* different density treatments *within* the same harvest. Second superscript letters denote statistically significant groups *within* the same density treatment *between* harvests. *a* = lowest, *c* = highest value.

Time (Days)	Density	Shoot N uptake (g pot^{-1})	Root N uptake (g pot^{-1})	Total N Uptake (g pot^{-1})	N withdrawal (g pot^{-1} day^{-1})	Shoot P uptake (g pot^{-1})	Root P uptake (g pot^{-1})	Total P Uptake (g pot^{-1})	P withdrawal (g pot^{-1} day^{-1})
199	1	15.67 (4.11)	0.92 (0.53)	16.59	0.083	0.36 (0.02)	0.66 (0.11)	1.02	0.005
	25	19.97 (1.47)	4.45 (0.28)	24.42	0.122	0.57 (0.06)	1.29 (0.14)	1.86	0.009
	40	25.75 (5.82)	10.41 (0.76)	36.16	0.181	0.81 (0.18)	1.14 (0.20)	1.95	0.010
370	1	65.29 (9.27)	10.10 (0.87)	92.49	0.440	1.17 (0.08)	4.24 (0.96)	6.43	0.032
	25	25.96 (1.31)	10.48 (0.53)	60.86	0.213	0.93 (0.04)	4.46 (0.58)	7.25	0.031
	40	18.58 (1.11)	11.26 (1.11)	66.00	0.174	1.01 (0.09)	5.79 (0.24)	8.75	0.039
617	1	66.25 (6.00)	13.29 (0.35)	172.03	0.322	0.95 (0.01)	6.91 (0.28)	14.29	0.031
	25	24.98 (2.39)	15.26 (1.36)	101.10	0.162	0.94 (0.06)	7.95 (0.47)	16.14	0.035
	40	14.59 (0.45)	17.69 (0.92)	98.28	0.130	1.02 (0.05)	10.78 (0.23)	20.55	0.047

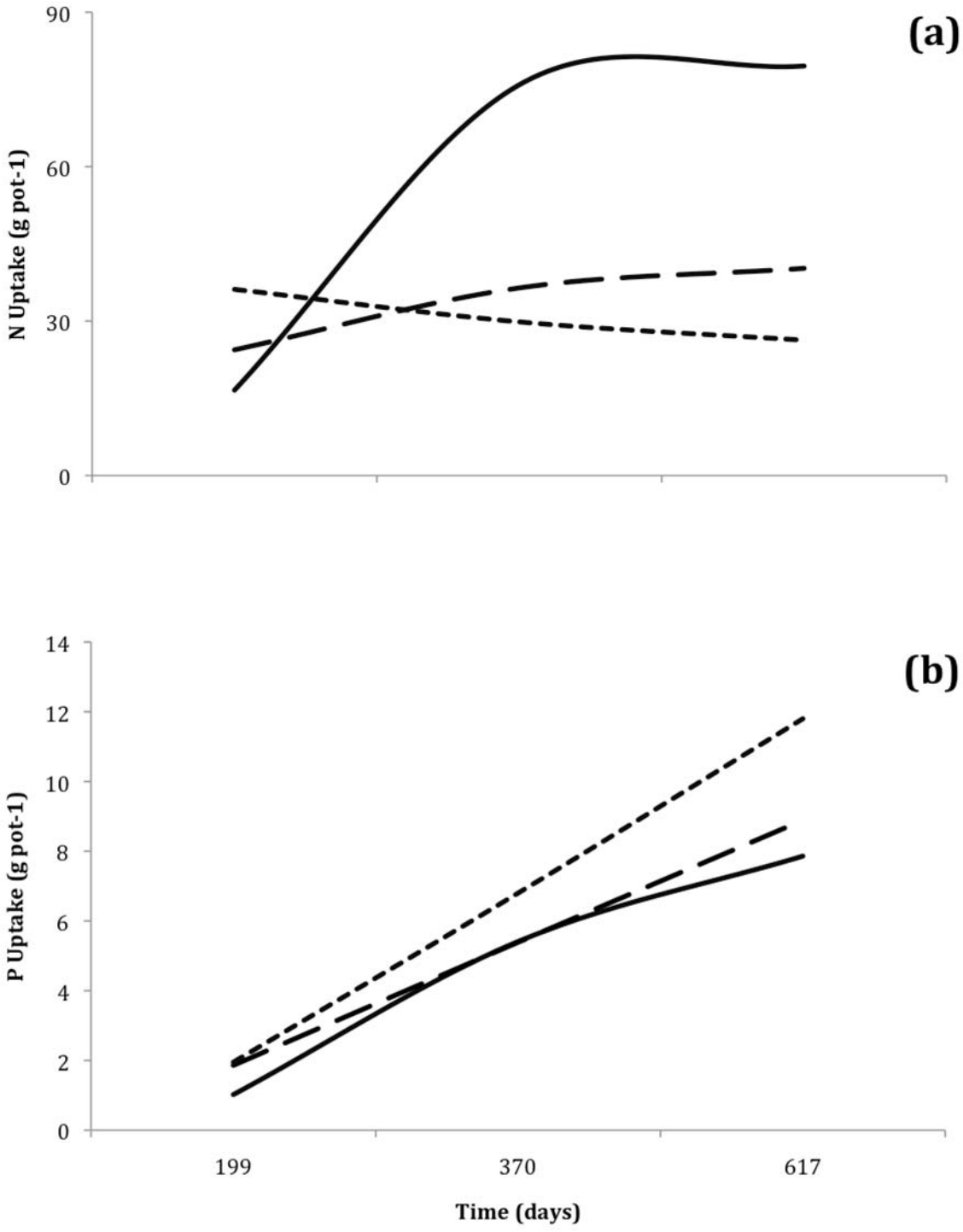


Figure 23. Total shoot + root N (a) and P (b) uptake over time in pots containing *C. glaucophylla* seedlings grown at three different planting densities – one seedling per pot (solid line), twenty-five seedlings per pot (broken line) and forty seedlings per pot (dotted line).

6.5. Discussion

This study has followed on from quantitative field-based investigations in Chapters Two, Four and Five, using an *ex situ* experiment to describe some of the competitive interactions

in dense *C. glaucophylla* populations. The results of this study suggest that *C. glaucophylla* is a morphologically plastic species, able to make phenological adjustments in order to maintain a high survival rate at high densities. The results of this study also provide new insight into the ecology and nutrient use of the species, which has implications for management.

Although the seed germination trial was not set-up to answer the specific objectives of this chapter, the results have yielded new information not previously made available in published literature. In this trial it was found that seed germination was inhibited without a continual supply of fresh water, which progressively decreased the concentration of a tea-coloured leachate in solution. This observation would suggest that field germination is limited by the availability of water to release seeds from endogenous (chemical) dormancy. As the seeds germinated in this study were continuously supplied with water throughout the germination trial, a prolonged rainfall event is most likely required to produce substantial regeneration episodes on agricultural land.

In the literature (e.g. Rolls 1981) it has been suggested that two substantial episodes of regeneration occurred on the north-western slopes and plains of NSW in the late 1890's and 1950's, which correlate with annual rainfall in the previous 5 years which was well above average (BM2008). In a study of the germination behaviour of two other *Callitris* species common to low-rainfall, Mediterranean climates of south eastern Australia, Adams (1999) noted a similar moisture-mediated response by seeds. This study also noted that time-to-emergence was significantly reduced after cumulative low-rainfall events, and that seeds did not appear to dry out in between and hence the period to emergence was not re-set. Should this same response to rainfall variation occur for *C. glaucophylla*, then it could be expected that germination success of the species is enhanced by increased availability of

water to the soil via land management modifications and agriculture. Substantial increases in irrigation of farming land in the region since 1950 might therefore have artificially enhanced the success of *C. glaucophylla* seed germination in the latter part of last century.

The effects of plant density had a significant impact upon seedling phenology in this study, and seedlings grown at higher densities exhibited lower shoot and root biomass, and were inhibited developmentally with a delayed onset of bark and lateral shoot production. A negative density-dependent relationship is usually expected between mean plant size and density in even-aged monocultures (Firbank and Watkinson 1987). Further, increasing plant density can also reduce plant development and reproductive capacity (Silvertown and Charlesworth 2001). Changes in root and shoot biomass have been observed in other plant density studies (Hutchings and John 2004; Lei 2004), but in these situations, increased plant density resulted in reduced root:shoot ratios as plants competed with each other spatially for light. In this study however, root:shoot ratios increased over time with increasing density. Lentz (1999) compared and contrasted root and shoot growth in bulrush populations in which both plant density and soil nutrient supply were experimentally manipulated, and found that root:shoot ratios were highest in high density pots with low soil nutrient concentrations. Alterations to root:shoot ratios favouring root biomass have also been demonstrated following experimental manipulations of soil phosphate availability to crop cultivars (e.g. Nachimuthu et al. 2009 in press). It is therefore possible that the change in biomass allocation observed in high-density pots reflects a shortage of below ground resources, which were intensely contested towards the completion of the trial.

In this study it appears that in addition to the expected reduction in plant biomass with increasing density, the effects of competition were so intense that by the completion of the

trial whole pot biomass was slightly higher in single seedling pots than pots with forty seedlings. A contributing factor to this result is more than likely that the densities trialled in this study were so high so as to almost certainly result in greatly reduced plant biomass in high-density treatments. However, this result is still very important when considering that size variation *within* pots was negligible, and therefore the degree of size asymmetry in each pot was small. Competition among individual plants for resources in limited supply can be placed along a continuum between completely size symmetric competition (i.e. resource usage not proportionate to plant size) and completely size asymmetric competition (i.e. largest plants obtain all contested resources) (Schwinning and Weiner 1998). Whilst most plant populations exhibit competitive interactions that are at least partially size asymmetric (Firbank and Watkinson 1987; Hendry et al. 1996), there are some general exceptions that might relate to the patterns observed during this study. Firstly, plant populations normally do not exhibit size asymmetric competition if the contested resource is belowground. Secondly, populations of plants that grow taller but not wider when competing (Ellison 1987) also appear not to acquire resources asymmetrically. That root biomass increased greatly over time, and that lateral branching decreased, in high-density treatments in this study, suggests that competition for resources is independent of plant size. The co-efficient of variation for shoot height was very small, and hence the potential for size-related partitioning was also low in this study.

Increasing allocation to roots versus leaves is a likely adaptation to soil and atmospheric water deficits, but one that comes at the expense of a slow relative growth rate (Warren and Adams 2005). As the results of this study suggest that enhanced root biomass was the result of intense below-ground competition for resources, it appears that these resources limited growth and development of plants in higher density treatments just after 12 months into the trial. At the completion of the trial, plants in the 40-seedling density treatment had

almost ceased in above ground aerial growth, and were appearing to approach 'lock-up'. Yet despite this growth plateau, within-pot aboveground size variation was almost negligible, and root biomass allocation was increasing. The morphological and physiological adjustments made by high-density treatments which were mediated by competition indicate that *C. glaucophylla* is a highly plastic species, and suggest that individuals grown at high densities adjust allocations to various plant parts in order to maximise growth under resource constraints (Bloom et al. 1985; McConnaughay and Coleman 1999; Schenk and Jackson 2002; Watkinson 1980). Models suggest that if plants can at least maintain highly 'plastic' shoot morphology, then the density threshold for the onset of asymmetric competition will be very high (Schwinning and Weiner 1998).

The plasticity of *C. glaucophylla* with change in plant density is the result of competition for below-ground resources, and as a result of the adjustments to plant morphology in response to this competition, biomass partitioning is homogenous and hence density-dependent mortality is greatly reduced. In this study, plants grown at high densities had almost a 100 % survival rate, and hence the function of survival over time greatly exceeded the theoretical -3/2 thinning slope specified for most plant populations (Yoda *et al.* 1963, Miyanishi *et al.* 1979). Ellison (1987) demonstrated the relationship between plasticity of shoot growth and a lack of size hierarchical responses to growth at high densities in a common saltbush. Two other study species made few adjustments to their above-ground morphology, and hence self-thinned once neighbourhood crowding occurred, whilst the highly plastic *Salicornia europaea* did not. It therefore appears that the spatial dimension to competition for above ground resources (such as light) enhanced by local branch interference in most species has been avoided by *C. glaucophylla* due to its highly plastic shoot morphology. Therefore, survival of *C. glaucophylla* is ensured even at high densities.

Demographic and phenological traits of *C. glaucophylla* grown at high densities suggest that morphological plasticity is strongly mediated by belowground resource competition. Tissue concentrations of N and P varied over time and were strongly influenced by plant density but altered biomass allocation from shoot growth to root production at high seedling density corresponded only with the uptake and allocation of P in this study. Shoot P concentrations decreased substantially over time in single-seedling treatments, which was consistent with rapid growth and development of the aerial portion. Root P concentrations decreased over time in all three treatments due to continued root growth in all treatments during the study. Despite the low ext. P concentration of the soil medium, seedling uptake continued throughout the trial, and increased with seedling density.

Yet differences in overall plant uptake and withdrawal suggest that, contrary to many other Australian systems (Attiwill and Adams 1993; Grove et al. 1996; Holford 1997; O'Connell and Grove 1985; Vitousek and Howarth 1991), the limiting nutrient for growth of *C. glaucophylla* was N and not P. The plasticity of root and shoot allocation in response to nitrogen limitation was critically analysed in five annual plants with different ecological demands grown under hydroponic conditions by Glimskär and Ericsson (1999). The authors found convergence in root: shoot ratios among the morphologically divergent study species when N was limiting, whereby root biomass greatly increased. These results are consistent with the growth response of *C. glaucophylla* in this study, where the effects of plant density heightened demand for N. Nitrogen-limitation in this study was most likely facilitated by low soil organic C concentration and hence the potential for N-mineralisation would also have been low. Decreases in reference soil C and N over time indicate that mineralisation did occur however, but losses of inorganic-N through nitrate leaching may also have occurred as pots were regularly saturated and water was not recycled through the pots.

A possible limitation of this study was that plants were grown at artificially high planting densities, and that growth was facilitated by a non-limiting supply of water. Given the time constraints of the study, both of these experimental measures were employed to ensure that plant growth / nutrient limitation could be observed over the duration of the study (field observations of 'lock-up' suggest that the phenomena occurs sometime during the first 10 years after germination – Lacey 1973). Nonetheless, single seedlings were almost two-thirds of 'tree' height by 617 days (>1.6 m) (Knott 1995), and the extremely slowed growth and negligible mortality of the 40 seedling treatments by the end of the trial provided the first *ex situ* support for 'lock-up' as a real demographic process in dense *C. glaucophylla* stands. Further work in this area could extend on the observations of N limitation in the study, and would require a 'closed-circuit' design, where water at the bottom of the pot was returned to the soil, ensuring that the fate of readily leached nutrients could be accounted for throughout the trial.

In summary, competition among plants in a confined space or at high densities normally induces a range of physiological responses, which ultimately determine the growth, reproductive success, and survival of individuals. For *C. glaucophylla*, growth in a low nutrient and low rainfall environment appears to result in allometric adjustments which represent a trade-off between reduced above-ground growth and the assurance that individuals will persist through time with negligible mortality, even at high densities. Therefore, active management of dense stands is the only option to minimise intense within-stand intra-specific competition for below-ground resources, and may in fact assist in the restoration of 'degraded' landscapes by also reducing inter-specific competition between the species and groundstorey vegetation.

Chapter 7. Management Experiment

Changes in soil quality and floristic composition following management of dense *Callitris glaucophylla* (White Cypress Pine) regrowth

7.1. Background

Chapters Two, Four and Five described small studies which quantified soil and groundcover parameters, as they existed in association with *C. glaucophylla* in a range of spatial configurations. These results have informed the debate with respect to the ecophysiological role of the species in agri-ecosystems in northwest NSW. A concern of landholders, which has been confirmed by this research, is that vascular plant cover is greatly reduced in close proximity to *C. glaucophylla* trees, irrespective of tree size, age, density or soil type. With respect to soil chemical parameters however, individual *C. glaucophylla* trees increase soil pH, and enhance soil C and ext. P in their immediate vicinity. These effects are greatly modified in dense stands to the point where soil C and ext. P gains are minimal and soil acidity is actually increased relative to managed paddocks.

Chapter six demonstrated that *C. glaucophylla* seedlings have a very high survival rate and also exhibit a 'plastic' morphology. Therefore the species not only impacts negatively upon the productive environment but due to some inherent aspects of its ecophysiology, will presumably persist in the environment at high densities over a long period of time, requiring active management to restore ecosystem services. This chapter will now describe the effects of managing *C. glaucophylla* in a variety of scenarios (retaining dense stands, thinning or clearing, with or without livestock grazing) for soils and groundcover. It will also document tree growth over time, vascular plant compositional change as well as the instances of secondary plant regeneration and other weed incursions throughout the study.

7.2. Introduction

Tree clearing and subsequent overgrazing of the woodlands of eastern Australia over the last century has, until recently, maintained agricultural land in an unstable savannah-like state. Since the 1950's these 'agri-ecological zones', like others worldwide, have undergone a transition in response to the altered grass species composition induced by grazing animals and increasingly variable climate. These transitions have been characterised by declines in perennial grass cover, increases in annual grass biomass and in some instances, there is a final transition to dense woody vegetation at the exclusion of most herbaceous plants (Walker et al. 1981). The worldwide significance of this final 'woody' state is that even when grazing animals have been removed for an extended period of time (over 20 years), there is no transition back to the original woodland or even the intermediate, savannah-like state (Walker et al. 1986). Dense woody vegetation, such as *C. glaucophylla* stands in agri-ecological zones of NW NSW, therefore require intervention in order to reverse the effects of the 'woody' state. Management options that balance both agriculture and ecological diversity and stability are now being sought but so far, there has been limited study conducted in Australian ecosystems that is concerned with addressing both interests (Williams and West 2001).

Studies that have documented the changes in agri-ecosystems following treatment of woody vegetation have reported mixed success. In some instances, management of the target species is followed by a secondary regeneration of the species or the invasion into the management zone by other woody species. The reasons for this are usually thought to be due to the reduced cover of vascular plants in the understorey that have either been reduced directly, or modified in composition, by grazing animals (Harrington and Johns 1990; Hobbs and Mooney 1986; Walker et al. 1981). Alternate theories ascribe woody vegetation invasion to changes in soil moisture enabled by agricultural irrigation and the exclusion of fire, thus allowing soil water to be retained over longer periods of time (Barker and Booth 1980; Denham and Auld 2004; Harrington 1991; Knoop and Walker 1985).

Changes over time following management of dense *C. glaucophylla* stands have been documented primarily in forestry literature (e.g. Lacey 1972, 1973, Horne and Robertson 1986, Johnston 1991, Knott 1995) and are focused on growth rates and regeneration characteristics of the species. An increasing volume of literature is now dedicated to describing plant compositional change beneath stands of different densities for the species, and these results suggest that variations in the composition of vascular plant cover in the understorey of stands are linked to climatic variation, especially rainfall (e.g. Nadolny, in Andrews 2002, Thompson and Eldridge 2005a, McHenry 2007). Whilst a decrease in cover of understorey vegetation has been demonstrated retrospectively among a variety of land-uses for *C. glaucophylla* stands (Chapter Two), there has been little attempt to compare the effects of managing the species over time. With the exception of the results reported in Chapter Two, there have been few studies that compare soil fertility in managed stands.

In this study, I compared understorey vascular plant cover and composition, litter cover, soil chemistry and tree growth/regeneration characteristics in managed dense *C. glaucophylla* stands (grazed/un-grazed dense stands, thinned and clear-felled stands) on three properties on the North-Western Slopes of NSW. The aim of this study was to describe changes in these parameters through time providing comparisons before, during and at the completion of a 2.75-year management trial for *C. glaucophylla*.

7.3. Methods

7.3.1. Site layout

Two 60 m x 20 m replicate plots were located not more than 100 m apart and established at each of the Mingoola, Yallaroi and Myall Creek sites and were selected on the basis that they were similar in stand density. The 5 x 5 m grid plots reported in Chapter Five were established within these plots and the results of that study provided baseline pre-treatment data for this chapter (see Figure 23 for an example of plot layout).

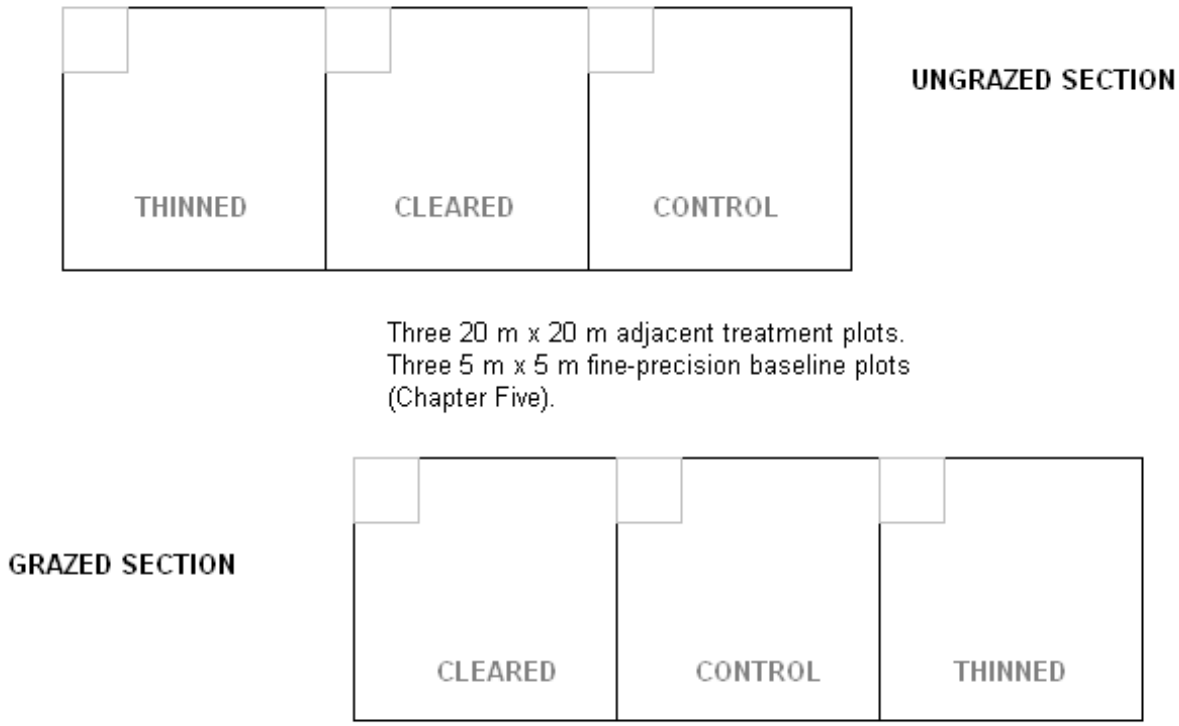


Figure 24. Example of the layout of the 60 x 20 m grazed and un-grazed sections at one property each containing a control, thinned and cleared sub-plot. The 5 x 5 m fine-scale sampling zones refer to the areas sampled in Chapter Five and data from these zones was used as pre-treatment data for the management experiment reported in this chapter.

Between December 2005 and January 2006 one of the replicate plots at each site was fenced to exclude domestic livestock (but not other grazing animals such as rabbits and kangaroos). This plot is referred to as the 'un-grazed' section hereafter, and the unfenced comparison is referred to as the 'grazed' section. Within each section, a 20 x 20 m 'control' plot was established, where trees were left standing. In the adjacent two 20 x 20 m plots in each section, one was clear-felled and the other thinned to 8 x 8 m spacing with a brush-cutter and a chainsaw near ground level. The felled timber was laid across the slope to remain throughout the duration of the trial. Treatments were allocated randomly within sections at each site. Throughout the duration of the trial, plots open to domestic livestock were grazed intermittently for approximately four months each year by cattle at Yallaroi and Myall Creek, and constantly by sheep at a low stocking rate at Mingoola.

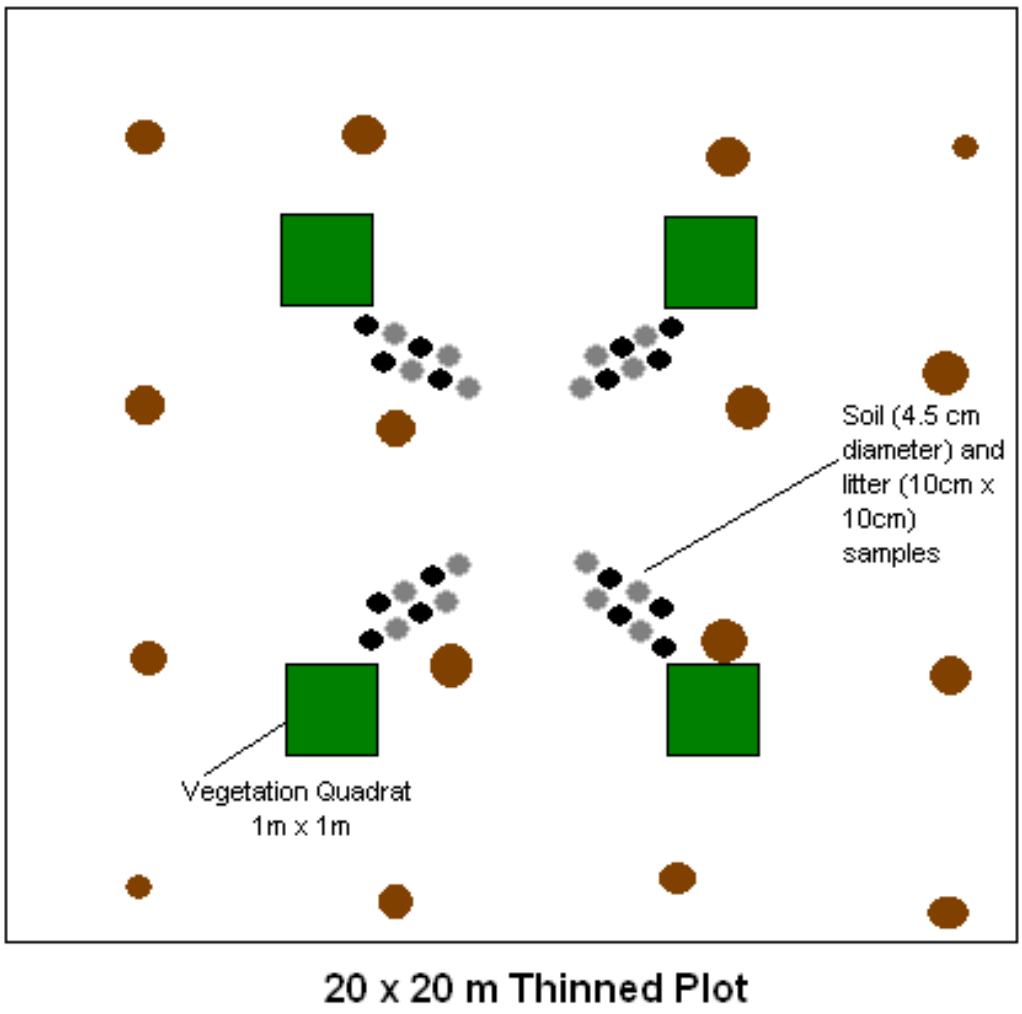


Figure 25. Example of the layout of the vegetation quadrats, and the location of soil and litter samples in a thinned *C. glaucophylla* plot (8 x 8 m spacing).

7.3.2. Sampling regime

Sites were sampled prior to management in October 2005 and then three-monthly until the conclusion of the trial in February 2008 for soil and October 2008 for groundcover. Within each treatment, four replicate 1 x 1 m quadrats were established in a square 5 m in from the edges of the plot to minimise edge effects. Groundcover was visually assessed in these quadrats. Litter and soil (0-5 cm bulked to form one sample per time period due to budgetary constraints) were sampled quarterly immediately outside the quadrats to ensure no disturbance to the vegetation. At each sampling time, the location of soil and litter samples was 10 cm further away than the last (Figure 24). Litter biomass was determined in a 10 cm square template by measuring the depth of litter and the dry weight of the sampled material.

Prior to treatment in October 2005 and again in September 2008, three 0-30 cm profiles were taken at each site with a 45 mm steel coring device and were separated into four depth increments – 0-5, 5-10, 10-15 and 15-30 cm.

Plant composition and abundance across the entire plot was determined on four separate annual excursions from October 2005 and including October 2008. The height and DBHOB of all trees remaining in the plot was measured quarterly, as was the incidence of any new *C. glaucophylla* seedling establishment over 30 cm tall.

7.3.3. Laboratory Analyses

All soil samples were dried to a constant weight at 40 degrees, sieved and ground to less than 2 mm. Soil C and N was determined by LECO combustion at 950 degrees and extractable P was determined by the Olsen method (Olsen et al. 1954) at Southern Cross University Environmental Analysis Laboratory (EAL). Soil pH was determined in a 1:5 calcium chloride suspension. Soil pH only was determined for the final profile samples.

7.3.4. Statistical analyses

Standardisation of data was undertaken to account for the substantial variation in soil chemical and groundcover parameters between sites that was established in Chapters Two, Four and Five. This involved relating soil and vegetation data collected during the trial to the initial site values collected at T-1 and converting data to a 'percent change with respect to T-1'. A number of GLM models were employed to assess variation in soil and groundcover parameters using MINITAB version 15. As the focus of the study was to apply the results of treating a small sub-set of dense *C. glaucophylla* stands to stands across the NWS of NSW, the effects of site, grazing regime and treatment ('control', 'thinned' or 'cleared') were all declared random factors.

7.3.4.1. Soil

Due to the lack of within-treatment replication for each time period, comparisons between sites were not included in a GLM in order to obtain 2 degrees of freedom (n – 1) for each treatment per time period. Variation in soil C, N, ext. P and pH was assessed using the model:

Y = grazing | treatment

Variation in soil C, N, ext. P and pH in the initial depth profiles, was analysed using the model:

Y = site | treatment | depth

Final pH profiles were compared with initial profiles using the above model, where all initial profiles were called control treatments and *F* values were calculated from sequential sums of squares.

7.3.4.2. Groundcover

Multiple GLMs for each time period were used to assess variation in percent cover of vascular plants in the understorey and litter biomass, each of which had 4 replicates per treatment per time period. The model terms were:

Y = site (random) | grazing (random) | treatment (random)

7.3.4.3. Vascular plant composition and abundance

As species richness data were assessed on a whole plot basis, only one value existed for each treatment and grazing regime per site. Therefore, standardised data were used to compare post treatment values with T-1 baseline data, and the site effect was dropped from the model:

Y = grazing | treatment

to provide 2 degrees of freedom for each time period. In order to account for the site effect, species composition and abundance were used to perform a multivariate classification of sites, treatments and time using similarity dendrograms in Minitab version 15.1.

7.3.4.4. Allometric and demographic characteristics

Since no grazing of seedlings by domestic livestock or other seedling mortality was observed throughout the trial, the number of seedlings (over 30 cm tall) were compared at the end of the trial by two-way ANOVA with the factors grazing and treatment pooled across all sites. Two-way ANOVA was also used to assess variation in tree height and DBHOB in control and thinned plots at the end of the trial.

7.4. Results

7.4.1. Soil profiles

Soil C and N varied with site and depth in depth profiles at the beginning of the trial (Table 14) due to significantly higher soil values in the top 10 cm of soil at the Myall Creek site. There were no other differences with depth between sites beyond variation in surface (0 - 5 cm) soil. All soil parameters were highest in the top 5 cm of soil, declining to 30 cm, except pH, which increased significantly at 15 – 30 cm depth. At the conclusion of the trial, thinning and clearing resulted in significantly increased soil pH in the upper 10 cm of the profile, but a significant decrease (0.2 pH unit to mean pH of 5.6) in pH occurred at 15-30 cm in grazed thinned and cleared treatments.

7.4.2. Surface soil monitoring

Treatment was the only significant source of variation for both C ($F_{(2,12)} = 8.84$, $P = 0.000$) and N ($F_{(2,12)} = 5.32$, $P = 0.023$) irrespective of time. Both parameters increased significantly relative to the original values found in the plots prior to treatment. Carbon increased by 10% in thinned plots irrespective of grazing and 15% in clear felled plots over the trial and for N the increases were 4% and 6% respectively (Figure 26). Carbon and N averaged a loss of two and three % respectively in the control treatments relative to the pre-treatment values for each site irrespective of grazing regime over the course of the trial. Extractable P and pH varied by

Table 14 *F*- and *P*-values (as denoted by asterisks) from a two-way ANOVA resulting from a preliminary investigation of soil chemical parameters prior to treatment in three 0 – 30 cm soil profiles collected from each of three sub-plots at three sites.

	C	N	P	pH
Site	23.58***	58.57***	138.97***	94.36***
Depth	44.04***	61.01***	2.79*	12.54***
Site | Depth	2.99*	5.95***	n.s.	n.s.

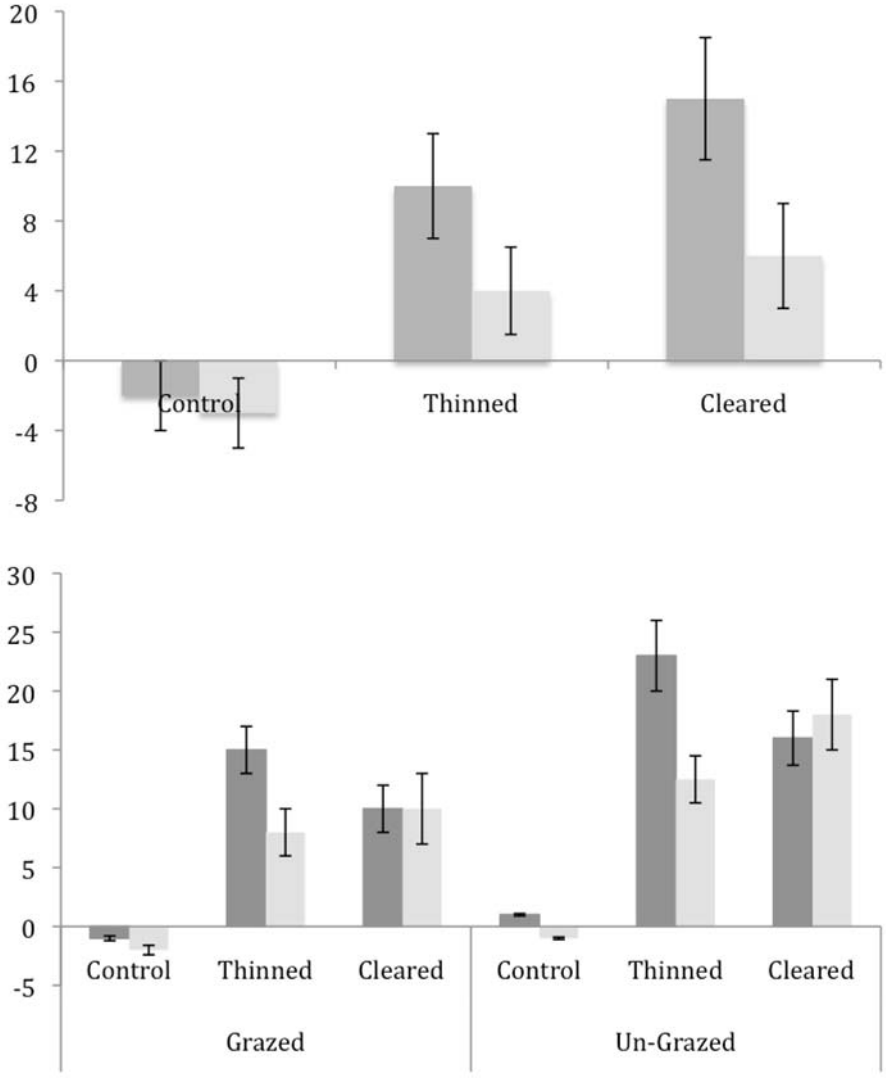


Figure 26. At the completion of a 2.75 year *C. glaucophylla* management trial, thinning and clearing resulted in significant increases in C (dark shading) and N (light shading) (top image). Soil ext. P (dark shading) and pH (light shading) increased following thinning and clearing, but were lower in grazed treatment plots (bottom).

grazing regime (ext. P - $F_{(1,12)}$ = 18.57, P = 0.000; pH - $F_{(1,12)}$ = 4.17, P = 0.045) and treatment (ext. P - $F_{(2,12)}$ = 3.53, P = 0.040; pH - $F_{(2,12)}$ = 9.76, P = 0.010) by the end of the trial. All grazing treatments had significantly lower concentrations of ext. P and lower soil pH than un-grazed treatments. Cleared plots had on average 13 % and thinned plots had 20 % more ext. P than the original pre-treatment. Soil remained acid with an average pH of 5.13 in control plots irrespective of grazing regime, with significant increases in pH observed in thinned plots (mean = 5.40) and cleared plots (mean = 5.53) after treatment.

7.4.3. Groundcover

For each time period, vascular plant cover differed significantly with the interaction between sites, grazing and treatment ($F_{(4,12)}$ = 6.15, P = 0.021). Plant cover increased in thinned and cleared plots within the first six months of treatment and fluctuated in response to grazing and also season in the first two years. Thereafter, irrespective of sites, all cleared and thinned plots became increasingly invaded with the exotic grass *Hypparhenia hirta* (Coolatai grass), which comprised an estimated 75% of all plant cover in un-grazed, and at least 50 % of all cover in grazed treatment plots (Plate 13). At the completion of the trial, plant cover ranged from approximately 15 % in control plots, irrespective of grazing regime, to 75 % cover in grazed treatment plots and 90 % cover in un-grazed treatment plots (Figure 27).

Litter biomass differed significantly between treatments at each time period, and at the end of the trial, thinned plots had the highest litter biomass, followed by cleared plots and then control plots, irrespective of site or grazing regime ($F_{(2,12)}$ = 18.49, P = 0.000). The time frame of 'peak' litterfall during the trial was variable between sites, but occurred somewhere between three and nine months after the trial at each site as a result of foliage falling from felled timber. Mean litter biomass then declined over time in the cleared plots and thinned plots, but was still higher than the control plots at the end of the trial.





Plate 14. The initial groundcover in the dense and clearfelled plots at the beginning of the trial (top) and in February 2008 (bottom), when much of the clearfelled plot had been invaded by *H. hirta*.

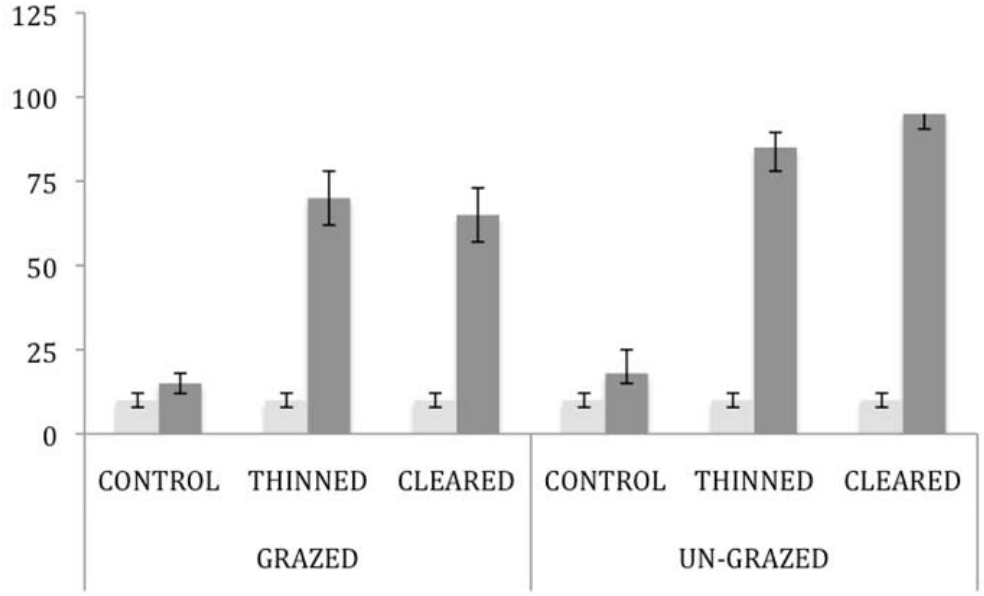


Figure 27. Mean vascular plant cover at the commencement of the trial (October 2005) and at the end of the trial (October 2008).

7.4.4. Plant community diversity and composition

The interaction between grazing and treatment was significant for native ($F_{(2,12)}$ = 44.41, P = 0.000) and exotic ($F_{(2,12)}$ = 33.25, P = 0.000) plant species richness at the conclusion of the trial. There was no change in native or exotic species richness in control plots during the trial, but there was significant variation between thinned/cleared plots and controls (Figure 28). Grazed sites had significantly more native and exotic species. Within the un-grazed section, only thinned plots had significantly more native species richness, whilst only cleared plots had more exotics.

Floristic composition increased in the thinned/cleared plots in the first year following treatment but then declined again almost to pre-treatment levels, especially in the un-grazed sites, towards the end of the trial as *H. hirta* replaced much of the understorey (Plate 13). The composition of grazed and un-grazed zones varied at all sites and by the end of the trial, perennial grasses such as *Aristida ramosa* and *Austrostipa scabra* replaced the exotic annuals (e.g. *Setaria pumila*) that more common in the grazed areas (see appendix 1 for species list).

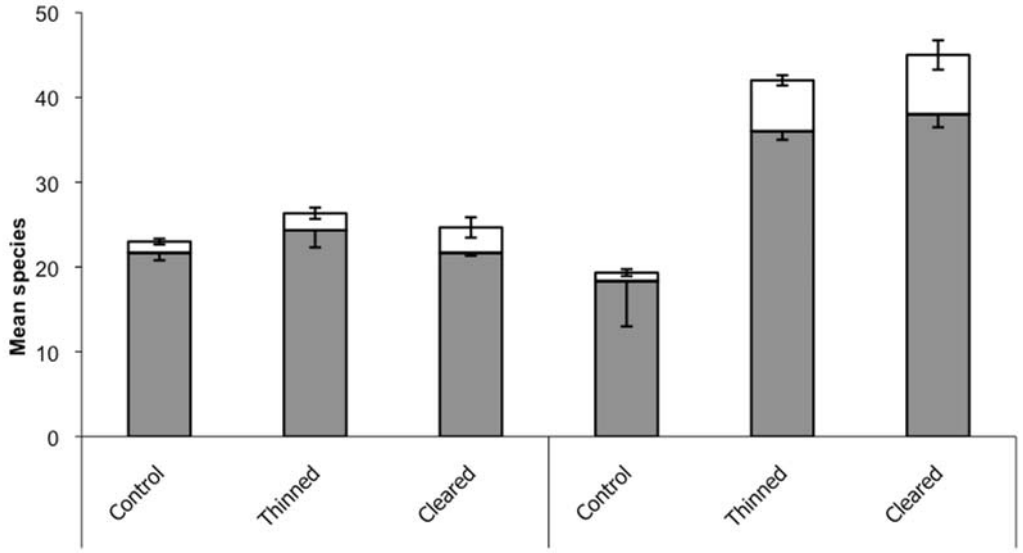


Figure 28. Mean species richness (± S.E.) of native (shaded) and exotic (unshaded) plants pooled across all sites at the conclusion of the trial.

7.4.5. Callitris glaucophylla *growth and re-establishment*

There were no significant differences between site or grazing for tree height, but the interaction between sites, grazing and treatments was significant for tree DBHOB ($F_{(2,576)}$ = 45.00, P = 0.000). Trees had a significantly larger DBHOB in un-grazed thinned plots relative to grazed thinned plots, and the amount of growth was significantly higher at the Myall Creek site than Mingoola or Yallaroi. Although growth increases were measured in control plots over the course of the trial, these increases were not significant (Figure 29).

There was substantial between-site variation in *C. glaucophylla* seedling recruitment (e.g. 40 seedlings in the grazed cleared plot at Myall Creek at the end of 3 years but only one at Yallaroi), and this resulted in all factors being statistically insignificant. There was a general trend however across all sites whereby cleared plots had more recruitment than thinned plots and grazed plots had more recruitment than un-grazed plots. There was no recruitment of any species in the control plots, including *C. glaucophylla*, after the first year of the trial at any site and at the end of the trial, recruitment was limited to three more *C. glaucophylla* seedlings in the control plot at the Myall Creek site.

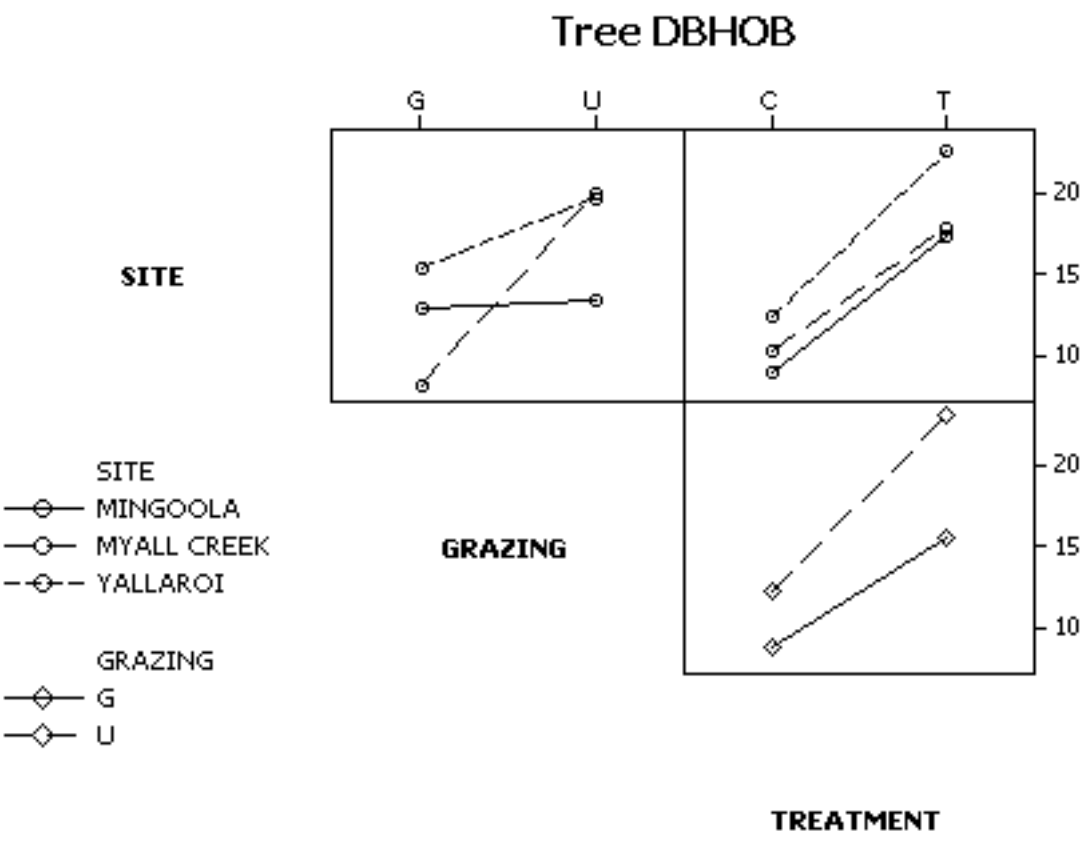


Figure 29. Significant interactions between site, grazing regime and treatment (control or thinned) for tree DBHOB. G = grazed, U = un-grazed, C = control plot, T = thinned plot.

7.5. Discussion

Despite the limited sample size of this study, the results have provided new information regarding the management of the species for both productive and ecological purposes. For almost every parameter studied, it was demonstrated that treatment (thinning or clearing) of dense stands resulted in favourable environmental outcomes, albeit that the magnitude of these effects was modified by grazing livestock. However, the results also suggest that the management of dense *C. glaucophylla* regrowth, without follow-up of a number of secondary management issues such as maintenance of groundcover, produced an unstable ecosystem state. Treated stands which are then left unmanaged are therefore likely to return to a more stable dense woody state without a series of further interventions.

The results of this trial have again highlighted the complex mechanisms which drive patterns of soil acidity in dense *C. glaucophylla* stands, and presumably measurable pH change occurred rapidly during this study due to the sandier texture and hence weak buffering capacity of each soil. Two concurrent mechanisms are proposed below to explain the significant changes in soil pH observed throughout the soil profile at each site during the course of the trial, nitrate leaching and biological pumping.

For most of the trial, north-west NSW experienced a severe rainfall deficit (see Chapter Two for seasonal rainfall data). Nitrogen supply to semi-arid woodlands and arid shrublands is driven by pulses of rainfall (Noy-Meir 1973, Gebauer and Ehleringer 2000, Chesson *et al.* 2004, Reynolds *et al.* 2004), and often inorganic nitrogen in the form of nitrate accumulates because the amount of rainfall sufficient to stimulate microbial activity is much less than that required to stimulate root activity (Schwinning and Sala 2004). Nitrate leaching, resulting in the acidification of sub-surface soil often occurs after infrequent, substantial rainfall events, when there is a lack of perennial, deep-rooted plants to withdraw excess nitrate from the soil. In this study, the final pH profiles were collected after a series of large spring rainfall events and abundance and cover of perennial plants in the grazed plots was significantly lower than in the un-grazed plots. A loss of nitrate from lower depths could therefore explain the observed acidification of the 15-30 cm soil depth (i.e. below the shallow roots) in the grazed plots, and is a process common in north-west NSW (e,g. Lockwood *et al.* 2003).

Increased surface soil pH may also have been explained by the biological pumping mechanism proposed by Noble and Randal (1989) and observed by Wilson (*et al.* 2007) for *Eucalypt* species in higher rainfall zones and which is now postulated for *C. glaucophylla* (Chapter Four). The redistribution of nutrients to the soil surface by perennial groundcover species in the form of alkaline litter, which occupied almost 100% groundcover in the un-grazed areas, may have significantly influenced surface pH. Further, substantial litter was

progressively lost from the felled timber over the course of the trial and the association between litter deposition beneath individual trees and increased soil pH beneath the canopy of individual trees was demonstrated previously in Chapter Four. In summary, it is likely that more than one key process contributes to soil pH change in managed *C. glaucophylla* stands, and further work is required to better understand these processes.

In this study, C, N and ext. P all increased significantly following treatment of dense stands. Although mean values were significantly higher for ext. P in un-grazed plots relative to grazed plots, all values were still significantly higher than control plots. These observations are not consistent with the results of Chapters Two and Five, in which it was noted that dense stands had significantly more ext. P and C than adjacent cleared managed paddocks. However, these observations *are* consistent with the time scale described in other literature pertaining to vegetation management and soil change (e.g. Burrows *et al*. 1990). Most of the nutrients liberated after tree thinning and clearing are likely to be a consequence of the return of nutrients stored in the phyllodes of the felled timber to the soil. Tree thinning and clearing is often associated with a flush of microbial activity and enhanced mineralisation of organically bound nutrients due to an increase in available soil water and enhanced soil temperature and light availability, however, these effects are short-lived (Attiwill and Leeper 1987, Attiwill and May 2001). Given these considerations and the observations from the preceding chapters it would therefore be erroneous to conclude that tree management is likely to result in sustained soil fertility increases. On the contrary, a study which documented groundcover, species richness and soil microbial biomass and pH over 30 years since clearing other invasive woody species found that optimum benefit from management was exhausted in as little as six years (Kaur *et al* 2005).

Changes in groundcover and plant composition observed in this study were generally consistent with other literature describing changes through time with management of woody

vegetation in grazing landscapes. Significant increases in groundcover have been observed to follow tree clearing or thinning in Australia (Walker *et al*. 1972, Burrows 1990, Kaur et al. 2005, Watson 1998) and internationally (e.g. Todd and Hoffman 1999), and is postulated to be the consequences of decreased competition for soil water and nutrient resources, as well as light and space (Silvertown and Charlesworth 1994). In an article documenting plant responses to livestock grazing in temperate NSW grasslands (Dorrough *et al.* 2004) similar patterns of increases in exotic species, decreases in native species and a predominance of annual plants in areas grazed by livestock.

In this study however, the exclusion of livestock also resulted in a dramatic increase in the invasive exotic grass *H. hirta*, which rapidly became the dominant species in the fenced plots at all three sites. At the conclusion of the trial the cover and richness of other vascular plant species in the plots was reduced, and if left unmanaged there is a serious risk of further increase in the local *H. hirta* population to the exclusion of other plants. Contrary to other species, which note an increase in weedy exotic species in managed, grazed landscapes (e.g. Dorrough et al. 2004 a, b, 2008) in response to varied and sometimes intense levels of disturbance, *H. hirta* appears to have invaded the un-grazed plots so successfully due to the lack of disturbance. Connell and Slatyer (1972) describe this process in the inhibition model of colonisation, whereby species already present at a site dictate the future composition of the remnant. Breaking this cycle, it is proposed, requires an intermediate level of disturbance (the 'Intermediate Disturbance Hypothesis') in order to provide opportunities for other species to establish. Future management of treated *C. glaucophylla* stands might therefore require follow-up management of secondary weed species in order to enhance pasture viability.

In previous studies, plant diversity and species richness has been linked to site rather than tree density or management (e.g. Nadolny 2001 in Andrews 2001, Thompson and Eldridge 2005b, Chapter Two of this thesis). The limited replication in this study meant that the effects of

treatment had to be pooled across sites, thus excluding site as a factor for comparison. Although site and species richness did appear to be related in this study (Mingoola = lowest species richness, Myall Creek = highest species richness), there were nonetheless relationships between tree density and richness, as well as grazing management and richness. These differences in the early years following treatment of dense *C. glaucophylla* stands have not been described before, and, given the subsequent invasion of the plots by *H. hirta*, presumably will not be long-lasting.

A further management issue made apparent in this study is that of secondary regeneration of *C. glaucophylla* seedlings, which varied between grazed and un-grazed treatments, but generally sites which had been grazed had higher incidences of regeneration. The interaction between vascular plant cover and the success of a secondary regeneration event has been discussed by Andrews (2001). Maintenance of cover in the understorey is considered pivotal to the reduction of new *C. glaucophylla* seedling establishment because cover functions at the very least as a physical barrier to seedling establishment. The dense groundcover in the un-grazed plots, much of which comprised of *H. hirta*, might therefore have provided beneficial coverage to the soil surface, therefore reducing the potential success for re-establishment by *C. glaucophylla*.

Tree growth was observed even despite drought conditions at every plot and site throughout the duration of the trial. In control plots, this result implies that whilst stands exhibit a pattern of extremely slowed growth, this growth does not cease when stands are 'locked up'. It has been suggested previously that the species may be more effectively utilised as a timber resource on private lands (Andrews 2001), especially given the recent increase in demand for the species following the conservation of substantial forest reserves in 2006. This study suggests that, provided that secondary regeneration is addressed, *C. glaucophylla* timber could be managed for future timber harvesting, whilst also providing environmental benefits.

In conclusion, this study, was described changes that occur in treated dense *C. glaucophylla* stands, and was the first to directly compare the effects of management with and without livestock grazing, Further research should now be directed at expanding the study to encapsulate and broader range of sites and land-use histories. The results of this study imply that treatment of dense stands must take into account the secondary effects of seedling regeneration and weed incursions and incorporate them into ongoing management strategies for the species.

Chapter 8. Summary and Conclusions

8.1. Background and Synopsis of Topic

Both anecdotal and published evidence suggest that dense *Callitris glaucophylla* regrowth has adverse consequences for production. The invasive nature of the species has been recognised under the provisions of the *New South Wales Native Vegetation Act (2004)*, where it is deemed to be *Invasive Native Scrub*. The Act now regulates management of dense post-1990 regrowth and removal of vegetation can only proceed if the proposed treatment satisfies the 'environmental test', that is, if it '*improves or maintains*' site condition. The process of determining appropriate management actions as bounded by the Act is hindered by a lack of information pertaining to the environmental test.

This thesis has taken a science-based approach to the specific management issue of *C. glaucophylla* regrowth in agricultural landscapes of the North-Western Slopes of New South Wales, where it is listed as INS. I have used soil and groundcover parameters to illustrate the effects of the species on site condition across a range of soil types and a variety of densities. I have also provided new insight into some of the ecological characteristics of the species that enhance its ability to colonise and sustain populations on agricultural lands. Finally, I have demonstrated the short-term effects of management of the species for a variety of outcomes.

In this chapter I will synthesise the data presented in the research chapters of this thesis to provide a summary of the research conducted, highlight the new information this research has contributed to the existing knowledge gaps for the species and identify future research priorities. I will also present some general management recommendations for the species given the provisions of the Act.

8.2. Research Summary and Implications

8.2.1. The effects of individual C. glaucophylla trees of different ages on environmental condition

The cycling of nutrients in individual *C. glaucophylla* trees results in the net increase in soil C, pH and ext. P in the upper soil profile. Tree size ('age') is important in determining both the size and spatial extent of soil change in the vicinity of the tree. In this study, tree size was strongly positively correlated with litter biomass. At sites where heavy grazing occurred, litter biomass was low, indicating that litter had been consumed or scattered, and soil-canopy enhancements were small.

Litter has a much longer residence time in semi-arid landscapes than in higher-rainfall zones (Chapman et al. 2006), and therefore a further understanding of the litter dynamics of *C. glaucophylla* is required. A number of theories to describe litterfall patterns and litter quality for coniferous plants in a range of environments have been proposed. The 'acceleration' model suggests that coniferous plants exhibit increased leaf abscission rates when herbivory is common, therefore litter which is dropped is higher in nutrition and potentially contributes to elevated soil nutrient patches (Ritchie et al. 1998). In semi-arid regions of the world, woody vegetation re-establishment into previously cleared landscapes exacerbates resource patchiness, resulting in fertile islands beneath tree canopies (Schlesinger and Pilmanis 1998). The higher soil pH observed in the surface soil beneath individual *C. glaucophylla* canopies is inconsistent with other literature pertaining to conifers and soil acidity, however, and is indicative of other sub-soil processes.

The biological pumping process first proposed by Noble and Randall (1999a, b) appears to be the most likely explanation for the elevated soil pH associated with single tree canopies, and is a process which has been observed in other species in semi-arid and subtropical zones close to the study area (e.g. Wilson et al. 2007). This process involves sub-surface acidification at

lower root depths as a result of the withdrawal of cations and the excretion of organic acids in the shallow (upper soil profile) root zone and via the deposition of anion-rich litter. Further confirmation is required to confirm this process for individual *C. glaucophylla* trees as soil acidity with depth was not determined in this study.

The invasion of woody vegetation into previously cleared pasture is a contentious issue and until now, very few effects of this type of vegetation had been clarified for the study region (Eldridge et al. 2003). With the exception of a reduction in vascular plant cover and the depletion of water in the canopy zone (which may have been enhanced by the drought), this study has demonstrated that individual *C. glaucophylla* trees do not deplete soil resources. Priorities for single tree management are discussed below in section 8.3.

8.2.2. Soil and vegetation patterning in high density stands and the impact of plant density on tree growth and survival

Competitive processes are pivotal drivers of change in *C. glaucophylla* populations and the impacts of competition have been demonstrated both *in* and *ex situ* in this thesis. Within dense stands, spatial anisotropy in the distribution of soil and groundcover variables could not be linked to the size or distribution of individual trees, except at lower tree density (i.e. the Yallaroi site). In higher density stands, patterns were either obscured by processes such as nutrient transport, or did not occur. Hence, the 'islands of fertility' principle evident for the canopy zone of scattered paddock trees, did not apply to individual trees in dense stands. Further, in most situations dense stands were lower in fertility than individual tree canopies despite the fact that canopies intersected in dense stands.

The retention of nutrients in the soil of dense stands appears to be very low relative to single trees, and is linked to lower levels of litter beneath the dense canopy. It is likely that the accumulation of litter and build-up of soil evident around scattered individuals is lost in dense

stands via lateral nutrient flow. Inter-specific competition between trees and other vascular plants for light, water and space favours dense tree cover, resulting in a bare surface devoid of physical obstructions to topsoil and litter loss in heavy rainfall and high wind events. Consequently, soil is eroded and nutrients are lost either directly or through a lack of litter deposition. Higher soil acidity in dense stands is therefore a further consequence of topsoil and litter loss; alkalinisation of the soil surface during the biological pumping process is not achieved due to continuous lateral transport.

Whilst the lateral transport of nutrients away from high-density stands has been observed anecdotally and throughout this study, it is also likely that intense within-stand competition resulted not only in reduced growth of individuals, but also a reduction in effective litter cycling, or a reduction in litterfall. In this study, nitrogen limitation was observed experimentally at high planting densities, which greatly affected plant morphology and resulted in significantly reduced above-ground biomass. Nitrogen-limited systems must maintain tight nutrient cycles, with much of the available N withdrawn from foliage prior to leaf abscission (Miller et al. 1979). A consequence of this biochemical cycling is however, that any litter deposited and subsequently incorporated into the mineral soil is has a high C:N ratio, which further exacerbates N-limitation (Vitousek and Howarth 1991). As above-ground stand growth becomes limited, and lower limbs and foliage have been shed, it is likely that most remaining foliage is retained within the canopy to minimise further N-loss.

Whilst many of the diminished soil quality indices, are a likely consequence of reductions in above-ground growth and hence litter quality and quantity at high population densities, the results of this study also highlight the paucity of knowledge pertaining to below-ground functionality in dense *C. glaucophylla* stands. Current allometric models for the species generated in similar environments suggest below-ground biomass to be merely 0.4 times the size of above-ground biomass (Burrows et al. 2001), yet in this study below-ground biomass

exceeded the aerial portion at high planting densities. Whilst this finding has obvious implications for carbon accounting (and therefore the estimates of C content in dense and thinned stands in Chapter Two could be grossly inadequate), it also potentially explains why there are such large differences in mean values between isolated trees and dense stands. In addition to the greater demand for resources created by a larger root volume, mass cation withdrawal from deeper in the soil profile is likely to have occurred during rapid stand growth, but due to 'lock-up' and / or litter transport, re-alkalinisation did not occur and act to counterbalance the substantial pH disparity throughout the profile. Further work is now required to understand nutrient cycling processes in *C. glaucophylla* and their impacts on soil acidity, nonetheless, the results of this study strongly suggest that high density stands require intervention to restore environmental condition.

Further to the argument for active management of dense stands is the experimental confirmation of 'lock-up' as a true biological process in *C. glaucophylla*, but one that may be restricted to the aerial portion. From an evolutionary perspective, this result supports the notion that plants which compete only for below-ground resources do not compete asymmetrically (Schwinning and Weiner 1998), and hence there is no competitive advantage for individuals within the population to increase in height in order to capture aerial resources such as sunlight. Phenological plasticity to nutrient limitation and neighbourhood crowding enables *C. glaucophylla* to persist in a reduced form until presumably conditions become favourable for further above-ground growth and development, instead of self-thinning. Future research should now be directed at understanding the functional biology of above- and below-ground biomass once aerial growth has become static, which will further understanding of the nutrient dynamics of dense stands. Given that soil N availability is limited by the availability of water, further understanding of stand water use and subsequent nutrient uptake in 'locked-up' systems is also a research need that is yet to have been addressed.

8.2.3. The effects of managing C. glaucophylla regrowth on environmental condition

Dense *C. glaucophylla* stands persist in a stable woody state, and normal succesional processes have been arrested (Chapman et al. 2002) As noted in section 8.2.2, and earlier in Chapters Two and Five, re-distributional processes within dense stands are either interrupted by erosional nutrient flow or are too inefficient to replenish nutrient-depleted soils. As dense *C. glaucophylla* populations self-thin along a very slow trajectory (see Chapter Six), restoration of stand growth will most likely only occur over an appreciable timeframe via a reduction in tree density. In this study, thinning dense stands resulted in a substantial increase in above-ground biomass just two years following management, despite drought conditions. Stand release and total clear-felling also provided substantial remediation of environmental condition, reducing soil acidity and facilitating rapid regeneration and re-establishment of diverse vascular plant cover. Many of the soil effects are presumably short-lived however, as litter and brush from felled retained timber is progressively lost from the system and incorporation of the remaining organic material reaches a peak. As time passes, the remaining trees in thinned stands may also grow to yield the same total site biomass as the previous dense stand, and it is unclear whether nutrients will again become limiting and vascular plant cover is again inhibited.

Although the trial was too small for many statistical models to support the data, in most situations clear differences were observed between site condition in grazed and un-grazed treatment contrasts. Somewhat unexpectedly however, total grazing exclusion favoured a secondary invasion of *H. hirta* into the understorey of thinned or cleared stands, irrespective of site. This represents a further restoration barrier to the rehabilitation of dense stands, and may in part be due to a reduction in tree density that is below optimum to ensure a range of light and shade tolerant species (Cummings et al. 2007). An intermediate level of disturbance in the form of periodic grazing and / or weed control might therefore be necessary to ensure

that secondary infestations don't become entrenched. Otherwise managed stands are at risk of taking another succesional pathway to a stable invasive grass – woody state that is neither productive nor diverse.

The technical aspects of managing dense *C. glaucophylla* stand on the NWS of NSW are discussed hereafter and are accompanied by a discussion of the relevant findings from the management trial.

8.3. Suggested Best Management Practices for Dense White Cypress Pine Stands

Given that thinning and clearing of dense *C. glaucophylla* stands has been demonstrated to maintain or improve environmental condition in some circumstances, there is a clear need to identify the key features of stand management which are most likely to sustain environmental and productive benefits. This section will draw together some of the results from the management trial in order to present some best management practices for dense stands on the NWS of NSW.

8.3.1. Consider the desired outcome of treating dense stands

Given the results of Chapters Two and Seven, it is clear that thinning, clearing or leaving stands untreated have distinctly different outcomes for production and environmental condition. The expense of thinning, clearing and fencing may not be viable unless the land has been identified for future use. Sometimes it may be best to leave dense stands as they are if the proposed treatment area is large, estimated gains from using the land for productive purposes are small and follow-up treatment of weeds or pine re-establishment is to be performed by a single person (i.e. the landholder).

8.3.2. (During treatment) Consider the effects of slope

Observations suggest that considerable soil erosion occurs in dense stands on the NWS (Chapters Two, Five and see Eldridge *et al.* 2003), presumably because of root competition for soil water (Chapter Six) and a lack of vascular plant cover in the understorey, resulting in mass transport of topsoil during rainfall events on sloping country (Chapter Five).

Given these results, it is suggested that areas of the property identified for thinning and clearing treatments be restricted as much as possible to areas of minimal slope. Where possible clear-felling of timber should be restricted to flatter areas with thinning treatments on sloping country. Mechanical timber removal by stump pulling, bulldozing, or any other treatments that disturb the soil surface, should be avoided at all costs.

8.3.3. (During Treatment) Retain felled timber

In anticipation of soil loss following treatment of the study plots in Chapter Seven, felled timber was lay across the slope and retained throughout the trial. This retained timber provided extra benefits for the site including substantial additions of litter, which may have assisted in raising surface soil pH and enhancing soil C and other nutrients in the short term. Felled timber provides additional environmental services as felled brush provides important biophysical benefits including enhancing the water-holding capacity of the soil (Harris et al. 2003).

In order to maximise post-treatment environmental condition, felled timber and woody debris should be retained wherever possible. If timber is removed from the site, it is likely that the short-term benefits demonstrated in Chapter Seven such as enhanced soil fertility and a decrease in soil loss following treatment will not occur at any appreciable level. Loss of topsoil and degradation of topsoil structure has been demonstrated to favour woody

vegetation (Walker 1981) and hence strategies that enhance soil stability are essential to restoring land 'degraded' by dense woody INS.

8.3.4. (Following treatment) Maximise vascular plant cover through sensible grazing management

From the results of Chapter Two and Chapter Seven, it is apparent that treated plots that have a substantial plant cover component (irrespective of the composition) following treatment exhibit much lower rates of *C. glaucophylla* re-establishment (and see plate 14). Maintenance of a high level of plant cover has two primary functions in treated, formerly dense stands – (1) grasses and other deeper-rooted perennial plants stabilise the soil and potentially mitigate topsoil loss, and, (2) dense vascular plant cover in the understorey provides a mechanical barrier to future seedling establishment of *C. glaucophylla*.

Although grazing was intermittent at two of the three study sites where the management trial was conducted (Chapter Seven), there were still clear differences between the number of new *C. glaucophylla* seedlings in grazed and un-grazed treated plots. It is therefore suggested that treated stands should be excluded from domestic livestock grazing for at least the first year following treatment, and that only periodic grazing be conducted within the treated area thereafter.

8.3.5. (Following treatment) Address further seedling regeneration and other weed issues.

Provided that substantial plant cover is maintained, *C. glaucophylla* regeneration should be minimal, especially in thinned stands where the subsequent growth of the retained trees will access many of the below-ground resources for trees (e.g. space for deep roots). Any future seedling establishment should be treated by manual felling techniques prior to tree maturity between 7-12 years of age.

Grazing often favours the establishment of exotic weeds over native plants (Prober et al. 2002). In this study however, whilst grazing resulted in the increased species richness of exotic plants, exclusion of livestock grazing facilitated the invasion of *H. hirta* (Coolatai grass), to the point where it comprised most of the groundstorey vascular plant cover. Similar results have been observed in Eucalypt woodlands in northern NSW invaded by the noxious weed *Lantana camara,* whereby dense weed cover re-established in the absence of ongoing management and impeded the transition back to forest following management (Cummings et al. 2007).

Therefore, in the absence of on-going disturbance, it appears that land managers might be faced with a trade-off between maximising plant diversity/promoting groundcover restoration and retaining a dense weedy understorey in order to minimise dense *C. glaucophylla* re-establishment. The decision to manage secondary weed outbreaks should be made on the basis that:

- The weed is noxious. If so, then by law it must be controlled.
- Does the weed have a value, e.g. as stock fodder? If so, then perhaps it can be retained to some degree, AND,
- What is the long-term stability of the understorey if the weed is not controlled? Is the weed likely to persist for years after tree management or is it only transient? If left unmanaged will the weed outcompete other native species?

8.4. Legislative implications

Since 2005 regulations under the Act have permitted the management of dense stands provided that doing so *maintains or improves* environmental condition. Chapter Four indicates that single trees maintain or improve upon the soil chemical parameters studied, but impact negatively on vascular plant cover. Given the results of chapters Five and Six, it is clear that competition within stands impedes tree growth and development, subsequently

exacerbating competitive interactions between trees in dense stands and vascular plant cover. These results provide a legitimate context for the lawful management of the species.

The preliminary research conducted in Chapter Two, as well as the results of Chapter Seven suggest that there are measurable benefits to be derived from the management of dense stands, from both a productive and ecological perspective. Thinning and retaining felled timber in the understorey maintains and in some situations improves upon soil chemical status and plant cover, and from a carbon storage perspective represents a suitable compromise between conservation and production for carbon trading purposes. Clearing of dense stands and retaining timber has also been demonstrated to have positive effects on environmental condition, however, derived benefits from enhanced soil nutrient status following treatment appear to be short lived (see Chapter Two). Nonetheless, either treatment represents substantial environmental gains, provided that appropriate general management practices are adopted.

8.5. Conclusions

A series of anthropogenic modifications to the landscape have created conditions suitable for the expansion of woody vegetation populations and the encroachment of woody vegetation into areas that previously did not support that vegetation type. Across much of north-western NSW, *C. glaucophylla* exists in a stable woody state at high population densities. Due to its phenological plasticity and extremely slow self-thinning characteristics, management of the species to reduce population densities is an outcome desired by many landholders and their entitlement to do so has now been supported by state legislation.

This thesis has quantified and highlighted the disparity in ecosystem services provided by the species at high or low populations densities. It has demonstrated that most of the deleterious impacts imposed on agricultural soils and pastures are a function of intense within-stand

competition and also poor grazing management, and are not due to the specific characteristics of the species itself (e.g. allelopathy). A number of knowledge gaps still remain for the species, especially pertaining to the biological pumping process, nutrient and soil loss from dense stands, and plant water relations. Nonetheless, this thesis has addressed some of the more fundamental questions about the role of the species in the agricultural landscape, clarifying its environmental impacts, its ecology and most importantly, its management. In order to address the ongoing ecological and economic threat imposed by .*C. glaucophylla* thickening and encroachment, a site-based, long-term management strategy must be adopted which recognises the impacts of agricultural management on system stability. In the absence of appropriate grazing management and continued soil degradation, areas cleared of the species will only continue to revert to the more stable dense woody state, reducing environmental condition and agricultural productivity.

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Appendix One. Species List

* Denotes introduced species

Species list of all vascular plants encountered across all three properties reported in Chapter Seven.

**Anagallis arvensis*
**Conyza* sp. *bonariensis*
**Conyza* sp. p*arva*
**Gamochaeta* sp.
**Geranium* sp.
**Hyparrhenia hirta*
**Hypochaeris glabra*
**Hypochaeris radicata*
**Opuntia aurantiaca*
**Opuntia stricta* var. *stricta*
**Sonchus oleracea*
**Sonchus oleracea*
**Sonchus* sp.
**Spergularia media*
**Trifolium* sp.
Alphitonia excelsa
Aristida personata
Aristida scabra spp. *scabra*
Aristida sp.
Asperula conferta
Austrodanthonium sp.
Austrostipa scabra ssp. s*cabra*
Boerhavia domini
Bothriochloa sp.
Brunoniella australis
Callitris glaucophylla
Calotis lappulacea
Canthium odoratum
Cassinia laevis
Cassinia quinquefaria
Chamaesyce sp.
Cheilanthes distans
Cheilanthes sieberi ssp. *sieberi*
Chenopodium pumilio
Chloris truncata
Chloris ventricosa
Chrysocephalum apiculatum

Crassula sp.
Cymbonotus lawsonianus
Cymbopogon refractus
Cyperus fulvus
Cyperus gracilis
Daucus glochidiatus
Desmodium brachypodium
Desmodium varians
Dicanthium sericeum spp. *sericeum*
Dichelachne micrantha
Dichondra sp. *A*
Digitaria brownii
Digitaria sp.
Dodonea viscosa spp. *augustifolia*
Einadia sp.
Enneapogon nigrans
Eragrostis leptostachya
Eucalyptus blakelyi
Euchiton sphaericus
Evolvolvulus alsinoides var. *decumbens*
Fimbristylis dichoform
Gallium gaudichaudii
Gallium propinquum
Glossogyne tannensis
Glycine clandestina
Glycine tabacina
Goodenia glabra
Goodenia hederacea spp. *hederacea*
Hymenochilus muticus
Isoetopsis graminifolia
Lagenifera sp.
Lomandra confertifolia spp. *pallida*
Lomandra filiformis
Lxauchenus sublyratus
Marsdenia viridiflora spp. *viridiflora*
Melichrus urceolatus
Mentha satureioides
Mentha sp.
Muellerina bidwillii
Notelaea microcarpa var. *microcarpa*
Ollearia sp. aff. e*lliptica*
Ophioglassum lusitanicum ssp. c*oriaceum*

Oxalis perennans
Oxalis sp.
Panicum effusum
Panicum queenslandicum
Parsonsia lanceolata
Paspalidium sp.
Phyllanthus virgatus
Pimelea curviflora
Pimelea neon anglica
Plantago debilis
Polycarpon tetraphyllum
Rostellularia ascendens spp. *ascendens*
Rumex brownii
Scleria macliaviensis
Senecio lactos spp. *dissectifolia*
Senecio quadrideutatus
Sida corrugata
Sida cunninghamii
Sida sp.
Sida subspicata
Solenogyne bellioides
Solenogyne sp.
Sporobolus creber
Stackhousia viminea
Stuartina muelleri
Swainsona galegifolia
Swainsona reticulata
Templetonia stenophylla
Tripogon lolliformis
Vittadinea dissecta
Vittadinea muelleri
Vittadinea sp.
Vittadinea sulcata
Wahlenbergia communis
Wahlenbergia sp.
Wahlenbergia sp. *2*
Wurmbea sp.
Zornia dyctiocarpa var. *dyctiocarpa*