THE PHYSIOLOGICAL AND PATHOLOGICAL IMPLICATIONS OF PRUNING EUCALYPTS

Danielle Wiseman

B.Sc. Australian Environmental Studies (Hons)

Griffith University

Submitted in the fulfilment of the requirements for the degree of

Doctor of Philosophy

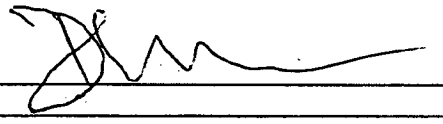
School of Agricultural Science, CRC for Forestry and

University of Tasmania

November 2010

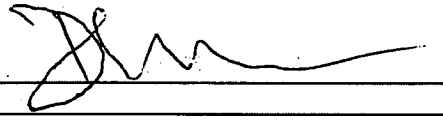
DECLARATIONS

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

Signed: 

Danielle Wiseman

This thesis may be made available for loan and limited copying in accordance with the Copyright Act 1968.

Signed: 

Danielle Wiseman

ABSTRACT

A major focus in Tasmania since 1988 has been research for the management of temperate eucalypt plantations for solid wood. Unpruned plantation eucalypts do not deliver high-quality appearance-grade sawlogs. The extent to which trees can be pruned before their growth is significantly reduced is a function of species and site. An understanding of the processes that optimise clearwood production after pruning is required to make informed decisions about the type and timing of silvicultural inputs.

The effect of fertiliser addition on pruning-associated decay was investigated at two nitrogen (N)- and phosphorus (P)-deficient sites. At one site, pruning of *Eucalyptus nitens* increased the level of decay and degrade in clearwood formed after pruning. Improved nutrition increased the longevity and size of branches in trees, and led to a higher incidence of decay infections compared to trees at a lower level of nutrition. At the second site, the responses of *Eucalyptus globulus* and *E. nitens* to pruning in two lifts and different rates of N-fertiliser application were compared. Pruning reduced growth, but the final measured volume (at ~ age 6 years) of pruned trees in fertiliser treatments was greater than in the unpruned trees with no fertiliser. *E. nitens* exhibited superior growth over the course of the experiment with a larger volume response to applied N than *E. globulus*. *E. nitens* had a higher incidence of decay infections in pruned stubs because of its tendency to have larger branches than *E. globulus*, though the overall incidence of decay in this experiment was very low.

A rapid rate of occlusion of the wound created by pruning is required to maximise the production of clearwood. Five years after pruning, trees over a range of early and late fertiliser treatments were harvested and dissected to assess branch occlusion and clearwood production. The occlusion rate of pruned stubs was low, being delayed by the exudation of kino from branch stubs and by thick bark. Branches growing higher in the tree were more likely to have occluded than lower branches. The amount of clearwood produced depended on branch height, status and diameter, stub length, growth before and after pruning, and the distance required for a stub to occlude. Fertiliser treatments did not significantly affect these relationships, which suggested that applications at age four years of age or later can be made as required for increasing growth rates and clearwood production.

Physiological responses to second-lift pruning have been investigated less intensively than those of first-lift resulting in less certainty in linking pruning strategies to outcomes. In an experiment to address this gap in knowledge, trees of *E. nitens* were pruned in two lifts. The responses to fertiliser nitrogen application of pruned and unpruned trees were also investigated. The physiological response to pruning was dependent on resource availability. Pruning did not initiate a physiological response in trees which did not receive fertiliser N. Where N fertiliser was applied, pruning increased levels of photosynthetic activity in comparison to unpruned trees. Fertiliser N also stimulated the production of leaf area. Due to low water availability post second lift pruning, it is hypothesised that the trees response to pruning involved an interaction between the effects of N on leaf area, increases in stomatal conductance due to pruning and the effect of N on the trees ability to increase photosynthetic activity.

Thesis results are discussed in relation to adoption of management strategies to maximise growth and solid wood products such as the application of supplementary fertiliser and the best timing and severity for pruning operations.

ACKNOWLEDGMENTS

The project was funded by the Australian Research Council, Forestry Tasmania, the Australian Centre for Agricultural Research, the School of Agricultural Research and the CRC for Sustainable Hardwood Forestry. Sites were made available by Forestry Tasmania, Gunns Ltd. and Norske Skog

I thank my supervisors, Associate Professor Caroline Mohammed, Dr Chris Beadle and Dr Libby Pinkard for their guidance, interest, encouragement, and their faith in my ability to complete this project.

The following people shared their expertise with me: Dr. Karen Barry, Dr Michael Battaglia, Associate Professor Noel Davies, Dr. Alieta Eyles, Dr Phil Smethurst, Dr Tim Wardlaw and all the staff who assisted at Forestry Tasmania, Ms Ann Wilkinson.

Malcolm Hall, Craig Baillie, Ann LaSala, Maria Ottenschlaeger, Petr Otahal, Phillip Grosse and David Page provided technical assistance. The talented and helpful staff and students of the School of Agricultural Science, the CRC and the CSIRO were always willing to help sort out problems, especially Jan Ellis.

I would like to extend a special thank you to my two children for their patience with me.

PREFACE

This PhD is composed of 4 experimental papers which have been either published or submitted for publication to refereed international journals. To improve the reading of this thesis, the following changes have been made including:

- References have been amalgamated to a single list of references at the end of the thesis,
- Acknowledgements for each publication have been detailed separately (see below),
- Figures and tables have been renumbered according to chapter,
- Additional details that were not originally included in the papers but considered worthy contributions to the thesis have been added as appendices where required

Publications arising from this project are as follows:

CHAPTER 1

Danielle Wiseman is a co-author on the following review paper which included material from her introductory chapter.

Beadle CL, Volker P, Bird T, Mohammed CL, Barry K, Pinkard EA, Wiseman D, Harwood C, Washusen R, Wardlaw TJ, Nolan G (2007) Solid wood production from temperate eucalypt plantations; a Tasmanian case study. *Southern Forests* **70**, 45-57.

Acknowledgements: Thanks go to Drs Jane Medhurst and Matthew Wood and three anonymous reviewers for their valuable comments on the manuscript and Ms Maria Ottenschlaeger for compiling the Figures and Tables.

CHAPTER 2

Wiseman D, Smethurst PJ, Pinkard EA, Wardlaw TJ, Beadle CL, Hall M, Baillie CC, Mohammed CL (2006) Pruning and fertiliser effects on branch size and decay in two *Eucalyptus nitens* plantations. *Forest Ecology and Management* **225**, 123–133.

Acknowledgements: Experimental sites were kindly made available by Gunns Ltd. and Norske Skog. Thanks go to Ann LaSala for her work in setting up the experimental site and to Karen Barry and Noel Davies for help with hydrolysable tannin analysis. Much appreciation goes to Karen Barry and Carolyn Raymond for their comments on the manuscript. This research was made possible through funding and assistance provided by the CRC for Sustainable Production Forestry, CSIRO FFP, University of Tasmania and Forestry Tasmania.

CHAPTER 3

Wiseman D, Smethurst PJ, Beadle CL, Pinkard EA, Wardlaw TJ, Baillie CC, LaSala A, Mohammed CL (2010) Clearwood prediction in *Eucalyptus nitens* from fertiliser history and tree characteristics at pruning. Reviewed internally by CSIRO review. Submitted to *Annals of Forest Science.*

Acknowledgements: Assistance from the following people was greatly appreciated. Help in the field was provided by Mr Malcolm Hall and Mr Phillip Grosse. Chemical analyses were carried out by Ms Anne Wilkinson. Sites were made available by Gunns Ltd. and Norske Skog and Dr. Michael Battaglia assisted with statistical advice.

CHAPTER 4

Wiseman D, Pinkard EA, Wardlaw TJ, Mohammed CL, Hall M, Beadle CL (2009) Growth responses of *Eucalyptus globulus* and *E. nitens* to pruning and fertiliser treatments in a plantation managed for solid-wood products. *Southern Forests* **71**(1), 21-29.

Acknowledgements: The support and co-operation of Forestry Tasmania is gratefully acknowledged especially in setting up the field site. Thank you to Maria Ottenschlaeger for her help in the preparation of the manuscript, and her expertise in the field.

CHAPTER 5

Wiseman D, Beadle CL, Pinkard EA, Hall M, Wardlaw TJ, Mohammed CL (2009) Effects of pruning and fertiliser on gas exchange, leaf area distribution and leaf chemistry. *Tree Physiology.* Manuscript under internal review.

Acknowledgements: The support and co-operation of Forestry Tasmania is gratefully acknowledged especially in setting up the field site. Thank you to David Page for his help in the preparation of the manuscript.

Other communications including research carried out in this thesis were:

Mohammed CL, Barry KM, Harrison KS, Wiseman D, Yuan ZQ, Yee M, Hopkins AJM, Wardlaw TJ, Bougher N, Tommerup I (2003) Decay fungi in eucalypts slowly reveal their true identity! In 'Pest Off! No. 18 Cooperative Research Centre for Sustainable Production Forestry'.

Mohammed CL, Wardlaw TJ, Barry KM, Eyles A, Wiseman D, Beadle CL, Battaglia M, Pinkard EA, Kube P (2003) An interdisciplinary approach to the study and management of stem defect in eucalypts'. In 'Abstracts of Invited Papers 8th International Congress of Plant Pathology, Christchurch, New Zealand, 69 (2003) [F3] '

Wardlaw TJ, Mohammed CL, Barry KM, Eyles A, Wiseman D, Beadle CL, Battaglia M, Pinkard EA, Kube PD (2003) Interdisciplinary approach to the study and management of stem decay in eucalypts. *New Zealand Journal of Forestry* **33**, 385-398.

Wiseman D, Beadle C, Mohammed CL (2003) Fertiliser produces larger branches and higher incidence of wood decay in *E. nitens*. In 'Pest Off! No. 24 '.

Wiseman D, Hall M, Baillie CC, Smethurst PJ, Beadle CL, Pinkard EA, Mohammed CL (2003) Tree nutrition influences wood decay. In 'Cooperative Research Centre for Sustainable Production Forestry Annual Meeting 2003'. 21-23 October 2003, Cradle Mountain, Tasmania. (Poster)

Wiseman D, Hall M, Barry K, Beadle C, Mohammed CL (2003) Tree nutrition affects the incidence and extent of wood decay. In '8th International Congress of Plant Pathology'. 2-8 February, Christchurch, New Zealand. (Poster)

CONTENTS

SYMBOLS AND ABBREVIATIONS

	Symbol	Unit
TREE CHARACTERISTICS		
Diameter of tree at breast height (1.3 m)	D	m tree-1
Tree height	H	m tree^{-1}
Stem volume (formulae p 42)	V	m^3 tree^{-1}
Tree stem radius	R	m tree^{-1}
Tree stem radius at pruning	RAP	m tree^{-1}
Tree stem radius over stub	ROS	m tree^{-1}
Tree stem radius over occlusion	ROO	m tree^{-1}
Bark width	BW	m tree^{-1}
Increment in diameter at breast height of tree over time	D_{inc}	cm tree^{-1}
Increment in tree volume between pruning and harvesting	DV	m^3 tree^{-1}
Tree stem diameter increments between age 3.7 and 4.3 years	DI_1	cm tree^{-1}
Tree stem diameter increments between age 4.3 to 5.7 years	DI_2	cm tree^{-1}
Increments in tree volume at age 4.3	$V_{I,4.3}$	m^3 tree^{-1}
Increments in tree volume at age 5.3	$V_{I,5.3}$	m^3 tree^{-1}
Increments in tree volume at age 5.7	$V_{I,5.7}$	m^3 tree^{-1}
Width of clearwood produced since pruning	CLW	m tree^{-1}
Average growth since pruning	GSP	m tree^{-1}
Green Crown depth	C_D	M
FERTILISER/NUTRIENTS		
Unfertilised treatment plot	UF	
No fertiliser applied following the "at planting" dose	HF	
Weight of fertiliser added		kg ha^{-1}
Aluminium	Al	

Ammonium	NH_4
Calcium	Ca
Carbon	C
Copper	Cu
Hydrogen	H
Magnesium	Mg
Nitrogen	N
Nitrate	NO_3
Phosphorous	P
Potassium	K
Sodium	Na

SITE CHARACTERISTICS

Tree density per hectare	stems ha^{-1}	Stems per hectare
Total C, N and P		mg g^{-1}
Net N mineralisation		kg ha^{-1} $year^{-1}$
Average rainfall per year		mm $year^{-1}$
Total incident radiation		GJ m^{-2} yr^{-1}
Altitude	M.A.S.L.	Metres above sea level

BRANCH CHARACTERISTICS

Emergence height of first green branch on tree	H_G	M
Branch status	ST	Alive/Dead
Average branch diameter	D_B	Mm
Branch height above ground level	H_B (m $tree^{-1}$)	m per tree
Branch cross sectional area	A_B	Mm
Branch stub length left at pruning	SL	Mm
Pruning stub diameter	SD	Mm
Diameter of the cut face at the branch stub	CFD	Mm
Average distance for a branch stub to occlude	DO	Mm
Tree stem diameter over stubs	DOS	m $tree^{-1}$
Branch decay - presence and extent	DEC	
Branch decay - pockets in the branch crotch	P_D	Present/Absent

Branch decay - length	DEC_L	Mm
Branch decay - width	DEC_W	Mm
Branch decay - protective zone breach	BPZ	Yes/No
Specific leaf area	SLA	$m^2 g^{-1}$
Leaf area	*L*	m^2
Leaf Area Index	LAI	
Kino trace defect	K_T	Present/Absent
Kino vein	K_V	Present/Absent

PHOTOSYNTHESIS

Net photosynthetic capacity	A_{MAX}	µmol CO_2 m^{-2} s^{-1}
Intercellular CO2 concentration	C_i	µmol mol^{-1}
Carbon assimilation rate	*A*	µmol CO_2 m^{-2} s^{-1}
Stomatal conductance	g_s	µmol m^{-2} s^{-1}
Rate of photosynthetic electron transport (based on NADPH requirement)	*J*	µmol e^- m^{-2} s^{-1}
Photosynthetically active radiation	*PAR*	µmol m^{-2} s^{-1}
Day respiration	R_D	µmol CO_2 m^{-2} s^{-1}
Mesophyll conductance	g_m	µmol m^{-2} s^{-1}
Maximum rate of photosynthesis at the ambient (360 mmol/mol of air) level of CO_2	A_{360}	µmol CO_2 m^{-2} s^{-1}
Maximum carboxylation rate limited by Rubisco	V_{CMAX}	µmol CO_2 m^{-2} s^{-1}

CHAPTER ONE

General introduction

1.1 Producing solid wood from plantations

Australia has a total forested area of around 150 million hectares - covering around 19% of the continent. This is made up of around 147.4 million hectares of native forest and around 1.97 million hectares of plantation forests (BRS 2010). Over the last two decades there has been a decline in the supply of sawn timber from Australia's native forest due to the changing management priorities for this resource from timber production to the preservation of environmental values. In 1997, the Australian, state and territory governments and the plantation timber-growing and processing industry formed a strategic partnership called *Plantations for Australia: The 2020 Vision*. The aim of the partnership is to increase the plantation estate to 3 million hectares by 2020. In the ten years to 2007, the plantation area increased by about 50% of 1997 levels, at an average annual rate of nearly 77 000 hectares, due mainly to private investment. Of the total Australian plantation estate in 2008, 950 000 hectares (48%) were hardwood species and 1014 000 hectares (52%) were softwood species (BRS 2010). In Tasmania there are nearly 300,000 ha of plantations of which 217,000 are hardwood.

Most of the hardwood estate is geared for the production of woodchip for pulp and paper production although hardwood sawlog supply from plantations is estimated to rise slowly to 2030. Particularly in Tasmania there is an endeavour to manage hardwood plantations for solid wood production (Beadle, Volker *et al.* 2008). In line with Forestry Tasmania's commitment to make available at least 300,000 m^3 per year of high quality eucalypt sawlogs from state forests, the plantation estate will play a vital role in supplying an increasing percentage of this volume over the next 10-15 years. Forestry Tasmania prunes approximately 35 000 ha of eucalypt plantations (out of a total of 50 000 ha) (Wardlaw, personal communication). All pruned areas are intended for thinning.

There are several difficulties and uncertainties in producing solid wood from eucalypt plantations:

- The balance between a relatively long rotation time and high silvicultural costs makes it difficult to source investment in the projects e.g. to create Category 3 sawlog of 6.2

m lengths with a small-end diameter >30 cm, no tension wood, defect-free clear wood and an acceptable Internal Rate of Return plantations are established at around 1000 stems ha-1, 250-350 stems ha-1 are pruned to 6.4 m height by age 6 yr and, after thinning, a final crop of 200-300 stems ha^{-1} established by age 11-12 yr. Sawlogs are harvested at age 25-35 yr.

- There is a need to refit sawmills and further develop technologies for the processing of smaller plantation logs which are more difficult to successfully process. Unpruned plantation eucalypts do not deliver high quality appearance-grade sawlogs (Nolan *et al.* 2005). Issues such as growth strain and tension wood that are often a feature of young eucalypt wood must be, and are being, addressed through new sawing and drying technologies. For example, hew-saw technology that relieves growth stresses during processing can produce structural hardwood timber from unpruned plantations that matches pine for strength in grades containing lower density heartwood (FEA Plantations 2007).

- Sound silvicultural practices, which will contribute to reducing rotation length, optimising production and improving log quality need development and refinement.

A key silvicultural practice for the development of high value solid-wood from temperate eucalypts is pruning. Of the current hardwood estate in Australia, 62% is planted to *Euclayptus globulus* and 19% to *E. nitens* (BRS 2010). Plantations of *E. globulus* and *E. nitens* must be pruned in order to produce high quality appearance grade sawlogs (Nolan, Greaves *et al.* 2005). Neither species is able to self prune effectively which leads to retained dead branches which serve as infection courts for wood decay (Wardlaw and Neilsen 1999). They also result in loose knots and kino associated defects which can cause downgrade in up to 75% of recovered wood volume (Waugh and Rozsa 1991). In contrast, pruned live branches result in clean tight knots and for these reasons it is recommended that only live branches be pruned (Gerrand, Neilsen *et al.* 1997). The earlier a tree is pruned the smaller the knotty core. The knotty core is the wood laid down before pruning, from the pith to the point at which pruned stubs occlude. Minimising the size of the knotty core maximises clear wood production.

For high quality solid wood production plantations must be pruned and pruned early. Crown lift is the process by which lower branches senesce and the height to the living or 'green' crown retreats upwards. To minimise the size of the knotty core and ensure only living branches are pruned, pruning must be scheduled early to pre-empt crown lift and therefore be carried out before or at canopy closure. Pinkard *et al.* 1998 suggest that pruning severity should be constrained by the capacity of the trees inherent responses to compensate for the loss in leaf area in order that pruning does not result in a significant change in growth in pruned compared to unpruned trees in the stand.

1.2 Pruning and canopy dynamics and physiological response

Pruning is a defoliation event and as such has the potential to affect growth. Growth suppression from pruning associated defoliation occurs at a lower threshold of leaf area removal pre-canopy closure than post canopy closure (Pinkard 2002a). If thinning is not carried out concurrently with pruning, pruned trees may become suppressed by surrounding un-pruned trees.

While pruning is not a natural event, some degree of defoliation by insects and leaf diseases is common. Trees and other plants have evolved compensatory responses to defoliation including changes in biomass allocation and an up-regulation of photosynthetic activity in remaining leaves. Both of these responses have been observed in *E. globulus* and *E. nitens* in response to defoliation (Eyles, Pinkard *et al.* 2009a; Eyles, Pinkard *et al.* 2009b; Pinkard 2002a; Pinkard 2003; Pinkard and Beadle 1998b; Turnbull, Adams *et al.* 2007). Therefore trees are able to compensate for a certain amount of defoliation before growth is affected.

In response to pruning defoliation, Pinkard et al. (1998) observed increased rates of leaf development in the upper crown, and an increased ratio of leaf area to branch cross sectional area which was attributed to decreased or delayed leaf senescence. Light-saturated rates of single-leaf net photosynthesis (A_{MAX}) increased up to 190% of those in adjacent unpruned trees and the magnitude of the response was greatest in the upper canopy (Pinkard, Beadle *et al.* 1998). Both responses are likely to be dependent on resource availability (Eyles et al. 2009a) and site (Pinkard and Beadle 1998b) or even seasonally dependent (Pinkard, Battaglia *et al.* 2007).

Most studies carried out to date have focussed on first lift pruning or single defoliation events (Pinkard, Beadle *et al.* 1998; Turnbull, Adams *et al.* 2007) and there is a paucity of information on how trees respond to second and subsequent pruning events. Evidence from artificial defoliation studies points to a greater impact on growth from repeated defoliations in comparison to one off events (Pinkard, Battaglia *et al.* 2007).

1.3 Effect of nutrition on tree form and response to pruning

Resource availability will influence the response to pruning. Growth is less affected by pruning on high as opposed to low quality sites (Pinkard and Beadle 1998b). Plantations comprising the pruned eucalypt resource in Tasmania are allocated to high-pruning (to 6.4 m) or low-pruning (to 2.6 m). Low pruning regimes are applied to low productivity stands to allow harvest of a single 2.6-m length clear-wood peeler-log from stands that would otherwise be managed for pulpwood.

Responses to the application of fertiliser in *E. globulus* and *E. nitens* plantations are most common in the period before canopy closure when nutrient demand is highest (Cromer, Cameron *et al.* 1993; Misra, Turnbull *et al.* 1998). However, all growth prior to pruning will be laid down in the knotty core, so return on investment of early fertiliser application may not be forthcoming. In addition, early fertiliser application has been linked to an increased incidence of multiple leaders and large branches (Beadle, Turnbull *et al.* 1994) and therefore may not be desirable in plantations destined for solid wood production.

The application of fertiliser has been shown to maintain growth in response to artificial defoliation simulating insect attack. Pinkard *et al.* (2006b) demonstrated that the application of 100 kg N ha^{-1} increased height growth in 50% defoliated trees in comparison to undefoliated trees which had no fertiliser. The application of fertiliser N may be effective in assisting trees to recover after defoliation.

1.4 Decay related defects, clearwood formation and pruning

The presence of knots, decay and kino associated with branches is most important for the production of conventional appearance grade products. Decay incidence and extent are determined by three fundamental factors: *fungal entry* (or the *infection court*) that is represented by pruning wounds, dead branches or stem wounds; *fungal species* that on

infection of wounds result in more or less decay depending on the "aggression" of each species; and *defence responses* that can be passive (e.g. heartwood) or active (e.g. reaction zones) and serve to restrict fungal spread. Variables that influence the expression of these factors include season, fungal species, site (nutrition), time and the genetic variation of the tree species (intra- and inter-specific variation) which may govern the type of defence response.

Initial studies of wood quality from plantation grown eucalypts noted the potential for decay entry via pruning wounds (Wardlaw and Neilsen 1999). The incidence of decay in pruned stubs was found to vary with site, but not with season (Mohammed, Barry *et al.* 2000b). It was hypothesised that site differences were the result of the effects that climate and site fertility had on branch size and status, with wetter and or more fertile sites developing larger branches and retaining living branches for longer in the lower stem. (Mohammed, Barry *et al.* 2000b). Living branches and the resultant large wound associated with pruning a large branch were both found to be associated with a higher decay infection risk (Mohammed, Barry *et al.* 2000b). Barry *et al.* (2005) confirmed the effect of wound size in a controlled wounding study conducted over three sites. No differences were found between sites when wound size and fungal inoculants were controlled (Barry, Hall *et al.* 2005). Pruned branch size is therefore a major determinant of decay risk.

Pruned large living branches are associated with a higher risk of decay, in comparison to small living branches or pruned dead or senescing branches. However, pruned dead or senescing branches are associated with other defects such as excess kino or loose knots, so pruning living branches is preferred. To minimise decay risk, branch size should be kept to a minimum. Initial stocking rate can influence the branch size with lower stocking rates associated with larger branches (Gerrand and Neilsen 2000). The application of fertiliser N may also influence branch size as evidenced by the association between site fertility and branch size (Mohammed, Barry *et al.* 2000b). As branch size can also increase above the pruned section in response to first lift pruning (Pinkard and Beadle 1998a), second lift pruning may also involve pruning a higher proportion of large branches.

Clear wood production begins when the pruned stub is sealed or 'occluded'. As the pruned stem increases in diameter, new wood, referred to as callus closes over the stub from either side of the wound. Eventually the wound is sealed and the vascular cambium is re-

established. Occlusion has been shown to be influenced by stub length (Petruncio, Briggs *et al.* 1997), branch status (living or dead) (Petruncio, Briggs *et al.* 1997) and wound size (Deadman and Calderon 1988; Solomon and Blum 1976), but is always influenced by stem growth (Deadman and Calderon 1988; Petruncio, Briggs *et al.* 1997; Solomon and Blum 1976). Therefore stimulating diameter growth post pruning will promote rapid occlusion and the onset of clear wood production.

1.5 Objectives

To investigate the interaction between pruning, decay and recovery from pruning defoliation a number of experiments with the objectives as listed below

- Chapter 2: Determine the effect of early fertiliser application on tree growth, branch size distribution, the size of the knotty core and pruning associated defects and decay

- Chapter 3: Develop an understanding of the factors influencing the onset of clearwood production and how these may be influenced by the early application of fertiliser

- Chapter 4: Compare the response of *E. globulus* and *E. nitens* to the application of fertiliser N and two pruning lifts. Investigate the ability of N application to alleviate growth suppression related to leaf area removal and effects on pruning associated decay and defects in both pruning lifts.

- Chapter 5: Examine the effect of fertiliser N application on the physiological response to pruning in order to better understand how N application may effect recovery from pruning defoliation

In conclusion we will examine the results in terms of refining silvicultural prescriptions for plantations managed for solid wood in terms of pruning prescriptions and fertiliser N application.

CHAPTER TWO

Pruning and fertiliser effects on branch size and decay in two *Eucalyptus nitens* plantations

Abstract

The effect of a high rate of fertiliser addition, (900 kg ha^{-1} nitrogen N : 150 kg ha^{-1} phosphorus P) on pruning associated decay was investigated at two N and P deficient sites in Tasmania, Australia. Decay infections from pruned stubs were found to be more common in trees that received additions of fertiliser N and P, but fertiliser addition was not found to have an effect on basic density, lignin or the concentrations of extractives. Crown depth, and branch size were greater, and kino production reduced on trees that received fertiliser N and P. The incidence of decay infections in the pruned branch stubs increased with the frequency of living and large branches. Hence, improved tree nutrition increased the longevity and size of branches, thereby leading to an increased incidence of decay infections.

2.1 Introduction

Plantation-grown *Eucalyptus nitens* has a limited ability for self-pruning (Gerrand, Neilsen *et al.* 1997) and retained branches are associated with knots, decay and kino-trace defect (Wardlaw and Neilsen 1999) which cause solid wood products to be downgraded in value (Waugh and Yang 1994). In Australia, down grading plantation-grown wood will lead to added pressure on native re-growth and old growth forests to supply high quality, appearance-grade products. As a consequence pruning regimes have been developed for the production of high-grade, solid wood products from *E. nitens* and *Eucalyptus globulus* plantations (Gerrand, Medhurst *et al.* 1997). The timing of pruning operations must strike a balance between allowing trees to achieve sufficient height that pruning can be undertaken without impacting on growth, yet pre-empting crown lift. Crown lift refers to the process where the lower branches senesce, and the base of the green crown recedes up the stem. For *E. nitens*, 40-50% of leaf area can be removed before growth is affected, if pruning is undertaken at canopy closure (Pinkard and Beadle 1998b). Stocking rates can also be manipulated to achieve growth targets as well as limit branch size in the lower stem. However, while high stocking rates are effective in

restricting the size of lower branches, they also result in trees of lower diameter and hasten the onset of crown lift (Gerrand, Medhurst *et al.* 1997; Marks, Incoll *et al.* 1986).

Early results from pruning studies raised concerns that decay fungi entering through pruned branch stubs may also cause downgrade in wood from plantations (Glass, McKenzie *et al.* 1989; Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999). At the time this research was conducted few eucalypt plantations managed for solid wood had yet reached harvestable age, little information is available on how far decay will spread over the course of the rotation and whether decay is likely to spread outward and infect knot-free clear wood formed after pruning. Thus, effort was directed towards identifying factors associated with an increased risk of decay entry and spread.

A number of these risk factors have been identified (Glass, McKenzie *et al.* 1989; Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999). Pruned living branches are associated with a higher initial risk of decay than pruned dead or senescent branches (Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999). Possibly, this is due to protective zones, formed in branches as they senesce, providing a physical and chemical barrier to fungal entry (Barry, Davies *et al.* 2002). Large, pruned branches are more likely to develop a decay infection (Glass, McKenzie *et al.* 1989; Marks, Incoll *et al.* 1986; Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999) and the risk of decay entry increases exponentially with branch diameter (Mohammed, Barry *et al.* 2000a). Site may also influence decay incidence (Wardlaw and Neilsen 1999) particularly in relation to rainfall and temperature (Mohammed, Barry *et al.* 2000a). These results inferred that wetter warmer sites have the greatest potential for solid wood production, but are also likely to have the highest incidence of decay infections initiated at pruning (Mohammed, Barry *et al.* 2000a).

In Australia, a great deal of effort is expended improving plantation productivity through the application of fertilisers (Smethurst, Holz *et al.* 2004). The main growth limiting nutrients are most often reported to be nitrogen (N) and phosphorus (P) (Bennett, Weston *et al.* 1997; Hooda and Weston 1999; May, Smethurst *et al.* 2009). Approximately 4000

ha $year^{-1}$ of eucalypt plantations managed for solid wood products are supplied with secondary fertiliser in state forests in Tasmania (Paul Adams, Forestry Tasmania, personal communication) primarily to alleviate deficiencies of N and P, increase growth rates and prevent branch death.

Fertiliser application may result in changes to branching, wood properties or the productions of antimicrobial extractives, which may affect decay entry and spread from the pruned stubs. Branch habit and form have been shown to deteriorate with the addition of fertiliser (Neilsen 1996).

Extractives containing antimicrobial compounds are important constituents of both sapwood and heartwood defences (Barry, Pearce *et al.* 2001; Pearce 1996). Active sapwood defence in eucalypts involves the rapid formation of reaction zones at the boundary between decayed and healthy wood (Barry, Pearce *et al.* 2001). The reaction zones are marked by accumulation of secondary metabolites such as hydrolysable and condensed tannins and phenols (Barry, Davies *et al.* 2001). Theories such as the Carbon Nutrient Balance (CNB) hypothesis predict that rapid growth induced by the addition of fertiliser N will utilise available carbon. This may constrain the production of carbon-based secondary metabolites used for defence (Bryant, Chapin *et al.* 1983).

Lignin acts as a passive defence as it is inherently resistant to degradation by many micro-organisms (Duchesne, Hubbes *et al.* 1992; Pearce 1996) and induced lignification has been identified as an active defence against pathogen ingress in eucalypts (Hawkins and Boudet 1996).

Wood density has been linked to wood durability in excised wood blocks (Wong, Wilkes *et al.* 1983) and coarse woody debris (Mackensen, Bauhus *et al.* 2003), and may influence decay spread in living trees. However, the effects of fertiliser on basic density are varied. Fertiliser increased density in *E. grandis* (Cromer, Balodis *et al.* 1998), but decreased density in *E. globulus* at low rainfall sites (Raymond and Muneri 2000). At a site adjacent to those used in this study, the density of *E. nitens* responded positively to fertiliser in all but small diameter trees (Smethurst, Baillie *et al.* 2003).

The objectives of this study were to (1) assess the effects of fertiliser and pruning at two sites on wood properties, branch characteristics and decay associated with pruned branches, and (2) indicate how the outcomes might assist in optimising silvicultural prescriptions that reduce the risk of pruning-associated decay.

2.2 Methods

2.2.1 Sites

Two sites were used in this study: the Tim Shea site in south-west Tasmania and the Nunamara site in north-east Tasmania, which were both adjacent to previously reported sites with a larger range of fertiliser treatments (Smethurst, Baillie *et al.* 2003; Smethurst, Holz *et al.* 2004). The sites differed primarily in soil type, temperature and average, annual rainfall (Table 2.1). Tim Shea is wetter and cooler than Nunamara. Low P availability at both sites was alleviated by P application at planting, but N deficiency in both plantations became evident by 2 or 3 years of age where high rates of N fertiliser were not applied (Smethurst, Baillie *et al.* 2003; Smethurst, Holz *et al.* 2004).

Site preparation involved ripping, mounding and weed control prior to planting in 1993. Tree spacing was 2 m (within rows) and 4 m (between rows) giving a total of 1250 stems ha^{-1}. Soon after planting all trees received ammonium sulphate (20.5% N) and triple superphosphate (20.0% P) at a rate of 100 g per tree at Tim Shea or 200 g per tree at Nunamara. This fertiliser was applied as a spot approximately 0.15 m from the tree. The subsequent fertiliser treatments used were (UF), an unfertilised control, where no fertiliser was applied following the at-planting dose and (HF), a high rate of fertiliser addition. HF plots received 500 kg N ha^{-1} and 150 kg P ha^{-1} between the ages of 1 to 4 years. At 5 years of age HF plots received an additional 400 kg N ha^{-1}. Pruning was undertaken 10 months after this application of fertiliser. Trees were harvested at 9 years of age.

2.2.2 Experimental design

The experiment was a randomized, complete block design consisting of two pruning and two fertiliser treatments in factorial combination. The pruning treatments were an

unpruned control or trees pruned to 2.5 m. Eight trees, from a total of 25 in each of the fertiliser plots were selected on the basis of their form according to pruning specifications (Beadle, Turnbull *et al.* 1994). Four were randomly allocated as un-pruned controls and the remaining four were pruned. All branches up to 2.5 m on the pruned trees were mapped and their status recorded prior to pruning. Status refers to whether the branches were living, dead or senescing at the time of pruning. No record was made of the status of branches on trees that were not pruned.

Table 2.1. Site characteristics (Moroni, Smethurst *et al.* 2002)

	Nunamara	Tim Shea
Soil type[A]	Ferrosol	Kurasol
Soil type[B]	Oxisol	Utisol
Elevation (M.A.S.L.)	1000	1500
Rainfall (mm/year)	1000 mm	1500 mm
pH[C]	5.8	4.6
Total N (%)	0.22	0.33
Total P (%)	0.08	0.08
NNM[D] ($kg/ha^{-1} year^{-1}$)	22	30

[A]Isbell (1996); [B]Soil Survey Staff (1990); [C]1 : 5 soil : water; [D]Net N mineralisation

2.2.3 Measurements

The diameter at breast height (1.3 m) over bark (*D*) was measured approximately annually over all the trees in a plot. Height (*H*) and *D* were measured on all treatment trees prior to tree harvest. The increment in diameter (D_{inc}) since pruning was calculated for the harvested trees from previous annual measurements. Trees were harvested and dissected at age nine, 4 years after pruning. Decay associated with pruning was assessed in the first 2.5 m of each tree. All branch stubs were numbered and their height above ground level recorded. Occlusion of branch stubs was recorded for pruned trees. All branches were given a rating for their degree of occlusion, which related to the extent to which the cambium had closed over the pruned stub. The occlusion classes used in this study were, 0%, 1-33%, 33-66%, 66-99% and 100%. Trees were cut into transverse sections containing the branch stubs. Radial longitudinal cuts were then made through the

centre of each branch stub using a bandsaw. The longitudinal and tangential spread of decay originating from branch stubs was measured. Branch diameter and the presence of excess kino were also recorded.

Wood density was measured on discs cut from the trunk at breast height using the water displacement method (TAPPI 1989)

Hydrolysable tannins (ellagic acid, catechin, trigalloylglucose, pedunculagin, tellimagrandin1 and tetragalloylglucose) in heartwood were quantified using liquid chromatography and mass spectrometry (LC-MS). Wood sections for heartwood extractives were taken from a height of 0.8 m above ground level. Sections were stored in plastic bags at -20 °C for approximately 7 days, after which wood shavings (~20 mg) were taken, placed in liquid nitrogen and freeze dried. Freeze dried material was kept in zip lock bags at -20 °C prior to extraction in 1.5 ml of 70% acetone. Extracts for hydrolysable tannins were analysed within 24 h using the methods of Barry *et al.* (2001a) with an internal standard of quercetin.

Lignin and extractive content of the heartwood were determined using the same discs. Heartwood samples were taken from the annual rings between 1 and 4 years of age, to coincide with wood formed in the years fertiliser was applied. Wood samples were air-dried and ground in a Wiley mill to pass through a 1 mm sieve. Lignin content was measured using the method described in Australian standard Appita P11s-78. Polyphenolic extractives were removed by extracting with methanol for 6 h to prevent interference with lignin determination. Total extractives content was measured after methanol was evaporated using a rotary evaporator and flasks were dried in an oven at 105 °C for 1 h. Lignin content and extractives content are expressed as a percentage of the air-dry weight of the wood.

2.2.4 Statistical analyses

All statistical analyses were carried out in SPlus 2000 Professional (Math Soft Inc.). In all cases significance is defined as $p<0.05$. All trees in a plot were used to compare D between the two fertiliser treatments. H, D, D_{inc}, average branch diameter (ABD)/D,

wood density, lignin content and kino were measured on the eight harvested trees per plot. *H, D,* D_{inc}, (ABD)/*D,* wood density, lignin content and kino were averaged within pruning treatments per plot and values compared using factorial ANOVA. As variances were not uniform over both sites, each site was analysed separately. Linear regression was used to investigate relationships between D_{inc} with basic density, average branch diameter and the incidence of decay, on a tree basis.

Frequency histograms were used to examine patterns in branch size, branch abundance and decay infection with height within the lower 2.5 m of trunk, which was divided into 10 classes, each covering a distance of 0.25 m.

Regression was also used to investigate the relationship between individual branch diameters and the length of associated decay columns. Results for decay column length were transformed by taking the natural log of (decay column length + 1). To compare branch diameter distributions between fertiliser treatments, the proportion of branches in each treatment in the following size classes: 0-5 mm, 5-10 mm, 10-15 mm, 15-20 mm and >20 mm were compared using a χ^2 statistic. The same method was used to compare the distribution of branches of different status, occlusion ratings between fertiliser treatments and the proportion of branches with decay infections.

Concentrations of hydrolysable tannins were analysed using agglomerative hierarchical clustering.

2.3 Results

2.3.1 Tree Growth

There were no significant differences between pruning treatments for *D* using only the eight treatment trees per plot. Pruning could then be excluded from the analysis and all trees in a plot compared for *D* between the fertiliser treatments. HF trees had greater *D* than UF trees at both sites, but were only significantly greater between 5 and 6 years of age at the Tim Shea site (Figure 2.1a) and from age 5 to 9 years at the Nunamara site (Figure 2.1b). For the harvested trees, there were no significant differences between treatments in *H,* or D_{inc} in (Table 2.2) at the time of harvest.

Table 2.2. Average height at harvest, diameter increment since pruning and basic density by fertiliser and pruning treatment

	UF		HF	
	Not Pruned	Pruned	Not Pruned	Pruned
Tim Shea				
H (m)	18.26a[A]	18.16a	16.26a	16.99a
D_{inc} (cm)	5.2a	4.1a	4.9a	3.6a
Basic density (kg/m$^{3)}$	427a	425a	445a	465a
(ABD[B])/*D*	0.58a	0.64ab	0.72b	0.71b
Nunamara				
H (m)	18.46a	19.12a	17.81a	18.06a
D_{inc} (cm)	3.9a	4.0a	2.9a	3.2a
Basic density (kg/m$^{3)}$	460a	455a	495a	467a
(ABD[B])/*D*	0.61ab	0.54a	0.75c	0.70bc

[A] Means with the same letter are not significantly different ($p < 0.05$)

[B] Average branch diameter (mm)/*D* (cm)

(High fertiliser (HF)= 900 N kg ha^{-1}: 150Pkg ha^{-1}; Unfertilised (UF) = 0 N kg ha^{-1}: 0 P kg ha^{-1})

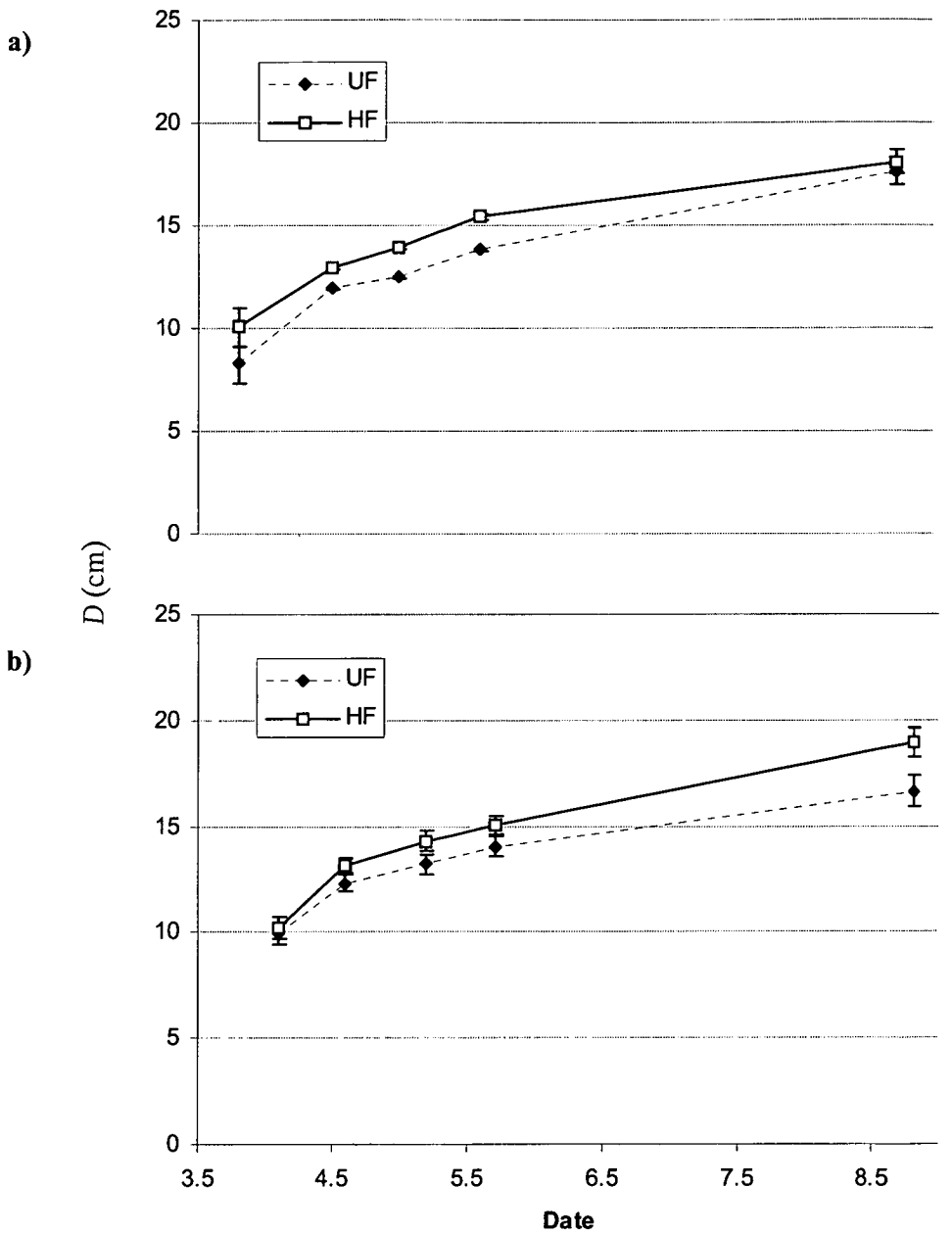


Figure 2.1. (a) *Diameter at 1.3 m (D)* averaged over all trees in a plot (n = 25) at the Tim Shea site
Bars = SE (High fertiliser (HF)= 900 N kg ha^{-1}: 150 P kg ha^{-1}, Unfertilised (UF) = 0N kg ha^{-1}: O P kg ha^{-1}).
Additional N applied October, 1997 (age four), pruning carried out August, 1998 (age four)
b) *D* averaged over all trees in a plot (n = 25) at the Nunamara site
Bars = SE (High fertiliser (HF)= 900 N kg ha^{-1}: 150 P kg ha^{-1}, Unfertilised (UF)= 0 N kg ha^{-1}: OP kg ha^{-1}).
Additional N applied November, 1997 (age four), pruning carried out September, 1998 (age five)

2.3.2 Branching

There was a significant ($p < 0.0001$, $R^2 = 0.35$) linear and positive relationship between average branch diameter (ABD) in the first 2.5 m, and *D*.

Comparing the ratio of ABD to *D* revealed HF trees tended to have a higher ABD/*D* ratio than UF trees, and in trees not pruned this was significantly higher ($p < 0.05$) (Table 2.2). Branch size distribution was significantly different between height classes ($\chi^2 = 154$, d.f. = 36, $p < 0.001$). Lower in the tree, branch size distributions were skewed towards a higher proportion of smaller branches, while higher in the tree the branch size frequency approached a normal distribution (Figure 2.2 (a-c)). Median branch size was 13 mm in the top two height classes (200-225 mm, 225-250 mm), 10 mm in the 100-125 cm height class and 11 mm in the remaining height classes.

Comparing branch abundance in relation to height showed few branches were located in the first 25 cm of the trunk (Figure 2.2 (a-c)). Branches were most abundant between the 25 cm and 75 cm after which abundance decreased with height. The abundance of branches was not significantly affected by fertiliser treatment.

For the pruned trees, the frequency of living branches increased with height, while the frequency of dead branches decreased with height (Figure 2.2 (a, b)), but no pattern was apparent in senescent branches. Trees at the wetter (Tim Shea) site had a higher proportion of living branches than trees at the drier (Nunamara) site. Fertiliser addition slowed crown lift at the wetter site as shown by an increased proportion of branches in the lower crown remaining alive in HF trees (Figure 2.2 (b)).

The distribution of branch size was significantly different between HF and UF trees ($\chi^2 = 187.4$, d.f. = 4, $p < 0.005$). HF trees had a higher proportion of larger branches than UF trees, i.e. in the 15-20 mm and >20 mm size class (Figure 2.2 (a-c)).

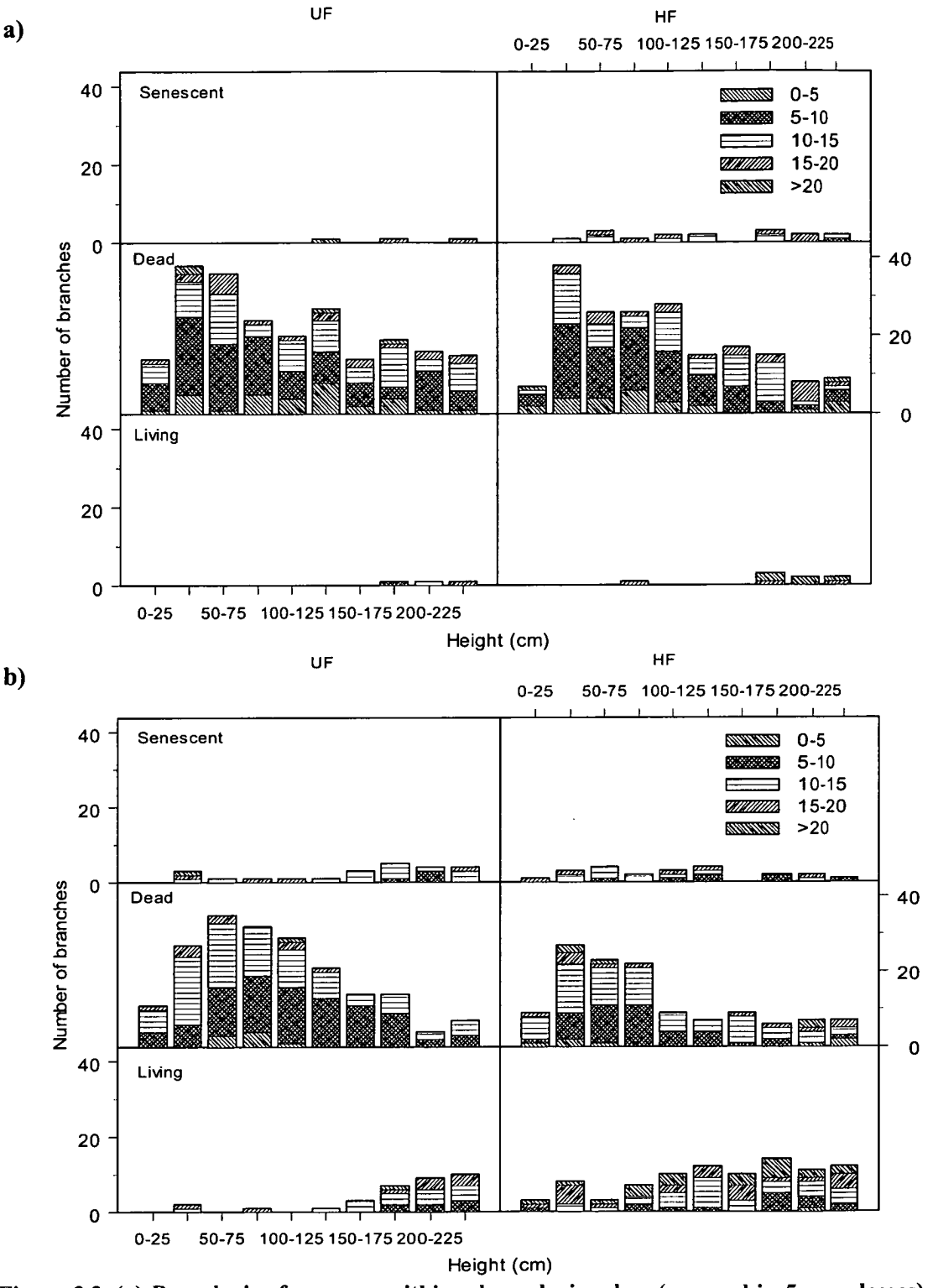


Figure 2.2. (a) Branch size frequency within a branch size class (grouped in 5 mm classes) and branch status at pruning (4.8 years old) of plantation-grown *E. nitens* subject to two fertiliser treatments at the Nunamara site
(High fertiliser (HF) = 900 N kg ha $^{-1}$: 150 P kg ha $^{-1}$, Unfertilised (UF) = 0 N kg ha $^{-1}$: 0 P kg ha $^{-1}$)
(b) Branch size frequency within a branch size class (grouped in 5 mm classes) and branch status at pruning (4.8 years old) of plantation-grown *E. nitens* subject to two fertiliser treatments at the Tim Shea site
(High fertiliser (HF) = 900 N kg ha $^{-1}$: 150 P kg ha $^{-1}$, Unfertilised (UF) = 0 N kg ha $^{-1}$: 0 P kg ha $^{-1}$)

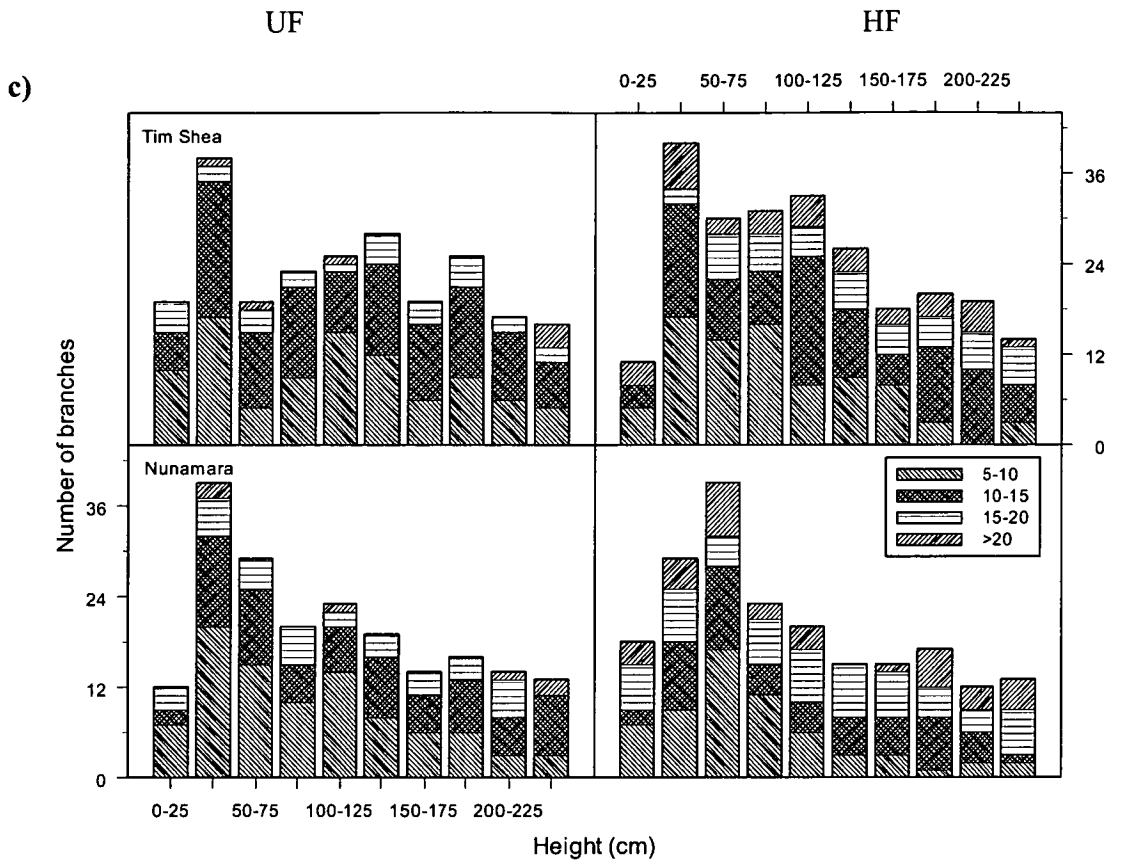


Figure 2.2. (c) Branch size distribution at harvest (9 years old) of un-pruned plantation-grown *E. nitens* subject to two fertiliser treatments
(High fertiliser (HF) = 900 N kg ha $^{-1}$: 150 P kg ha $^{-1}$, Unfertilised (UF) = 0 N kg ha $^{-1}$: 0 P kg ha $^{-1}$)

HF trees had a lower frequency of branches with complete occlusion and a higher frequency of branches with no occlusion (χ^2 = 23, d.f. = 4, p < 0.0001). However, most of this difference stemmed from the Nunamara site (Figure 2.3). Occlusion did not relate to branch size (Figure 2.3). There was no difference in decay incidence between occlusion ratings.

Results from ANOVA found HF trees had a significantly lower proportion of branches with excess kino than UF trees (F = 455.82, p < 0.005). Pruned living and senescent branches were never associated with excess kino, while 3% of dead branches exuded excess kino.

2.3.3 Decay

At the time of harvest no decay infection was found to have spread outside the knotty core. Decay infections were most frequent in the lower trunk (25-50 cm) where branches were most abundant, and in the upper sections of the pruned trunk (175-200 cm and 225-250 cm) where branches where larger. The incidence of decay as revealed by tree dissection is summarized in Table 2.3.

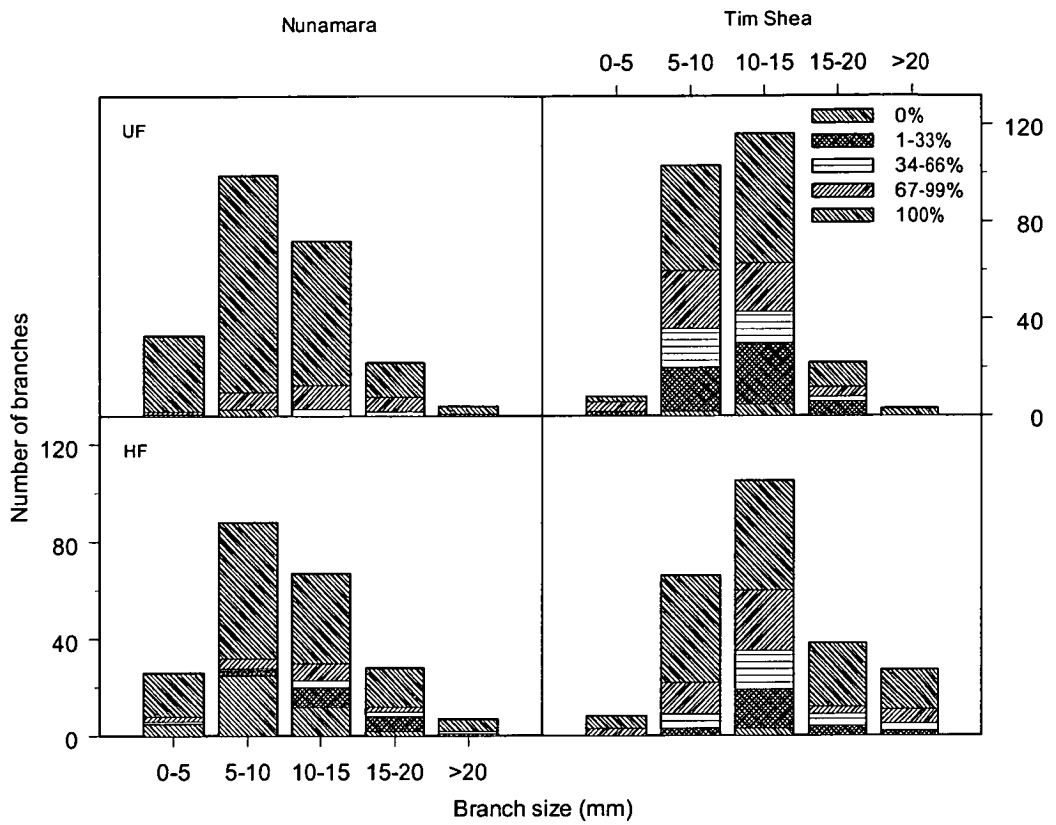


Figure 2.3. The number of pruned branches in each occlusion rating, 5 years after pruning
High fertiliser (HF) = 900 N kg ha^{-1} : 150 P kg ha^{-1}, Unfertilised (UF) = 0 N kg ha $^{-1}$: 0 P kg ha $^{-1}$

Table 2.3. The average proportion of branches in 9-year-old plantation grown *E. nitens* associated with decay infections as assessed four years after pruning

	Tim Shea pruned				Nunamara pruned			
	Living[A]	Dead[A]	Senescent[A]	Total	Living[A]	Dead[A]	Senescent[A]	Total
UF	0.11	0.01	0	0.12	0.19	0.00	0	0.19
HF	0.38	0.04	0.10	0.53	0.56	0.03	0	0.59
	Tim Shea not pruned				Nunamara not pruned			
	Living[A]	Dead[A]	Senescent[A]	Total	Living[A]	Dead[A]	Senescent[A]	Total
UF	NA	0.02	NA	0.02	NA	0.01	NA	0.01
HF	NA	0.01	NA	0.01	NA	0.02	NA	0.02

(High fertiliser (HF) = 900 N kg ha^{-1} : 150 P kg ha^{-1},), Unfertilised (UF) = 0 N kg ha $^{-1}$: 0 P kg ha $^{-1}$)
[A] Branch status

Overall, pruned trees had a significantly higher frequency of decay infections than trees that were not pruned (χ^2 = 32.7, d.f. = 1, p < 0.005) (Figure 2.4 (a-c)). Living and senescent branches were no longer present within the bottom 2.5 m of trees that were not pruned as

crown lift had extended beyond this height when the trees were harvested. The proportion of dead branches that became infected in the trees that were not pruned was negligible regardless of whether fertiliser was applied or not and branch size did not affect decay incidence (Fig 2.4c).

For the pruned trees, the incidence was significantly higher in the HF treatments compared to UF treatments ($\chi^2 = 39.6$, d.f. = 1, $p < 0.001$) (Fig 2.4a&b). Significant differences in the distribution of decay infections between living, dead and senescent branches were found ($\chi^2 = 185$, d.f. = 2, $p < 0.05$). Living branches had a higher than expected rate of infection, whilst dead branches had a lower than expected rate of infection (Figure 2.4 (a, b)). The number of decay infections associated with senescent branches differed only marginally from expected values.

Branches in the larger size classes had a higher proportion of decay infections after pruning than those in the smaller size classes (Figure 2.4 (a, b)). As branch diameter increased, the probability that a pruned branch would become infected also increased. The proportion of branches infected increased quite steeply in the 15–20 mm and >20 mm size classes (Figure 2.4 (a, b)). HF trees had more large branches than UF trees (Figure 2.4 (a, b)) and those large branches were more likely to become infected when pruned. In all branch size classes, HF trees had higher infection rates than UF trees (Figure 2.4 (a, b)).

a)

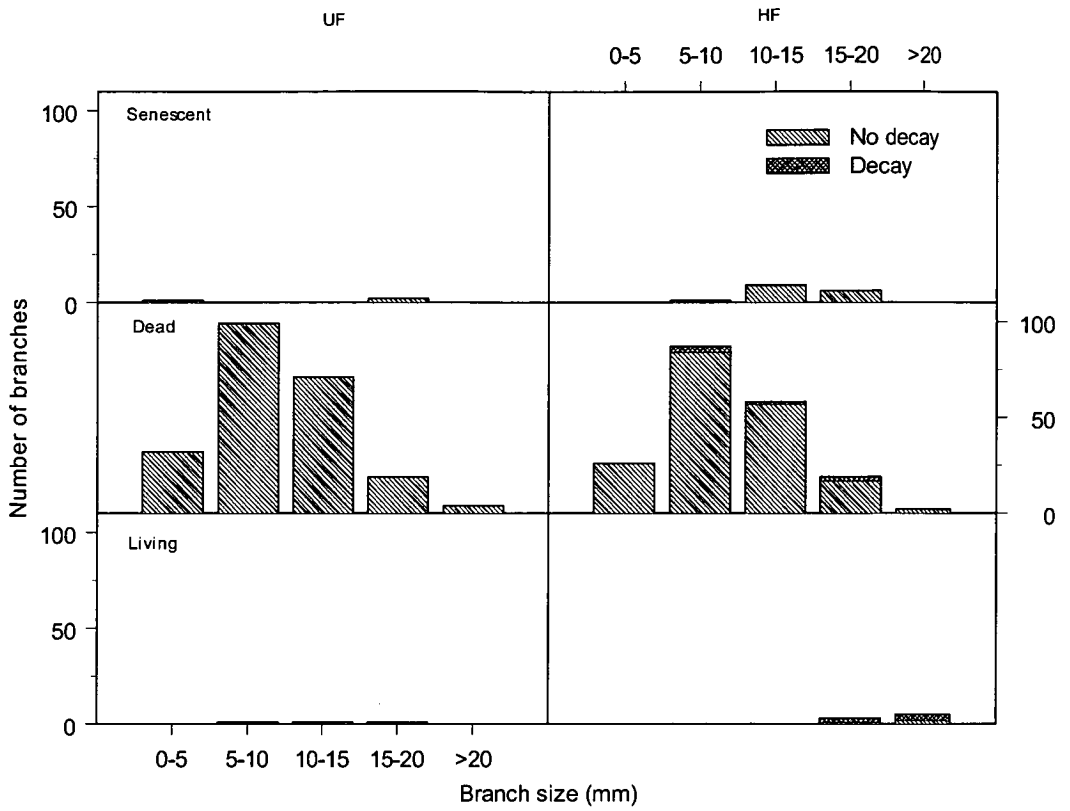


Figure 2.4. (a) The number of pruned branches associated with decay infections, 5 years after pruning at the Nunamara site. The branch status (senescent, living or dead) refers to the condition of the branches at pruning (age 4.8 years old)
(High fertiliser (HF) = 900 N kg ha^{-1}: 150 P kg ha^{-1}, Unfertilised (UF) = 0 N kg ha^{-1}: 0 P kg ha^{-1})

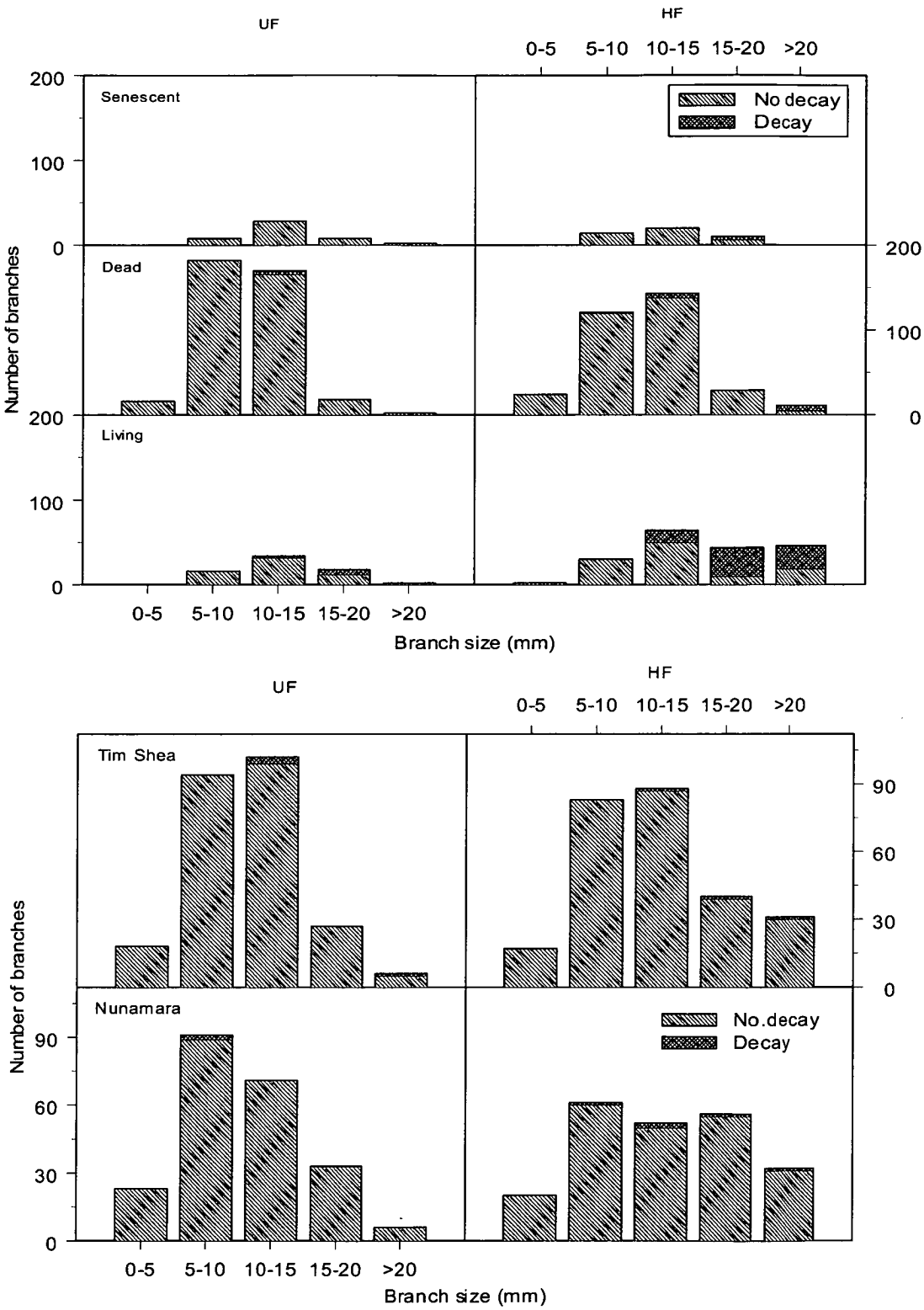


Figure 2.4. (b) The number of pruned branches associated with decay infections, 5 years after pruning at the Tim Shea site. The branch status (senescent, living or dead) refers to the condition of the branches at pruning (age 4.8 years old)
(High fertiliser (HF) = 900 N kg ha^{-1}: 150 P kg ha^{-1}, Unfertilised (UF) = 0 N kg ha^{-1}: 0 P kg ha^{-1})
(c) The number of un-pruned branches associated with decay infections at age 9 years
(High fertiliser (HF) = 900 N kg ha^{-1}: 150 P kg ha^{-1}, Unfertilised (UF) = 0 N kg ha^{-1}: 0 P kg ha^{-1})

The diameter of pruned living branches related positively with both the incidence and extent of decay. Large living branches were not only more likely to become infected, but the larger the branch, the more extensive was the associated decay column. There was no relationship between branch diameter and decay column length in senescent branches and only a very weak relationship in dead branches (Table 2.4). The strongest relationship between branch diameter and decay column length was found in living branches. The fitted equation explained 28% of the variation in decay column length (Table 2.4).

Table 2.4. Linear regression equations for the relationship between the diameter of a pruned branch (mm) and the associated decay column length (mm)

	Estimates			
Branch status	Intercept (SE)	Slope (SE)	R^2	*p*
Living	-1.95 (0.51)	0.23 (0.03)	0.28	<0.05
Dead	-0.15 (0.06)	0.02 (0.01)	0.02	<0.05
Senescent	-0.28 (0.29)	0.03 (0.02)	0.03	n.s.

2.3.4 Wood properties

No relationship was found for D_{inc} (from pruning to harvest) and decay extent. Basic density, lignin content and ABD were not related to D_{inc}. Nunamara trees had higher basic density than those at Tim Shea (Table 2.2). There was a trend toward higher densities in HF trees particularly at the Tim Shea site ($p < 0.10$). No difference in lignin or extractives content was found between fertiliser treatments (Table 2.5). No correlation was found between wood density, lignin or extractives content and the incidence or extent of decay. No fertilizer effect was evident upon hydrolysable tannins in the heartwood. No relationship with decay incidence or extent was found for any of the hydrolysable tannins identified.

Table 2.5 Lignin and extractives content of heartwood as a percentage of air-dry weight

	Tim Shea		Nunamara	
	UF (SE)	HF (SE)	UF (SE)	HF (SE)
Total Lignin (%)	29.0 (0.5)	28.4 (0.3)	27.3 (0.4)	26.7 (0.4)
Extractives (%)	4.6 (0.4)	5.1 (0.4)	4.4 (0.4)	3.9 (0.3)

Results from pruned trees. High fertiliser (HF) = 900 N kg ha^{-1}: 150 P kg ha^{-1}, Unfertilised (UF) = 0 N kg ha^{-1}: 0 P kg ha^{-1}

2.4 Discussion

2.4.1. Growth

In this study and at both sites, there had been no significant response in *D* to fertilisation prior to the first measurement at age 4 years. However, there were significant positive effects due to N (but not P) in adjacent fertilizer experiments at both sites that had more statistical power (Smethurst, Holz *et al.* 2004). A high rate of additional N fertilization at 5 years resulted in increased tree diameter at Nunamara by age 9 years, but no difference at Tim Shea. A significant effect on tree growth was expected because *E. nitens* plantations on ex-forest sites are often N limited and soil chemical indicators were consistent with expected N deficiency at both Tim Shea and Nunamara (Smethurst, Holz *et al.* 2004). No difference in *D* between harvested trees in the HF and UF treatments, was in agreement with whole-plot data at the Tim Shea site, but not at the Nunamara site. The failure to find greater *D* in harvested trees of the HF treatment at Nunamara may have been due to low replication (n = 3) and variability that biased the size of the few trees selected for harvesting.

2.4.2 Branching

Pruning operations should be timed to avoid removing more than 50% of leaf area which can suppress growth (Pinkard and Beadle 1998b) and yet, still be carried out while branches are small and live (Gerrand, Neilsen *et al.* 1997). Large branches are associated with large *D*, and this is compounded by the addition of fertiliser as shown by the increased branch size to *D* ratio, for HF trees. This implies that to minimise the occurrence of pruning associated decay, productive sites such as some ex-pasture sites will need to be pruned earlier in the rotation. Alternatively, stocking rates could be increased to control branch size (Neilsen and Gerrand 1999). Branch diameter may affect the rate at which pruning wounds occlude. Tree diameter growth, branch status at pruning (Petruncio, Briggs *et al.* 1997) and branch stub diameter (Marks, Incoll *et al.* 1986; Petruncio, Briggs *et al.* 1997) are important in determining the time taken for pruned stubs to occlude. While no relationship between occlusion and decay was found in this study, evidence suggests that the longer a wound is open the more favourable it is to fungal infection (Metzler 1997). The expectation that pruned stubs would occlude faster in HF trees was reversed at the Nunamara site, with better occlusion found in UF trees.

Patterns in branch size and abundance showed that branches became less abundant, but larger in diameter with tree height (Figure 2.2 (a–c)). Lower branches are the first to senesce

(Marks, Incoll *et al.* 1986) and as expected, dead branches were more frequent in the lower sections of the tree, whilst living branches became more frequent with height. As the risk of a decay infection increases when pruning both living and large branches, decay risk is expected to increase with height.

Results showed an increased frequency of decay infections in the 175–200 cm and 225–250 cm heights in the pruned trunk, in agreement with previous work with pruned *E. nitens* indicating that the risk of decay infection increased steeply above 1.5 m after which it stabilized between 3 and 6 m (Wardlaw and Neilsen 1999). Wardlaw and Neilsen (1999) ascribed this to the transition from pruning predominantly dead to predominantly living branches. Within a branch size class it was found that living branches were more likely to become infected than dead or senescent branches (Figure 2.4 (a, b)).

Of most significance were the effects that improved tree nutrition, had on branch size and status at the time of pruning. Leaf senescence can occur in response to environmental stresses such as drought or inadequate nutrition (Munné-Bosch and Alegre 2004). Leaf senescence, leading to branch death occurred less at the wetter Tim Shea site and less in the HF trees at the Tim Shea site (Figure 2.2 (a, b)). The remaining living branches were also of significantly greater diameter, indicating that improved nutrition not only allowed the trees to maintain lower branches, but to expand them. If care is taken not to promote excessive branch growth, early-age fertiliser additions could be a useful tool for maintaining living branches in the lower crown of trees grown for solid wood products.

While living branches carry a greater risk of decay entry after pruning, they are pruned in preference to dead branches in order to minimize defects in sawn timber associated with loose knots and kino-trace defect.

Kino is a resinous exudate, secreted by eucalypts as a means of sealing wounds and branch stubs (Eyles and Mohammed 2003). Excessive kino production is an undesirable feature in solid wood products as it reduces the appearance value and strength properties of timber (Waugh, Yang *et al.* 1997). Veins of kino are not found in *E. nitens*, but kino is exuded around branch stubs and is often effective at preventing fungal access (Marks, Incoll *et al.* 1986; Waugh, Yang *et al.* 1997; Yang and Waugh 1996). HF trees had a significantly lower proportion of branch stubs producing excessive kino in comparison to UF trees. From

observation, kino is associated with the stubs of pruned, dead branches, so this effect is most likely due to the influence that improved nutrition had on maintaining living branches in the lower crown.

None of the wood properties investigated were significantly affected by either the fertiliser or pruning treatments. No prior study on the effects of fertiliser addition on extractives and lignin content could be found for eucalypts, but fertiliser addition decreased extractive and Klason lignin content in *Pinus taeda* (Schupe and Yang 1995).

The effect of site on basic density may have been due to differences in rainfall. Rainfall has been shown to have a strong negative relationship with basic density (Raymond and Muneri 2000). The trend toward higher density with the addition of fertiliser at the wetter site is in contrast to results for *E. globulus*, which showed that the addition of fertiliser had no effect on density at high rainfall sites and decreased basic density at low rainfall sites (Raymond and Muneri 2000). However, the addition of fertiliser N and P increased basic density in *E. grandis* (Cromer, Balodis *et al.* 1998).

The association between large branches and decay infections is consistent with previous findings (Gadgil and Bawden 1981; Glass, McKenzie *et al.* 1989; Wardlaw and Neilsen 1999) and showed that the risk of decay increased dramatically when pruning live branches >15 mmin diameter at the Tim Shea site. Decay risk also increased at the Nunamara site in live branches >15 mm, but there were too few living branches for this to be conclusive. Wardlaw and Neilsen (1999) found a linear relationship between the proportion of branches with decay and average branch diameter within a branch diameter class. A threshold for decay risk based on pruned branch size diameter has been set at 35 mm (Neilsen and Gerrand 1999) and 30 mm (Wardlaw and Neilsen 1999), whereas results from this study suggest an upper branch limit of 20 mm to keep decay risk below 50%. Wardlaw and Neilsen (1999) found the relationship between branch diameter and decay risk to vary significantly between sites, so the lower threshold in this study may be the effect of site. Alternatively the branch size threshold in previous studies may have been higher as the branch size/decay risk relationship was not separated by branch status. If all branches (living, dead, senescent) were grouped together in this study, the decay risk would be reduced in the upper branch size classes.

Restriction of decay to the knotty core appeared to be effective for up to 4 years after pruning and is in agreement with earlier results (Barry, Hall *et al.* 2005; Glass, McKenzie *et al.* 1989). No association between D, wood density, lignin or extractives content and decay incidence or extent was found. Hence, differences in branch size and status can best explain the increased incidence of decay in the HF treatment.

The primary concern in plantation forestry is maintaining an adequate rate of tree growth. Eucalypts grown in plantations are more demanding from a site than many softwood plantations (Florence 2000). Currently, 30% of plantations in Tasmania are on low-nutrient soils and fertiliser must be applied to reach set productivity targets. This figure may increase as pressure to expand the plantation estate increases with the expected phasing out of logging in old growth forests or as a means of counteracting greenhouse emissions (Mercer and Underwood 2002).

The drawbacks to early fertiliser addition, as discussed above, are an increase in branch diameter that results in an increased risk of decay entry through pruning wounds. If decay is contained within the knotty core then clear wood is protected. However, there is some evidence from re-growth eucalypts that after 14 years barriers limiting decay spread break down (White and Kile 1994).

Early fertiliser application is desirable if the risk of decay infections from pruned stubs is minimised. Application of fertiliser N prior to pruning should be restricted to the level required to maintain living branches and care taken not to promote excessive branch growth in the lower crown. If so, the benefits provided through good growth, maintaining the green crown and reducing kino production associated with pruned stubs are likely to outweigh the risks posed by decay fungi entering through pruning wounds.

CHAPTER THREE

Clearwood prediction in *Eucalyptus nitens* from fertiliser history and tree characteristics at pruning

Abstract

An understanding of the processes involved in the formation of the defect core, branch occlusion and clearwood production after pruning is required to make informed decisions about the timing of fertiliser applications and pruning in *E. nitens* plantations in Tasmania, Australia. Growth of trees was monitored in factorial combinations of early (none or 500 kg N plus 150 kg P kg ha^{-1}) and late fertiliser treatments (none or 400 kg N ha^{-1}). At age nine years and five years after pruning, 11 trees over the range of treatments were harvested and dissected to assess branch occlusion and clearwood production. The number of occluded branches was low (46%). Occlusion was delayed by the exudation of kino from pruned stubs and by thick bark. Branches higher in the tree were more likely to have occluded than lower branches. The amount of clearwood produced depended on branch height, status and diameter, stub length, growth before and after pruning, and the distance required for a stub to occlude ($R^2 = 0.76$). Fertiliser did not significantly affect these relationships, which suggests that applications at four years of age or later can be made as required to enhance growth rates and clearwood production. However, high rates of N and P fertilisation earlier than this should be avoided to minimize the incidence of multi-stemmed trees.

3.1 Introduction

The trend towards decreasing rotation lengths in plantation forestry has been accompanied by greater investment in site selection and silviculture. For example, the use of fertiliser has become common practice for addressing nutrient deficiencies and increasing productivity (Bennett, Weston *et al.* 1997; Cromer, Cameron *et al.* 1993; Smethurst, Holz *et al.* 2004). In eucalypt plantations, fertiliser is usually applied at planting to encourage rapid establishment and growth and to maximize survival of the seedlings. Follow-up applications during the first few years of the rotation may be used to ensure trees 'capture' the site (Cromer, Turnbull *et al.* 2002). Early fertiliser N and P application has both potentially positive and negative implications for solid-wood production because rapid tree growth (Bennett, Weston *et al.* 1997; Cromer, Turnbull *et al.* 2002; Judd, Bennett *et al.* 1996) and the maintenance of living branches in the lower crown for green pruning (Pinkard and Beadle 1998b) are desirable outcomes, whilst larger cut surfaces associated with large branches and an increased risk of decay entry after pruning are not (Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999).

Pruning is used to maximise the development of knot-free or clearwood that surrounds the knotty core which contains the branch stubs. Prior to pruning, all growth is invested in the knotty core which has low value. Applying fertiliser potentially increases branch size and the diameter of the knotty core, so improved economic returns would be achieved by redirecting this growth potential into clearwood production.

Clearwood production is constrained by the rate of re-establishment of the vascular cambium over the pruned stub in a process known as occlusion or wound closure. With increasing diameter growth, the pruned branch stub is enveloped as new wood (callus) closes over the stub from each side. Eventually, both sides come together and the continuity of the vascular cambium is re-established. Thereafter, the new wood produced (clearwood), is free from stubs and other defects associated with stub occlusion. Defect may often arise from excess kino production (a resinous exudate) in response to damage. Kino is secreted by eucalypts as a means of sealing wounds and branch stubs (Eyles and Mohammed 2003). A number of factors appear to influence the occlusion process. For example, pruned stub occlusion in *Pseudotsuga menziesii* is influenced by stem diameter, the length of the pruned stub, the growth in stem diameter after pruning, the status of the branch at pruning (living or dead) and the type of pruning cut (smooth or non-smooth) (Petruncio, Briggs *et al.* 1997). Wound closure in *Betula alleghaniensis* was dependent upon wound width, wound length and annual stem increment (Solomon and Blum 1976). For *Eucalyptus regnans*, diameter at breast height, stub diameter, and height of pruned branch have been used to predict diameter over stubs (Deadman and Calderon 1988). Increases in stub length, bark thickness, and stub diameter will probably slow occlusion by increasing the distance over which new wood must form to occlude the stub before clearwood production commences.

This study tests the hypothesis that early fertiliser application increases the size of the knotty core and increases branch size, thereby potentially reducing the quantity and quality of clearwood production of plantation eucalypts. Concurrently, the effects of early and late fertiliser application on stem growth were determined, which are important for both pulpwood and solid-wood regimes. We also recorded the incidence of decay and kino production in relation to fertilizer treatment and branch attributes.

3.2 Methods

3.2.1 Site

The Tim Shea site is located in south-west Tasmania, adjacent to experiments that investigated the effects of a large range of fertiliser treatments on the growth and nutrient acquisition of *E. nitens* in plantations (Smethurst, Baillie *et al.* 2003). Tim Shea is a cool, wet site with low P availability (Table 1) alleviated by P application at planting. N deficiency became evident in the adjacent experiment by age three years in treatments where high rates of N fertiliser were not applied (Smethurst, Baillie *et al.* 2003; Smethurst, Holz *et al.* 2004).

Table 3.1. Soil classification, surface soil chemistry (0-10cm depth), and climate at Tim Shea (from Moroni, Smethurst et al., 2002, and Smethurst, Holz et al., 2004)

Australian soil classification[A]	Kurosol
Soil taxonomy[B]	Ultisol
pH[C]	4.6
Total C (mg g^{-1})	61
Total N (mg g^{-1})	3.5
Total P (mg g^{-1})	0.8
NNM (kg ha^{-1} $year^{-1}$)[D]	30
Elevation (M.A.S.L.)	430
Rainfall (mm $year^{-1}$)	1444

[A] Isbell (1996); [B] Soil survey staff (1990); [C] 1 : 5 soil : water; [D] Net N mineralisation

3.2.2 Establishment and fertiliser treatments

Site preparation involved ripping, mounding and weed control prior to planting in October 1993. Tree spacing was 2 m within rows and 4 m between rows giving 1250 stems ha^{-1}. Soon after planting all trees received ammonium sulphate (20.5% N) and triple super phosphate (20.0% P) at a rate of 100 g per tree. This fertiliser was applied as a spot approximately 0.15 m from the tree.

The site was divided into three replicate blocks. Each block was initially divided into two plots consisting of 7 rows x 5 trees = 35 trees per plot. Each plot was surrounded by a row of treated buffer trees, providing two buffer rows between plots. One plot was randomly designated UF and one HF. UF plots received no fertiliser whilst HF plots received 500 kg N ha^{-1} as urea and 150 kg P ha^{-1} as triple super phosphate split into three applications and applied annually between one to three years of age. At age 4.0 years, each of the initial UF and HF plots were split into two sub-plots, each containing 3 rows x 5 trees = 15 trees, leaving one row of buffer trees between the sub-plots. Within each plot, one sub-plot had 400

kg N ha^{-1} (UF + N, HF + N) and one had no additional fertiliser (UF, HF). This resulted in three replicates of the four sub-plots. The fertiliser applied between ages one and three is referred to as the 'early' application while fertiliser applied at age 4.0 years is the 'late' application. Early and late fertiliser applications were treated as factors.

3.2.3 Pruning

From the 15 trees in each sub-plot, four were selected for pruning after tree form was assessed using specifications from Beadle, Turnbull *et al.* (1994). Selection was carried out at age 4.0 years and the incidence of large branches and multiple leaders was recorded. Pruning was carried out at age 4.8 years, ten months after the second application of fertiliser. Prior to pruning, all branches below 2.5 m were mapped and their status recorded, i.e. whether a branch was living or dead at the time of pruning.

3.2.4 Growth

Diameter at breast height over bark (D) of all trees was measured at the ages of 3.8, 4.5, 5.0, 5.6 and 8.8 years. The height (H) of five trees per sub-plot over the range of diameters in each sub-plot was measured, and a regression of $H = f(D)$ was developed and applied over the remaining trees to predict H. Stem volume (V) was calculated using the formulae

$$V = (\exp(-10.316 + (1.8974*(\log_e(D - \exp(1.1817-(27.81/D)))))) + (1.1198*\log_e(H))))$$

from Candy (1997).

3.2.5 Harvest

At age 8.8 years, one pruned tree from each sub-plot was selected for harvest. The tree closest in diameter to the average D of the subplot was chosen. Unfortunately, due to harvesting for a separate experiment and tree death, no pruned trees were available for harvest in one subplot of the HF treatment. The trees that were able to be harvested were not always representative of the mean diameter of trees for that treatment (Table 3.2.). In total, 11 trees were harvested for dissection.

Table 3.2. Average *D* of harvested 9-year-old *E. nitens* in comparison to all trees in each fertiliser treatment

Treatment	*D* (cm)	
	Harvested trees	All trees
UF	16.9 (2.1)	16.8 (0.6)
UF+N	18.6 (2.4)	17.5 (0.8)
HF	17.6 (2.4)[A]	19.3 (0.6)
HF+N	15.9 (1.1)	18.5 (0.7)

(Standard error in parentheses: n = 3, except [A] where n = 2)

H and *D* were recorded and the first 2.5 m of each trunk was retained for dissection and further measurement. All branch stubs in the retained section were numbered and their height above ground level (H_B) recorded, after which transverse sections containing the branch stubs were cut. Radial longitudinal cuts were then made through the centre of each branch stub using a bandsaw. Variables measured were: stem radius (*R*), stem radius at pruning (RAP), stem radius over stub (ROS), stem radius over occlusion (ROO), stub length left at pruning (SL), stub diameter (SD), cut face diameter (CFD) and the presence (DEC) and extent of any decay (Figure 3.1). Occlusion was measured as the first point where new wood had formed over the stub that was free from any defect such as kino or bark. A disc was cut from a height of 0.8 m and the width of the tree rings measured.

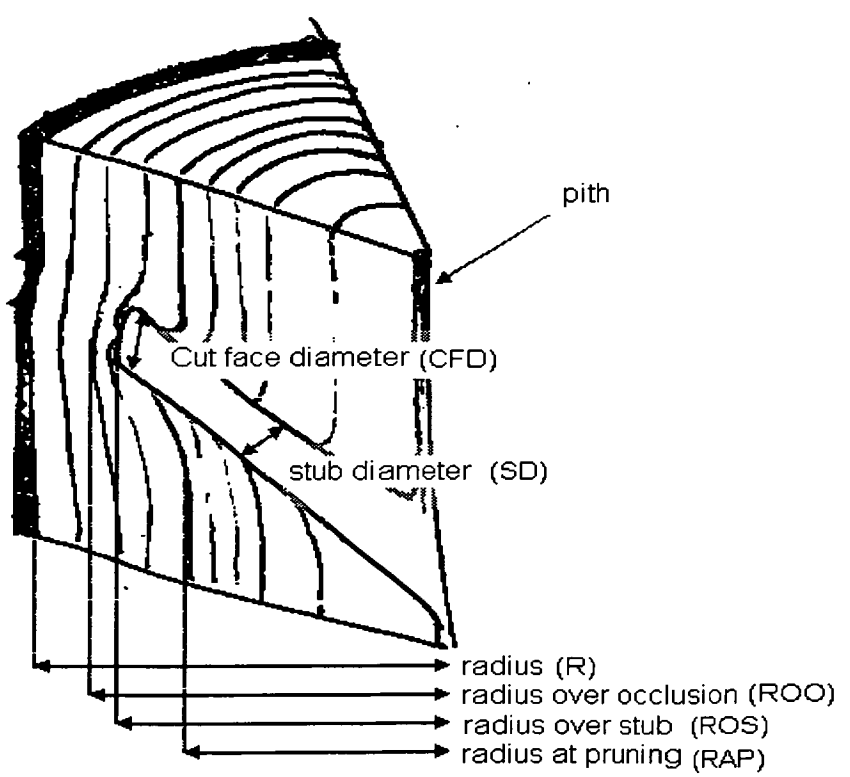


Figure 3.1. Variables measured on the harvested trees

3.2.6 Statistical analysis

Factorial analysis of variance for a split-plot-design was used to assess treatment effects on D, V and the increment in volume between pruning and harvesting (ΔV). Individual tree D or V at age 3.8 years was used as a covariate for the analyses of D and V, respectively. ANOVAs for D and V were performed on measures of all trees in a sub-plot (15 trees/sub-plot) unless otherwise stated.

For the harvested trees (1 tree/sub-plot), mean values per tree were used to assess treatment differences, except for ROS where the maximum value was used. The total number of branches examined was 474. The number of occluded branches was compared between treatments, and between living and dead branches using a χ^2 statistic. Branch diameters and heights were divided into intervals of 5 mm and 0.5 m, respectively. The numbers of occluded branches were compared between intervals also using a χ^2 statistic. Unless otherwise stated, $p = 0.05$ was used as the critical probability for significance.

At the time tree form was assessed and trees were selected for pruning (age four years), there were only two treatments in place, UF and HF. Thus the ANOVA model that compared the D at age 4 years of trees selected for pruning with those not selected included the early fertiliser treatment only.

Data for branches which had not occluded were not incorporated into analyses for distance taken for a branch stub to occlude (DO) and width of clearwood produced since pruning (CLW), giving a total of 214 branches as opposed to 474. A stepwise regression procedure that stepped in both directions (S-Plus 2000 Professional, Math Soft Inc.) was used to build the best model for predicting (DO) after pruning and (CLW). This procedure aimed to maximise the accuracy of the model while minimising the complexity. Only data points having a positive value for clearwood thickness (meaning they were fully occluded) were used in the analysis. The upper model for DO included growth since pruning (GSP), decay (DEC), the presence or absence of kino (KINO), bark width (BW), RAP, SL, CFD, branch status (ST) and H_B. The upper model for CLW included the same terms with the addition of DO. CFD was included in the upper model for DO in preference to stub diameter as it was more representative of the size of the wound to be occluded. Quadratic terms were included for all parameters. To determine how much each term contributed to the fit, the best model was applied, but with the exclusion of each of the terms in turn.

3.3 Results

3.3.1 Tree growth and form

At age 3.8 years, just before the late application of fertiliser, there were no significant differences between the treatments for *D* or *V*. Significant differences in volume became apparent at age 4.5 years, i.e. within six months of the late fertiliser being applied (Table 3.3). Differences between treatments were still apparent when the trees were harvested at age 8.8 years. At this time average volume (m^3 ha^{-1}) was greatest in HF + N (221) followed by UF + N (210), HF (198) and UF (191), with the UF treatment having significantly lower volume than the HF + N treatment (Table 3.3). There were no treatment differences for ΔV, which averaged 0.12 m^3 per tree.

Early fertiliser application affected tree form. Significantly more double leaders were found in the HF (24%) than the UF (17%) treatment.

At the time trees were selected for pruning (age 4 years) there was a significant interaction between early fertiliser treatment and tree selection for pruning (data not shown). Trees selected as being of 'prunable' form had significantly greater average *D* than those not selected in the UF treatment, but in the HF treatment, the average *D* of the selected trees was almost the same as for the trees not selected.

Table 3.3. Significance ($p <$) of early and late fertiliser treatments and their interaction on stem volume (*V*) as indicated by ANOVA using *V* at age 3.8 years as a covariate for later ages
N.S. = not significant

	Age (years)			
Source of variation	**3.8**	**4.5**	**5.6**	**8.75**
Early	N.S.	0.005	0.05	N.S.
Late		0.005	0.01	0.05
Early*Late		N.S.	N.S.	N.S.

3.3.2 Branching and defects

In total, 474 branch stubs from 11 trees were dissected and their characteristics recorded.

Of the dissected branch stubs, 17.5% had decay infections spreading from the pruned stub. Of the eleven trees harvested, only two had no decay infections. The average number of

branches with decay infections within each fertiliser treatment was UF = 4.4%, UF + N = 30.0%, HF = 17.9 % and HF + N = 14.5%. Treatment effects were not significant.

There was a positive linear relationship between average branch diameter in mm (D_B) and the percentage of branches per tree that had decay infections (% Decay) in the harvested trees. The relationship was significant ($p < 0.01$) with an R^2 value of 0.65 and can be described by Equation 1.

$$[1] \quad \% \text{ Decay} = -56.25\ (17.98) + 6.25\ (1.53) * D_B \quad (n = 11)$$

The overall mean for excess kino production from the pruned stubs was 18.6% of branches and there were no significant differences between treatments (UF = 25.3%, UF + N = 17.0%, HF = 16.7 % and HF + N = 14.7%).

3.3.3 Occlusion

The average distance to occlude (DO) measured from the end of the stub to the point of occlusion was 3.6 mm and the maximum DO for the branches occluded at harvest was 13 mm. Measured variables accounted for 23% of the variation in DO (Table 3.4). DO increased with cut face diameter (CFD), bark width (BW) and the presence of excess kino (KINO) and decreased with an increase in stub length (SL) and if decay was present in the stub (DEC). The terms that contributed most to the fit were KINO, CFD and BW. None of the variables was highly correlated.

Bark width (BW) increased as stem radius (R) increased and decreased with H. This relationship is set out in Equation [2] and explained 65% of the variation in BW ($p < 0.0001$). Numbers in brackets are the standard errors.

$$[2] \quad BW = -0.983\ (0.377) + 0.109\ (0.004) * R - 0.011\ (0.001) * H \quad (n = 474)$$

There were no differences in the number of occluded branches between branch size intervals. The number of occluded branches increased with height ($\chi^2 = 45.91, p < 0.0001$).

At harvest, 4.0 years after pruning, only 46% of branches examined were fully occluded. There were significant differences in occlusion due to branch status, i.e. living or dead at pruning ($\chi^2 = 26.08, p < 0.0001$), with 40% of dead branches and 68% of living branches

fully occluded at harvest. There was a significant and positive relationship between the percent of occluded branches and average growth since pruning (GSP) ($p < 0.01$, $R^2 = 0.80$). No significant differences between treatments for average GSP (UF = 26 mm, UF + N = 23 mm, HF = 23 mm and HF + N = 21 mm) were detected, although the lower than average diameters of the harvested trees in the HF and HF + N treatments may have influenced this result (Table 3.2).

Table 3.4. Coefficients selected by stepwise regression for estimating DO of *E. nitens* pruned at age 4.8 years and harvested at age 8.8 years ($R^2 = 0.23$, n = 214).
Only coefficients with $p < 0.05$ were included

Independent variables	Coefficient	S.E.	Contribution to R^2
Intercept	2.305	0.913	
BW	0.182	0.061	0.033
CFD	0.133	0.027	0.087
DEC	-0.433	0.201	0.017
KINO	1.070	0.183	0.123
SLGTH	-0.085	0.041	0.015

3.3.4 Clearwood

Tree ring width decreased with distance from the pith. Maximum ring width was observed during the first four years of growth (12 - 18 mm). Ring width then declined and was approximately 2 mm at the time of harvest.

Diameter over stubs (DOS; measured as the maximum value per tree of the ROS * 2) ranged from 136 mm to 214 mm in diameter and there were no significant differences between treatments for this variable. There was no significant relationship between SD and ROS.

Clearwood width (CLW) increased with *H*, radius at pruning (RAP) and GSP and decreased in association with living branches (ST) and with increased SD, SL and DO (Table 3.5). The terms that contributed most to the fit were GSP, SL and DO and none of the variables were highly correlated. This relationship described 76% of the variation in CLW, and a model using only the more easily measured variables GSP and SL described 64% of the variation ($p < 0.001$).

As GSP had the largest effect on CLW, the relationship between these two variables was used to investigate the effects of fertiliser application. The slope of the relationship appeared to be steeper for the UF and HF treatments than for the UF + N and HF + N treatments. However t-tests revealed no significant differences between treatments for the estimates of the intercepts or slopes of the fitted regression equations.

Table 3.5. Coefficients for estimating the radial thickness of CLW of *E. nitens* pruned when 4.8 years old and harvested at 9 years ($R^2 = 0.76$, n = 214).
Only coefficients with $p < 0.05$ were included

Independent variables	Coefficient	S.E.	Contribution to R^2
Intercept	-2.387	1.309	
DO	-0.565	0.075	0.065
GSP	0.669	0.032	0.496
H	0.012	0.003	0.019
RAP	0.068	0.016	0.021
SD	-0.175	0.046	0.016
SL	-0.600	0.053	0.143
ST	-0.689	0.224	0.011

3.4 Discussion

This is the first attempt to form quantitative links between clearwood production and the characteristics that define the growth of *E. nitens* trees that have been pruned and received fertiliser. Clearwood production was most significantly related to growth since pruning, but was also affected by the stub length left at pruning, and occlusion. Branch occlusion can be affected by stem diameter (Chiu, Lo-Cho *et al.* 2002; Petruncio, Briggs *et al.* 1997), stem growth rate (Chiu, Lo-Cho *et al.* 2002; Petruncio, Briggs *et al.* 1997), stub diameter (Chiu, Lo-Cho *et al.* 2002; Petruncio, Briggs *et al.* 1997), stub length (Chiu, Lo-Cho *et al.* 2002; Petruncio, Briggs *et al.* 1997), branch status (Gerrand, Neilsen *et al.* 1997; Petruncio, Briggs *et al.* 1997), type of pruning cut (Petruncio, Briggs *et al.* 1997) and site (Gerrand, Neilsen *et al.* 1997). We found the most significant negative effects on the process of branch occlusion were excess kino production, the length of the pruned stub and the width of the bark.

We found no significant effect of the repeated applications of fertiliser N and P early in the rotation on stem volume (*V*) or diameter over stub (DOS) in the harvested trees. It is probable

that nitrogen supply during the first one or two years after clearing is sufficient to meet tree demand in plantations on many ex-forest sites in Tasmania, after which N deficiency becomes apparent. This explains why the addition of fertiliser N only increased growth rates in the late fertiliser application, as illustrated in Table 3.3 (Cromer, Turnbull *et al.* 2002; Smethurst, Holz *et al.* 2004).

Fertiliser application increased the incidence of double and multiple leaders. This is consistent with findings in other experimental *E. nitens* plantations receiving similarly high rates of fertiliser (Cromer, Turnbull *et al.* 2002) and lower rates (100 –300 kg N ha^{-1} (Beadle, Turnbull *et al.* 1994) that are more consistent with current practices in Tasmania. Increased incidence of double leaders may only pose a problem if insufficient trees remain that are of suitable form for pruning (Beadle, Turnbull *et al.* 1994). In several cases application of N fertiliser has induced Cu deficiency resulting in stem malformation and branch sinuosity (Turnbull, Beadle *et al.* 1994). Application of fertiliser N has also been associated with the larger branches (Wiseman, Smethurst *et al.* 2006) and trees with branches greater than 3 cm in diameter are rejected for pruning in Tasmania as branch diameter is an important determinant of decay risk for pruned plantations (Glass, McKenzie *et al.* 1989; Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999). As in this study, the most vigorous trees in the stand may be rejected for pruning, if fertiliser application leads to deterioration in tree form. If the remaining single stemmed trees with small diameter branches selected for pruning are less vigorous than average for the stand, the pruned trees may become subdominant. In addition, the most vigorous trees provide the highest potential returns at the end of the rotation as log-end size has a marked effect on sawn-log recovery (Deadman and Calderon 1988).

While there was no effect of fertiliser application on the incidence of decay in this study, previous work at this site and another in northern Tasmania showed the incidence of decay increased in the HF + N treatment (Wiseman, Smethurst *et al.* 2006). The limited sample size in this study made it difficult to detect treatment differences.

Stub diameter (SD) had a negligible effect on occlusion and clearwood production but, as expected, greater SD was associated with a higher risk of decay. While incidence of decay was high (17% of branches), there is some evidence that decay entering through pruned stubs

will remain confined to the knotty core (Barry, Hall *et al.* 2005; Glass, McKenzie *et al.* 1989) in which case the impact of decay on wood quality will be minor.

Distance to occlusion was affected by cut face diameter (CFD) as found in Solomon and Blum (1976), Petruncio, Briggs *et al.* (1997) and Chiu, Lo-Cho *et al.* (2002) and stub length (SL) as found in O'Hara and Buckland (1996), Petruncio, Briggs *et al.* (1997) and Chiu, Lo-Cho *et al.* (2002). Bark width (BW) and the exudation of kino from the pruned stub (KINO) also affected DO and KINO had the most significant effect. This can be explained in terms of stub length as kino exuded around the end of the stub, effectively increases stub length. O'Hara and Buckland (1996) found occlusion to be more sensitive to stub length than wound size in *Pinus ponderosa.* Although no effect of fertiliser on the incidence of kino was found in this study, the addition of fertiliser P appears to reduce the incidence of kino under some circumstances (White, Raymond *et al.* 1999), and previous work at this site and another in northern Tasmania showed a significant reduction in the incidence of kino where fertiliser N and P were applied (Wiseman, Smethurst *et al.* 2006). Again the small sample size in this study may have masked treatment differences in kino production as no effect on kino was found.

Observations made while dissecting the harvested trees indicated that pruned living branches occluded more quickly than pruned dead branches, a result confirmed by the higher proportion of living branches which had occluded in comparison to dead branches. It was evident that kino was exuded most commonly and abundantly from pruned dead and senescing branches. The exuded kino prevented the cambium from sealing for some distance beyond the bark stub, forming a kino pocket. Dead branches were spuriously associated with a greater thickness of clearwood because only data with clearwood values greater than zero were used, which excluded many dead branches (60%) that had not occluded. Fertiliser N and P application can assist trees in maintaining living branches in the lower canopy (Neilsen 1996) and the addition of fertiliser reduces kino production by maintaining living branches in the lower canopy. Fertiliser application could be useful in promoting cleaner and more rapid occlusion, thereby reducing the size of the defect core.

Pruning of *E. nitens* in Tasmania usually commences at three to four years of age. While current annual increments in volume in plantation-grown eucalypts remain stable, radial increments in stem-wood decline after the first few years as the volume of wood added each

year is spread around an ever increasing core. Radial growth at three years of age in this study was more than double that in the subsequent year when the trees were pruned. On average, younger trees than those used in this study will have a greater proportion of living branches, thinner bark and larger growth rings at pruning, all characteristics which would promote clean, fast occlusion.

The importance of stem growth to occlusion and clearwood production is well documented (Chiu, Lo-Cho *et al.* 2002; Petruncio, Briggs *et al.* 1997; Solomon and Blum 1976) and proved to be the most important factor in the production of clearwood in this study. Four years after pruning, other factors that influenced occlusion had little effect on clearwood production. The next most significant factor was stub length (SL). This emphasizes the need for good pruning technique and early pruning to ensure that branches are trimmed as flush to the trunk as possible and that the pruned branches are still alive. The length of stub remaining after pruning is a function of bark width (BW). Bark width is related to radius, so a larger tree will have thicker bark and longer SL. SL will also increase toward the base of the tree where the bark is thicker. This, and the larger proportion of dead branches, may explain the lower level of occlusion towards the base of the tree also found by Reis, Pulrolnik *et al.* (2004).

GSP was clearly the main determinant of CLW and branch occlusion. As D increases most rapidly in young trees (<4 year of age), occlusion will also be most rapid in this time. Young trees also have thinner bark and are more likely to have retained living branches in the lower stem, two factors which will also encourage rapid occlusion. The effect of fertiliser treatment on clearwood and occlusion deserves further investigation, because the diameters of harvested trees were not ideally representative of the overall diameters of the treatments (Table 3.2) and tree growth was shown to be a factor in both occlusion and clearwood production. The outcomes of this study could have been more complete if branch occlusion was 100% at the time of harvest and if trees that better represented the fertiliser treatments from which they were sourced were available for harvest. However the scheduling of pruning operations must be delayed until the operation does not remove more than 50% of the leaf area as this has been shown to significantly reduce tree growth (Pinkard and Beadle 1998b). Despite these reservations, GSP was clearly the main determinant of CLW and branch occlusion. However pruning should not remove more than 50% of leaf area as this has been shown to significantly reduce tree growth (Pinkard and Beadle 1998b). Thinning or applying

fertiliser (where there is evidence of nutrient limitation) is highly recommended to encourage vigorous growth post-pruning and improve clearwood production.

CHAPTER FOUR

Growth responses of *Eucalyptus globulus* and *Eucalyptus nitens* to pruning and fertiliser treatments in a plantation managed for solid-wood products

Abstract

The responses of *Eucalyptus globulus* and *E. nitens* to pruning (removal of 0 or 60% of the green crown depth) in two lifts and nitrogen (N) fertiliser application (0 (N0), 100 (N1), 300 (N3) and 500 (N5) kg N ha^{-1}) were compared at a site in south-east Tasmania under conditions where both species can be successfully grown. Pruning reduced growth of both species, but the final measured volume (at age 5.7 years) of pruned trees in the N3 and N5 treatments was greater than in the unpruned trees in the N0 treatment. *E. nitens* exhibited superior growth over the course of the experiment and showed a larger volume response to applied N than *E. globulus* during one growth period. *E. nitens* had a higher incidence of decay infections in pruned stubs because of its tendency to have larger branches than *E. globulus*, though the overall incidence of decay was very low.

4.1 Introduction

Scheduling pruning operations for plantation eucalypts early in the rotation can overcome decay and defect risks described in previous chapters and which are associated with pruning large diameter living and/or dead branches. However, if growth rates are to be maintained, a smaller fraction of leaf area should be removed when pruning before, rather than at, canopy closure. By way of example, for two *Eucalyptus nitens* plantations, the removal of as little as 20% leaf area pre-canopy closure significantly reduced stem growth (Pinkard 2002b) whereas the removal of up to 55% of leaf area at canopy closure on a highly productive site did not reduce stem growth (Pinkard and Beadle 1998b). When *Eucalyptus globulus* was pruned pre-canopy closure at a low productivity site, removal of as little as 20% of leaf area also significantly reduced stem growth (Pinkard 2003).

Applying fertiliser N and P prior to pruning can result in a deterioration in tree form in terms of increased numbers of double leaders (Beadle, Turnbull *et al.* 1994) and the formation of larger branches (Wiseman, Smethurst *et al.* 2006) than without fertiliser application. An alternative strategy is to delay fertiliser application until just after pruning. This may lead to a number of benefits; firstly the increased nutrient supply may accelerate the recovery of the tree canopy, and secondly any stem growth response to fertiliser is now invested in laying down wood outside, rather than within, the knotty core. This results in a higher proportion of the stem being for high-quality solid-wood products.

Eucalyptus globulus and *E. nitens* are the plantation species of choice in Tasmania and most of southern Australia. *E. globulus* is mainly planted at low altitudes and *E. nitens*, a more frost-resistant species (Hallam, Reid *et al.* 1989), at altitudes >300 m. As plantations are increasingly managed for solid-wood production, a comparison of the two species in their growth response to pruning and addition of fertiliser is warranted. While *E. nitens* has been shown to have a broader optimal temperature range for photosynthesis (Battaglia, Beadle *et al.* 1996), *E. globulus* shows greater drought tolerance (White, Beadle *et al.* 1996). The experimental site used here was situated in the transition zone at 240 m in a high rainfall area where both *E. globulus* and *E. nitens* can be grown successfully, thereby providing a good environment for a species comparison.

This study compared the growth response of *E. globulus* and *E. nitens* to pruning across a range of fertiliser treatments. In particular, we assessed whether the response of stem-volume growth to fertiliser addition was superior in either of the species, if recovery from defoliation (in terms of stem-volume growth) varied between species and whether there was an interaction between fertiliser treatment and growth response to pruning. In addition the incidence of decay and other defects was compared between the species in two pruning treatments and two contrasting fertiliser treatments.

4.2 Methods

4.2.1 Site

The site was located at 240 m in the Esperance valley, in south-east Tasmania (43°17.110'S, 146°52.276'E). In a previous study at this site (Battaglia, Beadle *et al 1996.*), mean weekly maximum and minimum temperatures were 19.5 °C and 3.7 °C, respectively, rainfall was 1412 mm yr^{-1}, and total short-wave radiation was 4.16 GJ m^{-2} yr^{-1}. The summer of 2002 – 2003 was warmer and drier than normal with maximum temperatures 2° C above average and rainfall very much below average (Australian Government: Bureau of Meteorology 2003).

Soils in the area are formed from a mixture of Triassic sandstone and Jurassic dolerite and are classified as Yellow Chromosols (Isbell 1996). The site has a north-easterly aspect with a maximum soil depth of >1 m, the mid slope having shallower soils and the lowest area prone to waterlogging during winter, and possibly cold air drainage. The site was mounded along the planting rows and trees were planted every 2.5 m along the row with 4 m between rows, giving an overall density of 1000 stems ha^{-1}. The *E. globulus* trees were planted in April 1998

and the *E. nitens* in August 1998. However, as both species were planted during a period when growth rates are minimal, a reference planting date of July 1998 is used to calculate tree age of both species here. Three months after each planting, dead seedlings were replaced. As well as an at-planting dose of fertiliser, 200 kg ha^{-1} of urea (46% N) and 320 kg ha^{-1} of triple super phosphate (21% P) were aerially applied in May 2001. In early March 2002 (age 3.7 yr) the site was brush-cut to remove an abundance of woody weeds and 100 kg P ha^{-1} was applied as a spot of fertiliser to all trees to ensure trees were not P deficient.

4.2.2 Experimental design and treatments

A split-split plot design was applied over four blocks located along a slope, with Block 1 located at the bottom of the slope through to Block 4 at the top. Each block was split into two equal plots, one of which was planted with *E. globulus* and the other *E. nitens*. Each plot held 9 × 11 trees. Four N-fertiliser treatments were applied within each plot, creating four sub-plots. The treatments were N0 – 0 kg N ha^{-1}, N1 – 100 kg N ha^{-1}, N3 – 300 kg N ha^{-1} and N5 – 500 kg N ha^{-1}. Each sub-plot contained 3 × 4 trees, and was surrounded by a single row of buffer trees (Figure 4.1). Species and fertiliser treatments were allocated randomly.

Within each sub-plot, the six trees having the best growth and form were selected and three were randomly allocated for pruning and three for unpruned controls. The remaining trees in the plot and buffer trees were not pruned. Therefore approximately one in eight trees was pruned in contrast to about one in three in a commercial pruning program. The heights (H) and diameters at breast height (D) of the six selected trees were measured, as well as the height of emergence of the first green branch (H_G), which was used to calculate green crown depth ($C_D = H-H_G$).

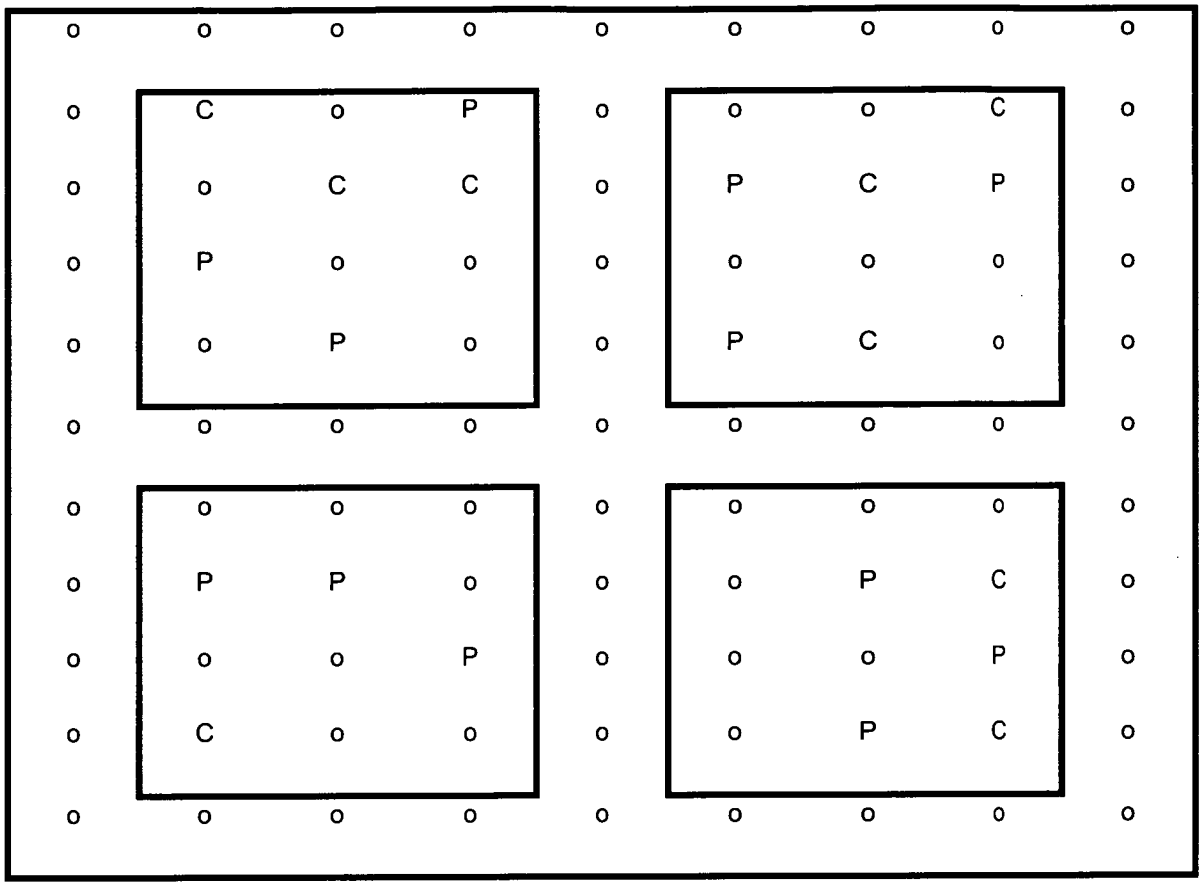


Figure 4.1. Schematic representation of one plot, containing four sub-plots.
'o' represents an unmeasured tree, 'P' a pruned tree and 'C' a measured, unpruned control tree

The fertiliser treatments were manually broadcast over the sub-plots. First-lift pruning was carried out immediately after the fertiliser was applied (late March 2002 at age 3.7 yr) and removed 20% of the green crown depth. Branches were pruned with pruning shears, flush to the trunk but retaining the branch collar, except for very large branches (>25 mm), where a pruning saw was used. Second-lift pruning removed 40% of green crown depth and was carried out 0.8 yr (at age 4.5 yr) after first-lift pruning. In this time the pruned trees had gained between 1.3 and 3.6 m in height.

4.2.3 Soil profile

Soil profiles were examined to a depth of 1.5 m, or to the level of the underlying rock, within each block. Approximately twenty soil samples within each sub-plot were taken from the 0-10 cm layer in the undisturbed inter-row area using a soil auger. Samples were bulked within a sub-plot, air-dried and passed through a 2 mm sieve. The fraction < 2 mm was retained for

analysis. The methods of Rayment and Higginson (1992) were used for pH (4A1), conductivity (EC) (3A1), moisture content (2A1), Colwell P (9B1), organic carbon (C) (6A1), total N and P (digestion – 7A1; colorimetric determination for N using LACHAT Instruments QuikChem 8000 method 13-107-06-2D; and for P using LACHAT Instruments QuikChem 8000 method 10-115-01-1D), ammonium (NH_4) and nitrate (NO_3) (extraction – 7C1; colorimetric determination for NH_4 using LACHAT Instruments QuikChem 8000 method 13-107-06-2D; and for NO_3 using LACHAT Instruments QuikChem 8000 method 12-07-04-F). Calcium (Ca), magnesium (Mg), potassium (K), sodium (Na) were extracted using method 15A1 (Rayment and Higginson 1992), and analysed by atomic absorption spectrometry (Varian SpectrAA-400). Exchangeable (Ex) acidity, hydrogen (H) and Aluminium (Al) followed the methods of Dai and Richter (Dai and Richter 2000). Loss on ignition (LOI) was performed at a temperature of 375 °C.

4.2.4 Biomass distribution

Just prior to the fertiliser application and first-lift pruning, four trees of each species were harvested from the buffer strips to estimate biomass distribution. The range of tree sizes in the measurement plots was divided into quartiles and a tree representative of the size in each quartile was selected for harvest. The trees were felled and their H and D measured. The height of emergence of the first green branch (H_G) was measured and used to calculate green crown depth (C_D). C_D was divided into three height zones which corresponded with the pruning heights to be used in the experiment, 0 – 20% (Zone 1), 20 – 60% (Zone 2) and 60 – 100% (Zone 3) of green crown depth. The diameters of all the branches in each height zone were measured. Five branches representative of the range of branch diameters were selected in each zone. Selected branches were bagged and taken back to the laboratory for leaf area, specific leaf area (SLA) and biomass determination using the methods of Pinkard and Beadle (1998a). Specific leaf area is the ratio of fresh leaf area to dry leaf mass. Relationships between leaf area (L) and branch cross sectional area (A_B) within each height zone were used to estimate the leaf area removed by pruning.

These relationships were developed using the information from the five selected branches, in each of the crown zones. A logarithmic transformation of the power function

$$y = ax^B$$

was used, giving the linear regression equation

$$\ln(L) = \ln(a) + b*\ln(A_B)$$

A nested regression model was applied in S-Plus (Mathsoft Corporation), providing a separate slope estimate for each zone of each tree of each species. ANOVA was used to test for significant differences in slope estimates between zones and species. Where no differences occurred, a single regression was applied to predict the leaf area of the remaining branches, providing an estimate of leaf area removed from first- and second-lift pruning.

4.2.5 Measurements and analysis

Growth measurements

Green crown depth (C_D) was analysed for an effect of species. Heights (H) and D of the six selected trees in each plot were remeasured at ages 4.3, 5.3 and 5.7 yr. An additional measurement of H was made just prior to the second-lift pruning at age 4.5 yr to ensure the calculated pruned heights were correct (H_G at age 4.5 yr was the same as that after first-lift pruning).

Diameter increments between age 3.7 and 4.3 years (DI_1) and 4.3 to 5.7 years (DI_2) were calculated and tested for effect of species, fertiliser and pruning. Height (H) and D measurements were used to calculate individual tree volume (V). A single volume equation (Candy 1997) was used as stem taper is unaffected by pruning (Pinkard and Beadle 1998b). Volume per hectare could not be calculated as only the selected trees were measured. The increments in V (V_I) between each measurement were also calculated for measurements at ages 4.3 ($V_{I,4.3}$), 5.3 ($V_{I,5.3}$) and 5.7 ($V_{I,5.7}$) yr. ANOVA was used to test for main effects and interactions of the three treatments viz species, fertiliser and pruning on the variables V, V_I. Species, fertiliser and pruning effects were compared using the error term associated with blocks, plots and sub-plots respectively.

Branching and defects

Trees were harvested for dissection between April and June 2004 (age 5.7 – 5.9 yr). As levels of decay at the site were low, the harvesting was limited to at least one pruned and one unpruned tree in each replicate of the N0 and N5 treatments.

The pruned part of the stem, or in the case of the unpruned controls the first 5 m of the trunk, was returned to the laboratory. Prior to dissection all branch stubs were numbered and their height above ground-level recorded. The stems were cut into transverse sections containing the branch stubs. Radial longitudinal cuts were then made through the centre of each branch stub using a bandsaw. Recorded variables for each branch stub included branch diameter, excess kino (K), kino-trace defect (K_T), kino vein (K_V), pockets of decay in the branch crotch (P_D), branch with decay infection spreading out of stub (DEC), length of decay (DEC_L), width of decay (DEC_W), branch protective zone breached by decay (BPZ) and occlusion which recorded whether the cambium had sealed over the branch stub or not. Kino-trace defect occurs when a branch stub breaks off and becomes trapped in the bark. As the tree grows, the stub is dragged outward, leaving a kino-filled void in its wake. The data for defects were tested using a chi-squared statistic based on the count data of the defect information and compared between species, fertiliser treatments (N0 and N5) and pruned and unpruned trees. Pruned trees only were compared for DEC, BPZ and occlusion, as there was no decay in the unpruned trees, and as they had not been pruned there was no opportunity for them to occlude. Branch sizes were grouped in classes of 0 - 5, 5 - 10, 10 - 15 and >20 mm to examine branch size distribution.

4.3 Results

4.3.1 Soil

Block 4 had a deeper A2 horizon (30 cm) than the other blocks (10-13 cm). Blocks 2 and 4 were free draining to a greater depth than Blocks 1 and 3 as indicated by mottling in the soil profile. Mottling in Blocks 1 and 3 began at a depth of 0.13 and 0.10 m, respectively, whereas no mottling was encountered in Block 2 until a depth of 1.4 m. Soil chemical properties did not differ significantly within a block (data not shown). In contrast, soil chemical properties showed significant differences between blocks with the exception of EC, and Ex. Acidity, Ex. Al and Ex. H (Table 4.1). Block 4 had significantly higher levels of organic matter (LOI and organic C) and nutrients (Total N, Total P, NH_4, NO_3, Ca, Mg, K and Na.) (Table 4.1).

Table 4.1. Results of soil analyses for each block

Different letters within a row represent means that were significantly different ($p < 0.05$); no letters indicates no significant differences

Soil property	Block			
	1	2	3	4
pH	5.02^{A}	5.10^{B}	5.18^{C}	5.18^{C}
EC (dS/m)	0.051	0.048	0.048	0.056
Moisture content (%)	2.19^{A}	2.15^{A}	2.52^{B}	3.63^{C}
LOI (%)	8.25^{A}	7.63^{A}	8.08^{A}	15.62^{B}
Organic C (%)	4.05^{A}	3.45^{B}	3.23^{B}	6.41^{c}
Total N (%)	0.120^{A}	0.114^{A}	0.119^{A}	0.206^{B}
Total P (%)	0.017^{A}	0.018^{A}	0.022^{B}	0.030^{C}
Colwell P (mg kg^{-1})	22.12	23.90	25.14	17.46
NH_4 (mg kg^{-1})	5.73^{A}	3.77^{B}	3.03^{B}	7.25^{C}
NO_3 (mg kg^{-1})	0.086^{A}	$0.0.67^{AB}$	0.060^{B}	0.203^{C}
Ca (cmol kg^{-1})	0.83^{A}	1.16^{B}	1.37^{B}	2.38^{C}
Mg (cmol kg^{-1})	0.66^{A}	0.89^{B}	1.11^{C}	1.41^{D}
K (cmol kg^{-1})	0.22^{A}	0.23^{AB}	0.26^{B}	0.33^{C}
Na (cmol kg^{-1})	0.17^{A}	0.16^{A}	0.17^{A}	0.26^{B}
Ex. Acidity (cmol kg^{-1})	3.83	3.36	3.78	2.46
Ex. H (cmol kg^{-1})	0.12	0.10	0.14	0.14
Ex. Al (cmol kg^{-1})	3.71	3.26	3.64	2.32

4.3.2 Biomass distribution

Branch size varied between the species with *E. nitens* having a significantly higher average branch diameter, but lower branch numbers, in zones 1 and 2 than *E. globulus* (Figure 4.2 (a,b)). Branch size and abundance was similar between the species in zone 3 (Figure 4.2 (a, b)).

In both species larger leaf area was associated with larger tree volume (V) (Figure 4.3). *Eucalyptus nitens* tended to have a larger total leaf area in each zone, but this difference was not significant (Figure 4.4a). The proportion of total leaf area in each zone was consistent between the species (Figure 4.4b). In both species, zones 1 and 2 carried just over 20% and 60%, respectively, of the total leaf area (Figure 4.4b). Pruning 60% of the green crown depth would then have removed a total of approximately 80% of total leaf area if the two lifts had been done together at first-lift pruning, but was less than this because of incremental growth between the two pruning lifts.

Specific leaf area (SLA) was significantly different between species, but not between zones (Figure 4.4c). The higher SLA was observed in *E. nitens*.

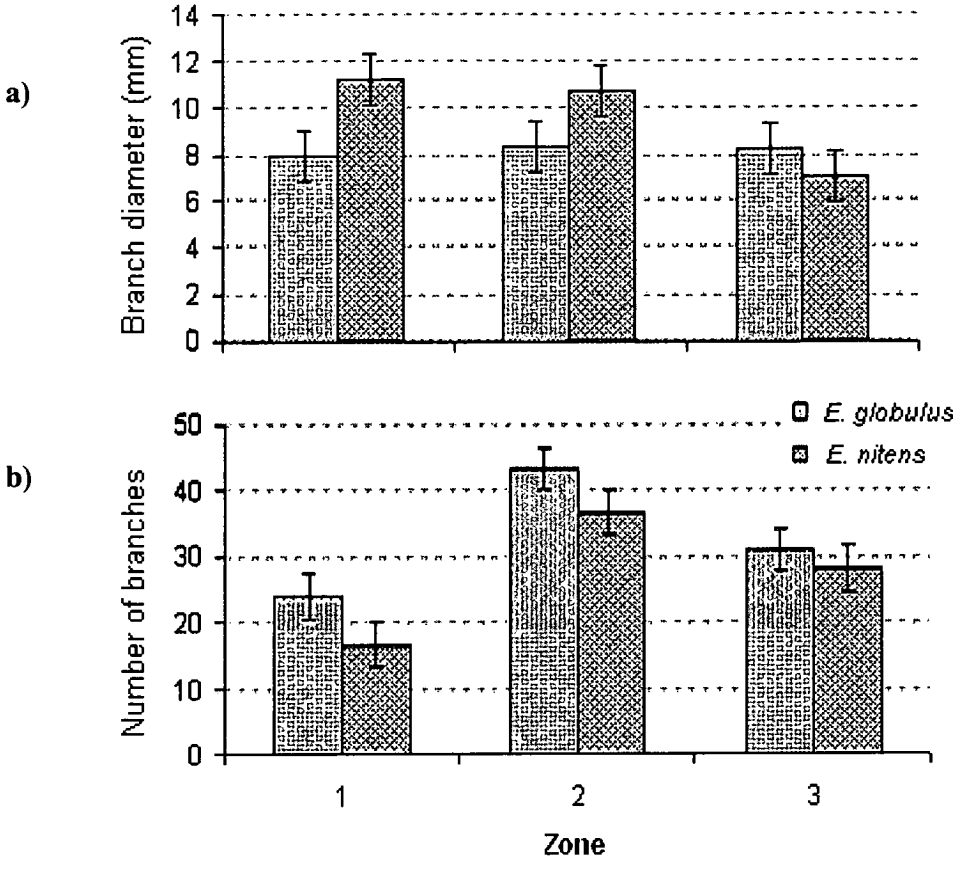


Figure 4.2. Average branch diameter
(a) and number of branches (b) compared between *E. globulus* and *E. nitens* for each zone
(1 = 0-20%, 2 = 20-60%, 3 = 60-100% of C_D), at age 3.7 years, just before first-lift pruning. Bars = S.E.

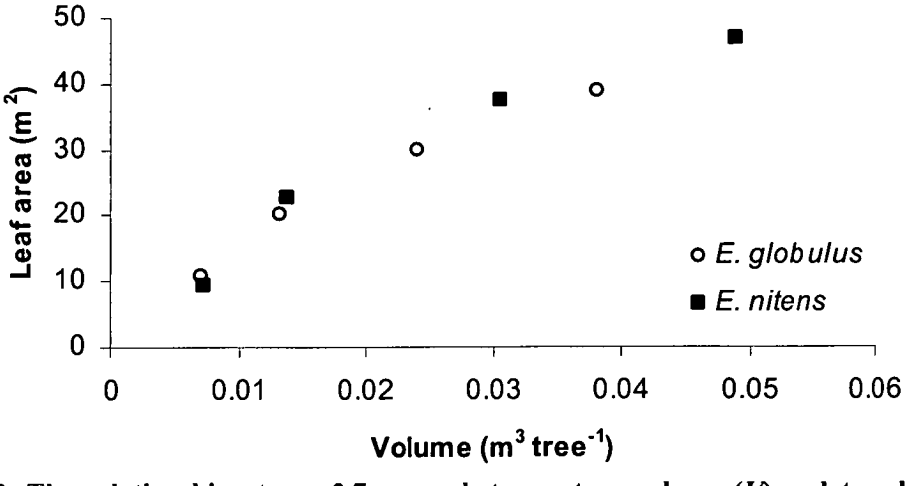


Figure 4.3. The relationship at age 3.7 years, between tree volume (V) and tree leaf area in *E. globulus* and *E. nitens*

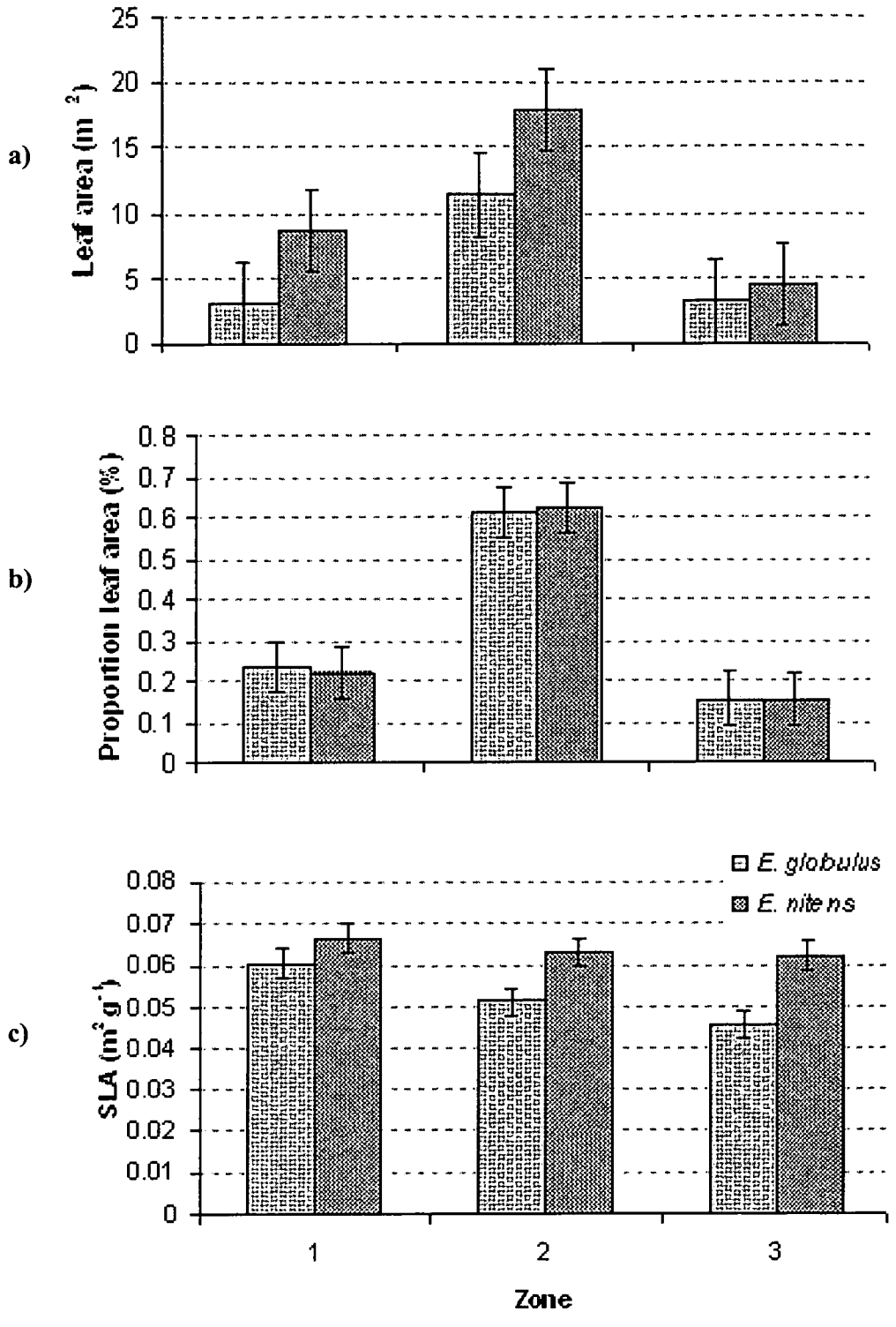


Figure 4.4. Average total leaf area
(a) proportion of total leaf area (b) and specific leaf area, SLA (c) in each zone
(1 = 0-20%, 2 = 20-60%, 3 = 60-100% of C_D), at age 3.7 years, just before first-lift pruning. Bars = S.E.

4.3.3 Growth

At age 3.7 yr, just prior to first-lift pruning and fertiliser application, *E. nitens* had significantly lower C_D (93% of *H)* than *E. globulus* (96% of *H*) (Table 4.2).

Both DI_1 and DI_2 significantly increased with increasing fertiliser N application (Figure 4.5, Table 4.2). Pruning also had a significant effect on DI_2 (Table 4.2), with unpruned trees having a greater increase in *D* than pruned trees. However the effect was not as large as that of applying fertiliser N (Figure 4.5).

Eucalyptus nitens had superior *V* to *E. globulus* at age 3.7 years, and maintained significantly greater *V* over the course of the experiment (Table 4.2, Figure 4.6). $V_{I,4.3}$ was not affected by the first-lift pruning, but did show a significant species and fertiliser effect (Table 4.2).

A reduction in *V* became evident 0.8 yr after second-lift pruning, at age 5.3 yr (Table 4.2) and this removal of a further 40% of C_D reduced growth in both species (Figure 4.6) with one exception: *V* of *E. globulus* in the N5 treatment was not significantly different from that of unpruned trees. Species, fertiliser and pruning effects were apparent on *V* until the final measurement at age 5.7 yr. There was a significant interaction between species and fertiliser on $V_{I,5.3}$, *E. nitens* having a greater response to the addition of fertiliser N during this period than *E. globulus*.

The effect of each of the factors on mean tree volume at the end of the experiment is summarised in Figure 4.7. Block had the smallest effect and only Blocks 3 and 4 were significantly different. Pruning reduced tree volume by an average of 0.01 m^3 $tree^{-1}$. The volume of *E. nitens* was on average 0.016 m^3 $tree^{-1}$ larger than that of *E. globulus*. The most significant effect on tree volume was through the addition of fertiliser N. Mean tree volume was increased by approximately 0.01 m^3 $tree^{-1}$ with the addition of 100 kg N ha^{-1} and 0.02 m^3 $tree^{-1}$ with the addition of 300 kg N ha^{-1} compared to the unfertilised control. Applying 500 kg N ha^{-1} did not significantly increase tree volume over the application of 300 kg N ha^{-1}.

Table 4.2. ANOVA results for crown depth (C_D), mean diameter increment (DI), tree volume (V), and tree-volume increment (V_I). Only significant interactions are shown.

Source of Variation	C_D	DI_1	DI_2	V (age 3.7 yr)	V (age 4.3 yr)	V (age 5.3 yr)	V (age 5.7 yr)
Species	0.001	N.S.	N.S.	0.01	0.01	0.05	0.05
Fertiliser		0.01	0.001		N.S.	0.01	0.001
Pruning		N.S.	0.001		N.S.	0.05	0.01
					$V_{I,4.3}$	$V_{I5.3}$	$V_{I5.7}$
Species					0.05	N.S.	0.001
Fertiliser					0.01	0.001	0.001
Species x Fertiliser					N.S.	0.05	N.S.
Pruning					N.S.	0.001	0.001

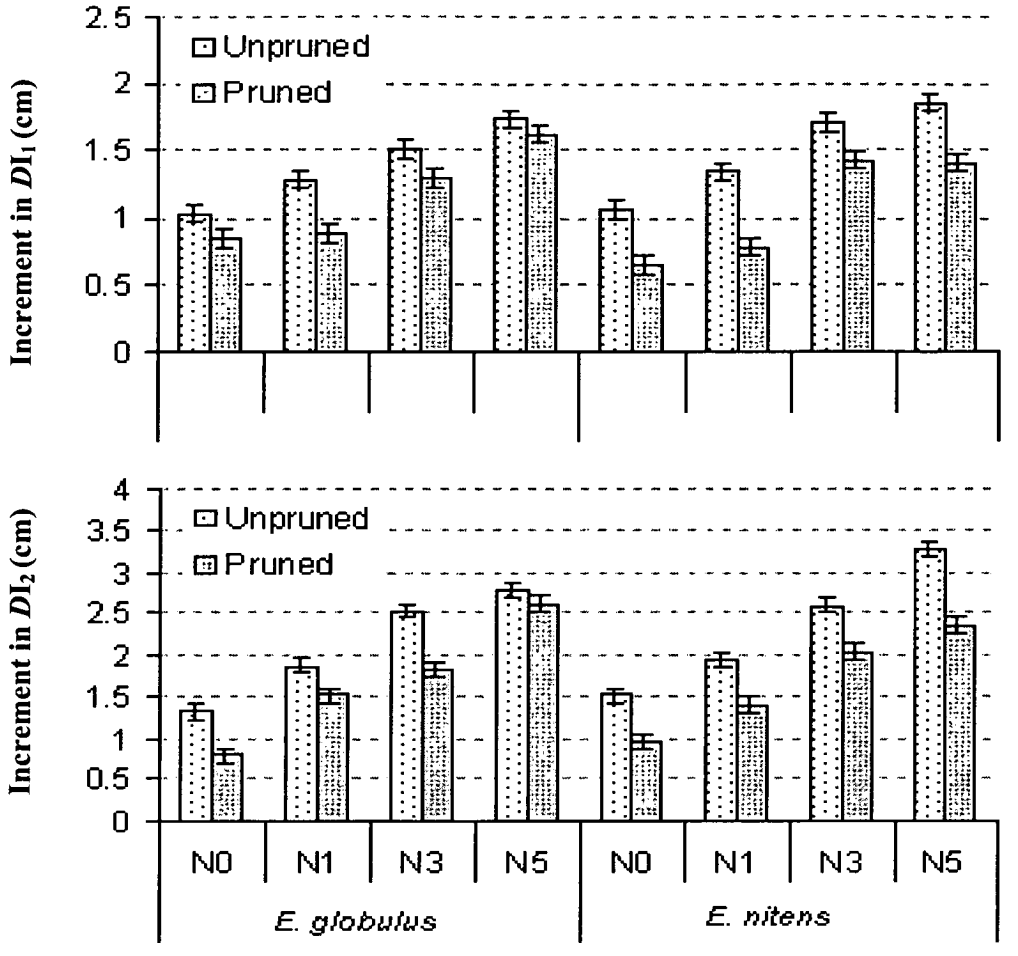


Figure 4.5. Increment in diameter between age 3.7 – 4.3 years (DI_1) and between 4.3 - 5.7 years (DI_2)

4.3.4 Defects and Decay

There were no differences in the incidence of kino (K), kino vein (K_V), or kino-trace defect (K_t) between the treatments (Table 4.3). There was no decay in any of the unpruned trees and only a small proportion (~ 1%) of pruned branches had decay infections. The incidence of decay, BPZ, and occlusion was not evenly distributed between species and treatments. The incidence of decay and BPZ was greatest in *E. nitens* receiving the N5 treatment. The most pronounced difference was the number of occluded branches in the N5 treatment of both species compared with the N0 treatment (Table 4.3).

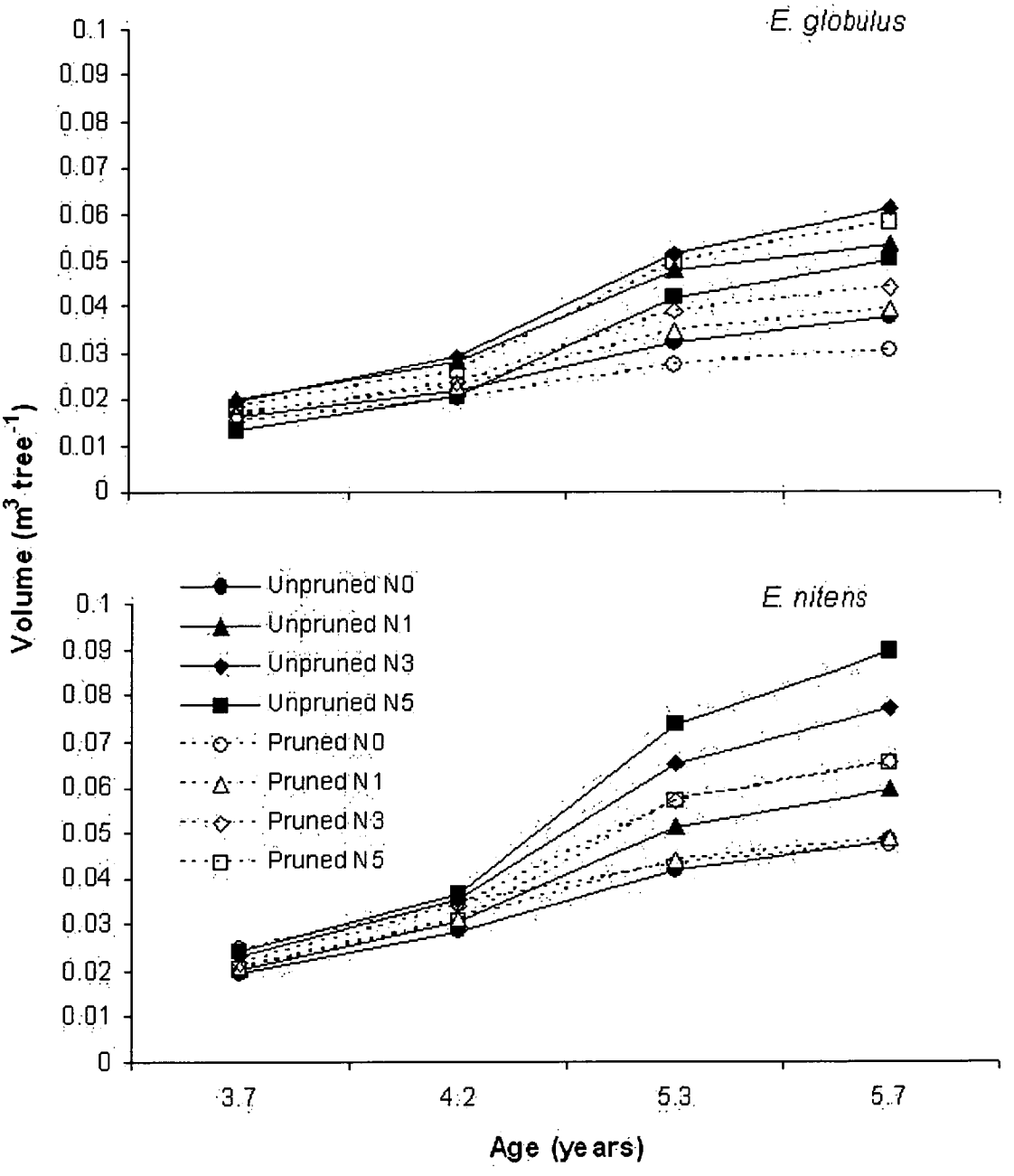


Figure 4.6. Tree volume from age 3.7 to 5.7 years
Fertiliser treatments were applied at age 3.7 yr when first-lift pruning removed 20% of C_D
Second-lift pruning removed a further 40% of C_D at age 4.7 years
N0 = 0 kg N ha^{-1}, N1 = 100 kg N ha^{-1}, N3 = 300 kg N ha^{-1}, N5 = 500 kg N ha^{-1}

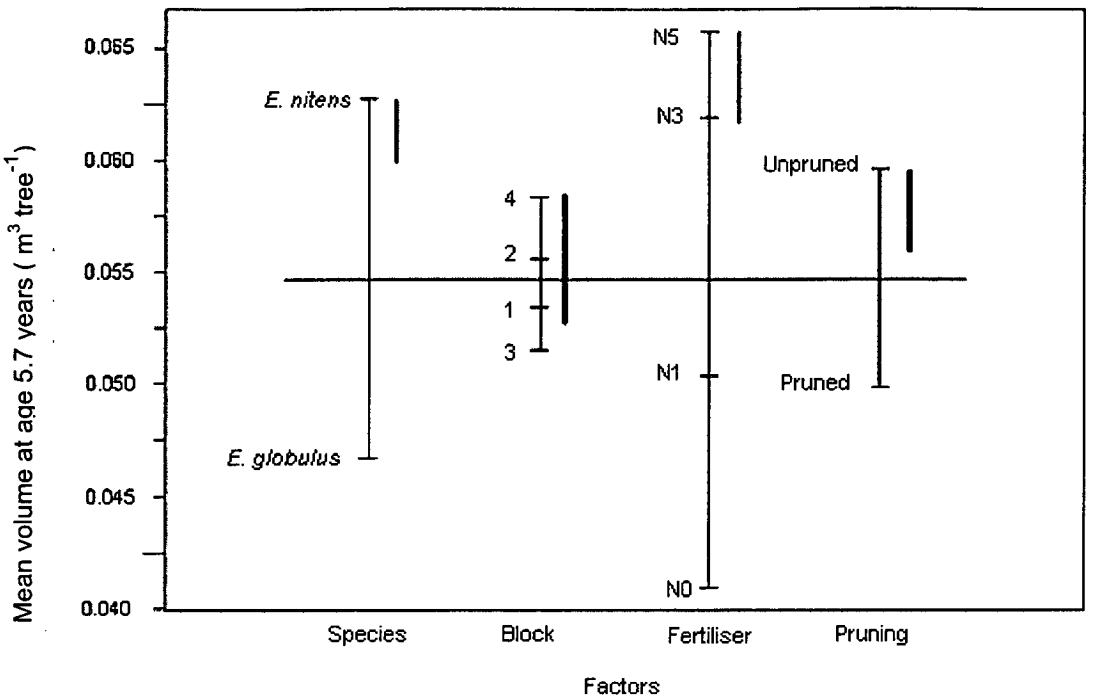


Figure 4.7. Effects of species, block, fertiliser and pruning on mean tree volume (m^3 $tree^{-1}$) at age 5.7 years. The horizontal line represents mean tree volume over the whole experimental site at ag 5.7 years. The vertical lines represent the variation around mean tree volume that can be attributed to each of the factors.
Dark bars represent standard errors

Table 4.3. Incidence of defect and decay in the harvested trees (n = 2125 branches)

Species	*E. globulus*				*E. nitens*				Total	χ^2
Pruned	No		Yes		No		Yes			
Fertiliser	N0	N5	N0	N5	N0	N5	N0	N5		
Excess kino, K	4	1	11	26	6	8	4	20	80	N.S.
Kino vein, K_V	0	2	9	19	0	0	3	0	33	N.S.
Kino trace, K_T	1	1	0	4	5	1	5	4	21	N.S.
Pocket decay, P_D	0	0	0	3	4	11	10	29	57	N.S.
BPZ*	-	-	31	21	-	-	26	55	133	0.000
Occlusion*	-	-	103	285	-	-	70	546	719	0.000
Decay, DEC	0	0	11	8	0	0	13	22	54	0.013
Decay width, DEC_W (mm)	-	-	15	5	-	-	7	10		
Decay length, DEC_L (mm)	-	-	87	45	-	-	76	29		

* Results for pruned trees only, n = 1541 branches. Decay width and length presented as averages for species and treatments

4.3.5 Branch size distribution at harvest

Branch size data collected from unpruned trees that received level N5 fertilizer at the time of harvest (age 5.7 years) showed *E. globulus* had a higher proportion of branches in the 0-5 mm

size class than did *E. nitens* (Figure 4.8). In the pruned trees, branches in the larger size classes (15-20 and > 20 mm) were rare in *E. globulus*, but common in *E. nitens*, especially in the second-lift pruning (Figure 4.8).

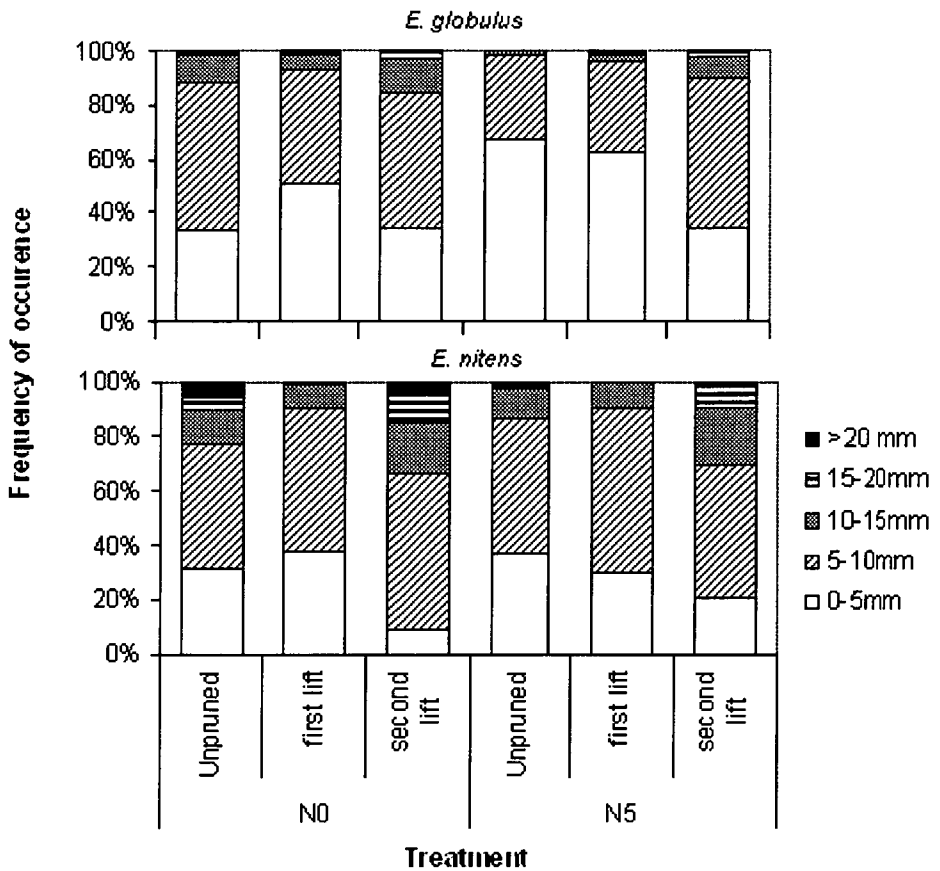


Figure 4.8. Branch size distribution in unpruned trees at age 5.7 years, and the size distribution of branches removed in first and second lift pruning.

4.4 Discussion

This study has shown that there are small but nevertheless significant differences in the growth patterns and response to pruning and fertiliser application of the two major eucalypt species, *E. globulus* and *E. nitens*, grown for wood production in southern Australia. Variation among blocks was observed but this could be explained by the examination of the soil profiles and soil chemical analyses undertaken at the commencement of the experiment. Block 4, located at the top of the slope, supported trees of the highest volume followed by Block 2, Block 1 and Block 3. The basis for this may be that Blocks 4 and 2 were free-draining to a greater depth than Blocks 1 and 3 as well as having greater amounts of ammonium and nitrate.

The major structural difference between the species was in branch size and numbers. *E. globulus* had smaller though more branches throughout most of the crown than *E. nitens*. This is a favourable trait if trees are to be managed for solid-wood production since large diameter branches have a higher incidence of decay infections than small diameter branches following pruning (Glass, McKenzie *et al.* 1989; Marks, Incoll *et al.* 1986; Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999; Wiseman, Smethurst *et al.* 2006). Differences in branch size between the species can also explain the higher incidence of decay in *E. nitens* than *E. globulus*.

As expected tree leaf area was related to tree volume for both species. The proportion of total leaf area invested in each zone was similar for both *E. nitens* and *E. globulus*. However E. nitens had on average greater total leaf area than E. globulus despite having a shorter crown. As tree leaf area expressed as leaf area index (LAI) is related to biomass production, this goes some way to explaining the higher productivity of *E. nitens* in this trial (Smethurst, Baillie *et al.* 2003). *E. nitens* was found to have fewer, larger diameter branches in comparison to *E. globulus* which had more and smaller branches. As there is a linear relationship between branch cross sectional area and branch length (Medhurst, 2000), the crown width of *E. nitens* would have been greater than that of *E. globulus*, giving them a greater area of light interception and this may have powered their productivity.

Eucalyptus nitens also had significantly greater specific leaf area (SLA) than *E. globulus*. Species with higher SLA are associated with a greater incremental change in net photosynthetic capacity (A_{MAX}) per unit variation in N (Reich, Ellsworth *et al.* 1998). This observation is supported by the significant interaction for species and fertiliser for $V_{1,5.3}$ which showed that *E. nitens* exhibited a greater increase in volume to applied N than *E. globulus*.

The amount of leaf area which can be removed during pruning from *E. globulus* or *E. nitens* without reducing the rate of growth will depend on the time of pruning (pre- or post-canopy closure) (Pinkard 2002b) and the productivity of the site (Pinkard 2003). The onset of canopy lift at the start of this experiment was evidence that canopy closure had taken place. The pruning treatment was severe, first removing 20%, and then eight months later an additional 40% of C_D, equivalent to 80% of leaf area present at first-lift pruning. This substantial loss of leaf area over a short period of time reduced the volume of the pruned trees compared to the unpruned trees in both species, with the exception of the pruned *E. globulus* in the N5

treatment. However, the pruned trees were still able to respond positively to fertiliser addition and in the N3 and N5 treatments they had higher volumes than the unpruned N0 trees for both species. Pinkard, Baillie *et al.* (2006b) have also shown that the application of N or N+P ameliorated the effect of a simulated defoliation in south-east Tasmania.

The impact of the second-lift pruning on growth may have been exaggerated, as the ratio of pruned to un-pruned trees was lower in the experiment (1:8) than in commercial plantations (1:3), potentially providing increased competition with surrounding unpruned trees. A negative correlation between pruning severity and growth has been found for a number of species (Alcorn, Bauhus *et al.* 2008; Chandrashekara 2007; Nielsen and Pinkard 2003). The impact occurs when too severe a pruning results in the pruned trees becoming subdominant to surrounding unpruned trees. However there was no evidence of such an effect during the course of the experiment.

While volume growth is important in terms of productivity, diameter increment is directly related to branch occlusion and clear wood production (Chiu, Lo-Cho *et al.* 2002; Petruncio, Briggs *et al.* 1997; Solomon and Blum 1976; Wiseman, Smethurst *et al.*), and is important for solid-wood production. Fertiliser had a significant effect on diameter growth between age 3.7 yr and 4.3 yr (DI_1). The first-lift pruning removed 20% of C_D, equivalent to removing 20% of leaf area and this did not affect diameter growth. The second-lift pruning which removed a further 40% of C_D (60% of leaf area at first-lift pruning) reduced diameter growth between age 4.3 and 5.7 yr (DI_2) in both species and in most of the fertiliser treatments. However, DI_2 in the pruned trees in the high N treatments (300 kg N ha^{-1} and 500 kg N ha^{-1}) was still significantly greater than that of unpruned trees in the low N treatments (0 kg N ha^{-1} and 100 kg N ha^{-1}). This is similar to findings by Pinkard, Baillie *et al.* (2006b), where fertilised defoliated trees had greater stem diameter than unfertilised controls. However analysis of variance showed there was no interaction between pruning and fertiliser application, indicating that during the course of the experiment the response to the application of fertiliser was independent of pruning.

The addition of fertiliser had a significant impact on branch occlusion following pruning. Rapid branch occlusion may help prevent the entry of decay-causing fungi (Metzler 1997) and promotes the onset of clear-wood production. The level of decay in the pruned stubs was very low, despite the pruning of large living branches which are usually predisposed to decay

entry (Mohammed, Barry *et al.* 2000a; Wardlaw and Neilsen 1999; Wiseman, Smethurst *et al.* 2006). This may have been due to the relatively warm, dry conditions at the time of the second-lift pruning, or indicate that this area is low risk for wood decay. Interestingly, the results suggested that *E. globulus* was less prone to decay entry than *E. nitens* under these conditions, a factor that may also be related to its smaller branches.

Although *E. nitens* had superior tree volume growth to *E. globulus* at this site and was better able to convert the applied N fertiliser into wood volume during an extended period of growth there was no evidence that either species responded differently to the loss of leaf area from pruning and require species specific pruning regimes. The response to the application of fertiliser N was similar for both species. It improved growth in both the pruned and unpruned trees, but there was no difference in the response to N between the pruning treatments. Branch occlusion was significantly better in trees which received 500 kg N ha^{-1} than trees which had no N applied. No decay was found in the unpruned trees. *E. globulus* had a lower incidence of decay infections in pruned stubs than *E. nitens*, and this can be explained by *E. globulus* having smaller branches at this site, not necessarily by a greater genetically based resistance to decay.

As a proportion of the trees in this study were harvested for examination of defects and decay at the end of the experiment, it was not possible to compare how trees in the control treatment recovered from pruning compared to the trees that had received fertiliser N. Tracking the growth of pruned and unpruned trees subject to a range of N fertiliser treatments over a rotation would provide useful information on the long term effects of both pruning and the addition of fertiliser N.

Pruning living branches produces tight knots and promotes clean, rapid occlusion. The drawback to green pruning is the risk of significantly reducing the rate of tree growth through the removal of leaf area. This study has shown that in some conditions it is possible to compensate for the loss in leaf area by the addition of fertiliser N just prior to pruning. While removal of leaf area did impact negatively on growth, the improvements attainable by the addition of fertiliser N can mitigate this loss. However the indication from this trial was that the ability of added N to assist trees to re-establish lost leaf area following green pruning was likely to be limited by water availability on lower rainfall sites. This is supported by the work of Eyles, Pinkard *et al.* (2009a) who demonstrated that recovery from defoliation was not

limited by either nutrient or water availability in isolation, but was limited if both nutrition and water availability were constrained.

CHAPTER FIVE

Effects of pruning and fertiliser on gas exchange, leaf area distribution and leaf chemistry

Abstract

Trees can respond to the loss of leaf area through green pruning by increasing photosynthetic rates and changing patterns of biomass distribution. In order to examine the response to defoliation and how this may be affected by N supply plantation grown *E. globulus* trees were subjected to the removal of 60 % leaf area and the application of 500 kg nitrogen ha^{-1}. Control treatments were undefoliated and unfertilized. Measures of photosynthetic response to CO_2 concentrations were used to construct carbon assimilation (A) to intercellular CO_2 concentration curves. The period following defoliation was abnormally dry and trees were subject to water limitation. We found that there was no increase in photosynthetic rate, or the activity of photosynthetic enzymes in response to defoliation in the unfertilised treatment. In the fertilised treatment pruned trees exhibited higher rates of photosynthesis, photosynthetic enzyme activity and stomatal conductance in comparison to unpruned trees. Pruning did not suppress growth in the fertilised treatment and pruned trees had higher leaf area than unpruned trees in the N0 treatment within 11 months of pruning. The stimulatory effect of N on leaf area was important in aiding recovery from defoliation. Leaf chlorophyll concentrations declined in both the fertilized and unfertilised treatments in response to pruning, but there was little response in leaf concentrations of N, P or chlorophyll to the application of nitrogen. It is hypothesised that resource limitation influenced the response to pruning defoliation. Where both water and N were limiting trees were unable to respond to defoliation by up-regulating photosynthetic activity.

5.1 Introduction

The production of quality timber from temperate eucalypt plantations can only be achieved by green pruning. Recovery of appearance grade wood is dramatically reduced in unpruned stands in comparison to pruned stands (Moore, Siemon *et al.* 1996; Washusen and Reid 1996) and retained dead branches are associated with decay (Mohammed, Barry *et al.* 2000b). In addition, loose knots and kino-trace defect result if dead branches are pruned (Washusen, Waugh *et al.* 1998; Washusen, Waugh *et al.* 2000; Yang and Waugh 1996). This necessitates scheduling pruning operations to precede green crown rise, whereby lower branches senesce and the height of the green crown (the lowermost living branches) increases.

Green pruning (the removal of living branches) is a defoliation event and as such has the potential to reduce tree growth (Bredenkamp, Malan *et al.* 1980; Pinkard 2002a). The amount

of growth potential for a tree is related to its leaf area (Smethurst, Baillie *et al.* 2003). Therefore removal of leaf area, either through herbivory, disease or pruning has the potential to suppress growth. However trees, like many plant species have evolved mechanisms to compensate for lost leaf area and are able to respond in a number of ways. These include channeling resources into replacing lost leaf area, increased rates of carbon assimilation in remaining leaves and retaining existing leaves longer. The value of a pruned stem increases in proportion to its diameter, so optimizing growth in pruned stems within a plantation is of great importance to plantation managers. In addition it is desirable to maintain growth rates in pruned stems so that they are not out competed by surrounding unpruned stems. For these reasons an understanding of the effects of green pruning on growth and a trees inherent ability to compensate for lost leaf area can inform management options for mitigating growth suppression.

Plantation grown eucalypts, particularly on ex-forest sites exhibit a positive growth response to the application of fertilizer nitrogen (N) (Bennett, Weston *et al.* 1997; Moroni, Smethurst *et al.* 2002; Smethurst, Holz *et al.* 2004). Nitrogen is a requirement for the production of leaf area and is a major component of photosynthetic compounds, such as ribulose 1•5-biphosphate carboxylase/oxygenase (rubisco) and chlorophyll in leaves. Applying fertilizer N just preceding pruning may promote recovery by stimulating the production of leaf area and improving photosynthetic efficiency thus creating a synergy with the trees inherent response to defoliation, i.e. supplying the resources needed to replace lost leaf area and increasing photosynthetic efficiency. Pinkard, Battaglia *et al.* (2007) found that applying N fertilizer either pre or post-defoliation (to simulate insect defoliation) increased rates of crown recovery and reduced the impact on tree growth.

The relationship between carbon assimilation rate (A) and intercellular CO_2 concentration (C_I) (A/C_I) can assist in determining the mechanisms behind photosynthetic up-regulation following defoliation. By fitting the curve of the response in A to changing levels of C_I, allows the estimation of parameters which describe the underlying biology of factors affecting changes in A (Caemmerer and Farquhar 1984). Two factors influence the rate of assimilation. One is the activity of photosynthetic enzymes (especially ribulose biphosphate carboxylase (RUBISCO) and the enzymes which limit the regeneration of the ribulose biphosphate acceptor in the carbon reduction cycle. The second is the rate of supply of CO_2 to

the reaction sites which is determined by the concentration of CO_2 in the air bathing the mesophyll cells (C_i).

A trial was established and determined that the application of fertilizer N mitigates growth suppression due to green pruning; the results from the larger trial (Chapter 4) showed pruned trees in the N0 treatment were significantly smaller than unpruned trees. Both pruned and unpruned trees in the N5 treatment were significantly larger than N0 trees and there was no difference in volume between pruned and unpruned trees in the N5 treatment. In this trial the physiological processes behind both the response to pruning and the response to N are explored by testing the following hypotheses;

1. Increased N supply will offset the effects of defoliation due to green pruning by stimulating leaf area production.
2. The physiological response to increased N supply is related to increased leaf N or chlorophyll content.
3. Increased N supply will magnify the expected up-regulation of photosynthesis in response to defoliation, in terms of A, g_s, V_{MAX} or J.

5.2 Methods

5.2.1 Site description

The site was located in the Esperance valley, in South-East Tasmania (43°17.110'S, 146°52.276'). The climate is characterised by warm to hot, dry summers and cool, wet winters (Figure 5.1). The summer marking the start of the experiment was one of the driest on record with rainfall for the summer 7.5 mm in contrast to the long term average of 183 mm. Site description and site preparation are as detailed are detailed in Chapter 4.

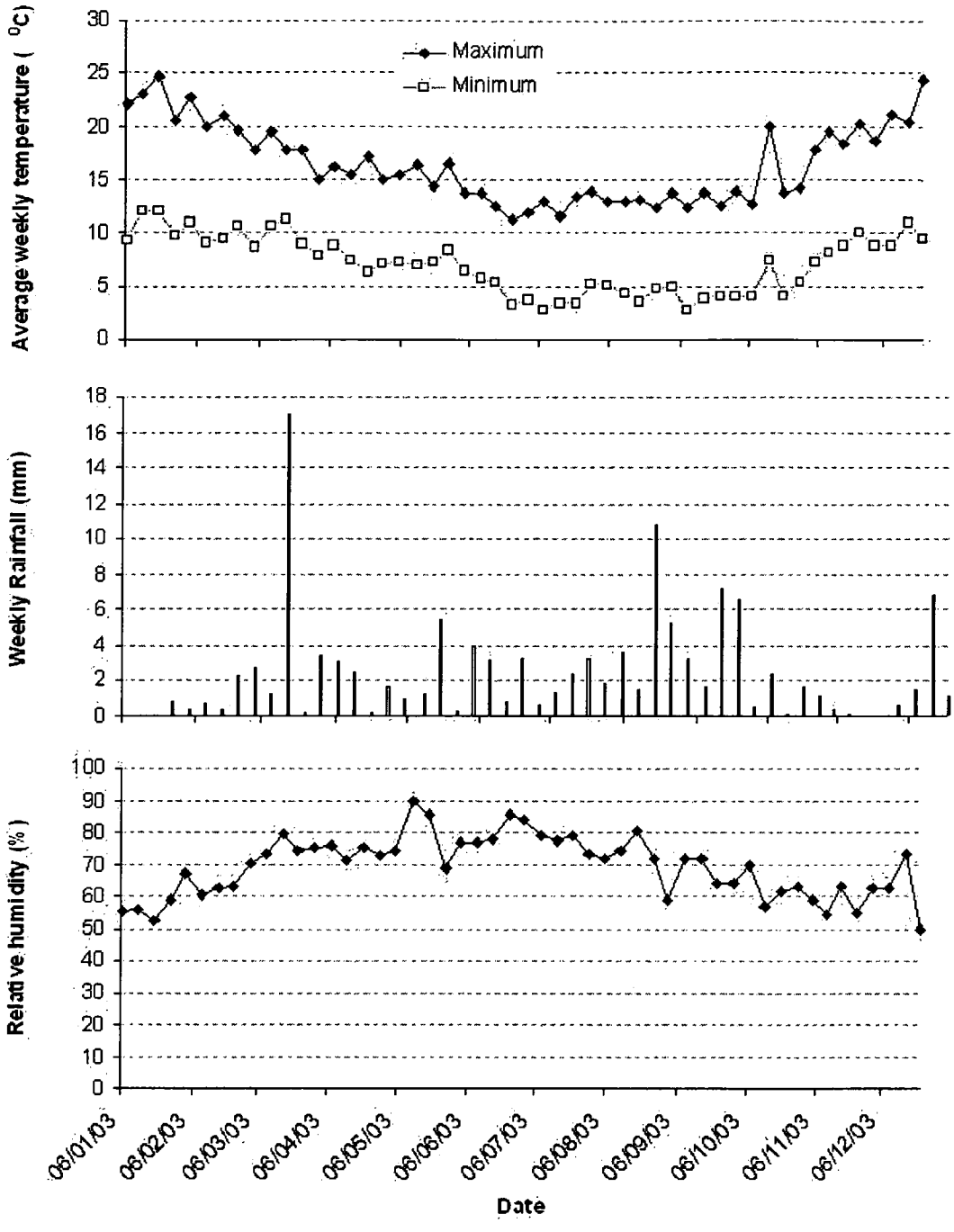


Figure 5.1. Weekly climate statistics for the experimental period for the closest weather station (Dover, Tasmania)

5.2.2 Design

This experiment formed part of a larger trial carried out for this thesis and additional detail and description of the larger trial is available in Chapter 4. In this particular trial, a split-split plot design was applied over four blocks located along a slope, with Block 1 located at the

bottom and Block 4 at the top of the slope. Each block was split into two equal plots, one of which was planted with *E. globulus* and the other *E. nitens*. The experiment described here was located in Block 4 and was concerned only with *E. globulus*. Two fertiliser nitrogen treatments were applied within the trial area. The treatments were N0 – 0 kg, N $ha^{-1}$and N5 – 500 kg N ha^{-1}. Each sub-plot contained three x four trees, and was surrounded by a single row of buffer trees.

Within each sub-plot, the six trees having the best growth and form were selected and three were randomly allocated for pruning and three for unpruned controls. The heights (H) and diameters at breast height (D) of the six selected trees were measured, as well as the height of emergence of the first green branch (H_G), which was used to calculate green crown depth ($C_D = H-H_G$).

The fertiliser treatments were manually broadcast over the sub-plots in late March 2002 at age 3.7 yr. First-lift pruning was carried out immediately after the fertiliser was applied and removed 20% of the green crown depth. Branches were pruned with pruning shears, flush to the trunk but retaining the branch collar, except for very large branches (>25 mm), where a pruning saw was used. Second-lift pruning current of green crown depth and was carried out 0.8 yr (at age 4.57 yr) after first-lift pruning. In this time the pruned trees had gained between 1.3 and 3.6 m in height.

5.2.3 Leaf area distribution

Just prior to the fertiliser application and first-lift pruning, four trees were harvested from the buffer strips to estimate leaf area distribution. The range of tree sizes in the measurement plots was divided into quartiles and a representative tree of the mean size in each quartile was selected for harvest. The trees were felled and their H and D measured. The height of emergence of the first green branch (H_G) was measured and used to calculate green crown depth (C_D). The C_D was divided into three height zones which corresponded with the pruning heights to be used in the experiment viz 0 – 20% (Zone 1), 20 – 60% (Zone 2) and 60 – 100% (Zone 3) of C_D. The diameters of all the branches at 150 mm from their base in each height zone were measured. Five branches representative of the range of branch diameters were selected in each zone. Selected branches were bagged and taken back to the laboratory for leaf area and specific leaf area (SLA) determination using the methods of Pinkard and Beadle (1998a). Specific leaf area is the ratio of fresh leaf area to dry leaf mass.

Relationships between leaf area (L) and branch cross sectional area (A_B) within each height zone were used to estimate the leaf area removed by pruning. This process was repeated at the end of the experiment at age 5.8 yr, selecting unpruned trees within the N0 and pruned and unpruned trees within the N5 treatment. These relationships were developed using the information from the five selected branches in each of the crown zones. A logarithmic transformation of the power function

$$y = ax^b$$

was used, giving the linear regression equation

$$\ln(L) = \ln(a) + b*\ln(A_B)$$

A nested regression model was applied in S-plus, providing a separate slope estimate for each zone of each tree. ANOVA was used to test for significant differences in slope estimates between zones and species. Where no differences occurred, a single regression was applied to predict the leaf area of the remaining branches, providing an estimate of leaf area removed from first- and second-lift pruning.

5.2.4 Physiology

The physiological response of trees to the addition of fertiliser N and pruning was assessed. Trees from each of the four treatments were selected; pruned trees in N0, unpruned trees in N0, pruned trees in N5 and unpruned trees in N5. Measurements were taken in the upper canopy. Access was via scaffolding towers, which could be raised as the trees grew.

Measures of CO_2 assimilation rates (A) over a range of external carbon dioxide (CO_2) levels were taken to construct A/C_I response curves; C_I is the intercellular CO_2 concentration. This was done to provide a means of separating the effects of pruning and N supply on photosynthetic behaviour. The system used was a Li-Cor 6400 portable photosynthesis system, fitted with a 6400-01 CO_2 mixer and 2x3 cm leaf chamber. The block temperature was set at 18°C, the incident level of photosynthetically active radiation (PAR) to 1500 μmol and the flow rate to 400 ml min^{-1}. The external CO_2 levels used were in the following sequence; 700, 600, 450, 360 (close to ambient), 250, 150, 0 and finally 360 mmol of CO_2 per mole of air.

Each measurement period was at least two days, with measurements taken over nine periods between January 2003 (tree age 4.56 years) and December, 2003 (tree age 5.5 years) (Table 5.1). For each period, the order in which the towers/treatments were measured was chosen randomly as was the tree and leaf order of measurements within each treatment. Three trees were measured within each pruning treatment. As there were two pruning treatments within each of the two fertiliser treatments, there were a total of 12 measurement trees. Within each tree three leaves were measured, all in the upper canopy. Where possible, the first fully expanded leaf of the current year's growth was used. However during winter and spring leaves of this age were not always available and the most suitable alternative was used.

A/C_I curves were parameterised using the model of Sharkey, Bernacchi *et al.* (2007). The parameters fitted by the model were V_{MAX} (maximum carboxylation rate allowed by ribulose 1•5•biphosphate carboxylase/oxygenase, RUBISCO), J (rate of photosynthetic electron transport (based on NADPH requirement)), TPU (triose phosphate use), R_D (day respiration) g_m (mesophyll conductance). The data used in the model were the data collected for each leaf measured for each tree at the eight levels of external CO_2. Parameters were generated for each leaf on each measurement tree and then averaged to give a value for each measurement tree. Limits were set according to the specifications of the model, ie, points below 200 ppm were Rubisco limited, above 300 ppm were RuBP-regeneration limited and the last point TPU limited. The exceptions were when the uppermost point of the curve showed no sign of levelling out, and then the final point was set as RuBP-regeneration limited.

The maximum rate of photosynthesis at the ambient (360 mmol/mol of air) level of CO_2 (A_{360}) and g_s were analysed by averaging the two measurements of A/leaf over the three leaves.

Results for A, V_{CMAX} and J were analysed using a nested, random effects ANOVA model in Splus:

$$x = period(n = 45) + fertiliserin(period)(n = 6) + pruningin(fertiliserin(period))(n = 3)$$

Where x = A, x = g_s, x = V_{CMAX}

Leaves were collected at the end of each measurement period for total chlorophyll, N and P analysis and stored on ice during transport after which they were kept at –20°C. A single disc was removed from each leaf and its chlorophyll concentration determined using the US EPA method SOP#:2030.

Leaf area was measured using a leaf area meter and corrected for the missing disc. Leaves were then dried at 60°C after which they were finely ground in a mortar and pestle.

Dried and ground leaf material was used for Trichloroacetic acid (TCA) extraction for N and P determination. 0.4 g of dried material was placed in a centrifuge tube for cold then hot extraction with 3M and 1.5M TCA, respectively. Extracts were then digested in sulphuric acid following the standard method for plant extracts (Lowther 1980). N and P in extracts were analysed on a Lachat FIA using the methods specified in Lachat Quickchem 8000 method 13-107-06-2D and 10-115-01-1D, respectively.

As for the physiological measurements, the results from the three leaves sampled were averaged and the results analysed using the same ANOVA model. For clarity, a summary of time of measurement and parameter measured is provided (Table 5.1).

Table 5.1. Summary of the measurement schedule for the experiment

Measurement Period	1	2	3	4	5	6	7	8	9
Date	10 Jan	3 Feb	19 Feb	24 Mar	13 May	25 Jun	20 Aug	12 Nov	15 Dec
Season	Summer			Autumn		Winter		Spring	Summer
Tree Age (yr)	4.56	4.62	4.67	4.76	4.90	5.02	5.17	5.41	5.50
Time since pruning (yr)	-0.1	0.05	0.1	0.19	0.33	0.45	0.6	0.84	0.93
				Measurements					
A	✓	✓	✓	✓	✓	✓	✓	✓	✓
g_s	✓	✓	✓	✓	✓	✓	✓	✓	✓
A/C_I	✓	✓		✓	✓	✓	✓		✓
Chlorophyll	✓	✓	✓	✓	✓	✓	✓	✓	✓
N & P	✓	✓	✓						

5.3 Results

5.3.1 Total chlorophyll

Significant variation in chlorophyll content of leaves (up to 50-60%) occurred with season (Figure 5.2 (a,b)). Chlorophyll content trended higher in the summer months and declined over winter.

Pre-pruning (age 4.62 yr) chlorophyll content was higher in the pruned trees. The effect of pruning was to cause significant declines in leaf total chlorophyll, but the effect was slower where trees were nitrogen limited. Post pruning, chlorophyll content declined in the pruned trees, 47% and 29 % in the N5 and N0 treatments respectively. Within 6 months of pruning, unpruned trees had had higher chlorophyll content than pruned trees and this difference was significant in the N5 treatment (Figure 5.2 (a,b)).

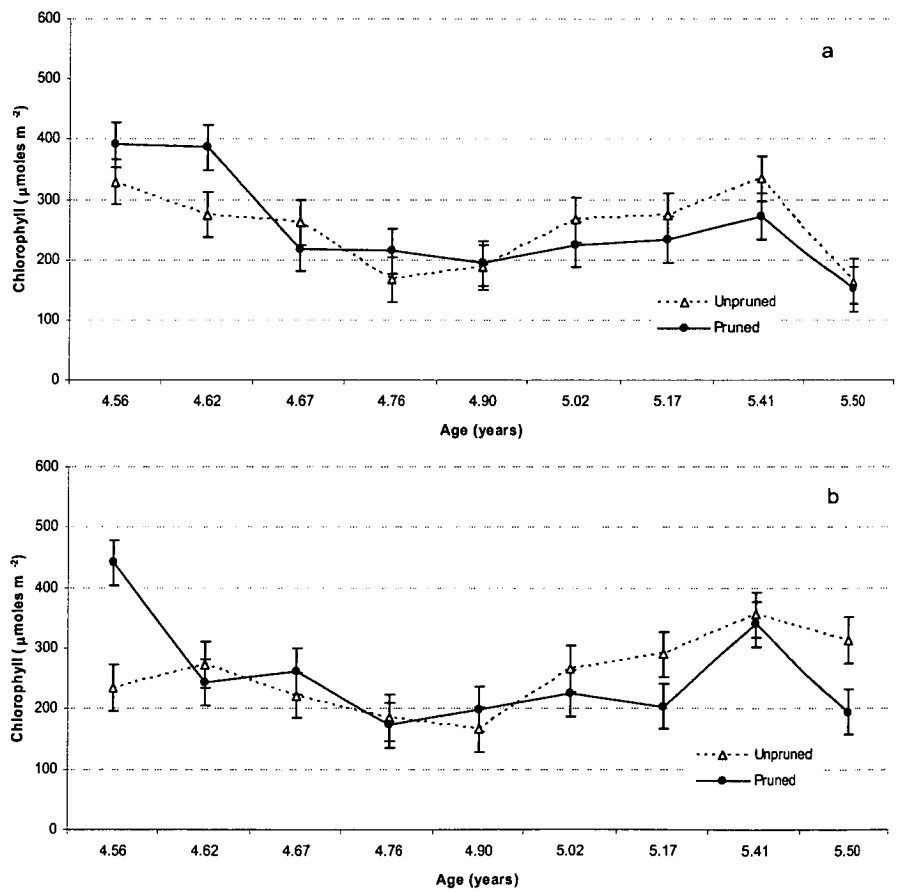


Figure 5.2. Chlorophyll content (µmol m^{-2}) in the upper canopy of *E. globulus* subject to two fertiliser treatments (a = N0 – 0 kg N ha^{-1} and b = N5 - 500 kg N ha^{-1}) and two pruning treatments (unpruned and pruned - 60 % green crown removal). Second-lift pruning was carried out immediately after the first measurement period at age 4.56 yr

5.3.2 Leaf nitrogen and phosphorus

There were no significant differences between pruning treatments for insoluble nitrogen (N) (Figure 5.3 (a, b)) or phosphorus (P) (Figure 5.3 (e, f)). Insoluble N was initially 30 % higher in the N5 treatment, after which levels declined in both N0 and N5 fertiliser treatments, settling at the same level by age 4.67 yr (Figure 5.3 (a, b)). Insoluble P declined slightly between the measurement periods between (4.56 yr) and immediately after pruning (5.62 yr), after which it increased in both the N0 and N5 treatments (Figure 5.3 (e, f)). Soluble nitrogen (nitrate, ammonium and amino acids) was generally higher in unpruned trees, although not significantly so (Figure 5.3 (c, d)). Concentrations of soluble nitrogen increased in N5 trees in the second measurement period, following which they decreased to previous levels, which were not significantly different from the N0 treatment. Soluble nitrogen remained stable in N0 trees (Figure 5.3c). Levels of soluble P (organic and sugar phosphate) declined after pruning (Figure 5.3 (g, h)). Levels in pruned trees were generally higher than unpruned trees, but this was only significant in N5 trees prior to pruning.

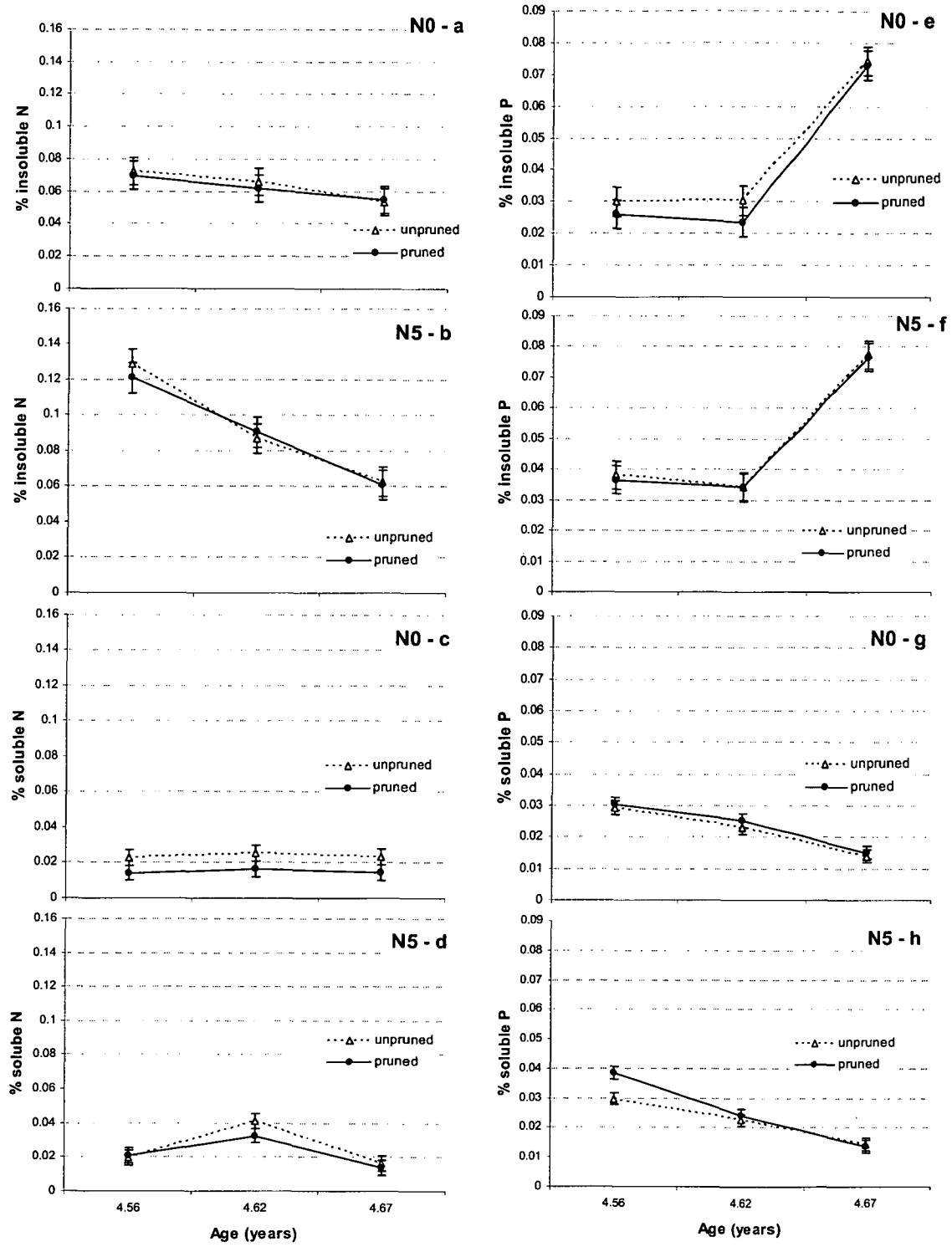


Figure 5.3. Insoluble (a, b & e, f) and soluble (c, d & g, h) nitrogen (N) and phosphorus (P), respectively, in the upper canopy of *E. globulus* subject to two fertiliser treatments (N0 – 0 kg N ha^{-1} and N5 - 500 kg N ha^{-1}) and two pruning treatments (unpruned and pruned - 60 % green crown removal) during the first three measurement periods. Second-lift pruning was carried out immediately after the first measurement period at age 4.56 yr

5.3.3 CO2 assimilation

A_{360} increased post pruning in the N0 treatment, but in both pruned and unpruned trees. The CO_2 assimilation rate of pruned trees in the N0 treatment was 14-21% higher for the first three measurement periods, but this was not significant (Figure 5.4a). A_{360} declined in the N5 treatment post pruning in both pruned and unpruned trees. In contrast, trends in A over time differed between pruned and unpruned trees in the N5 treatment (Figure 5.4b). Pruned trees in the N5 treatment maintained a significantly higher (25-38%) A_{360} for the first two measurement periods after pruning (Figure 5.4b), but this was due to a decrease in A_{360} in unpruned trees. In all treatments A_{360} declined significantly between age 5.41 and 5.50 yr. Chlorophyll, V_{MAX} and J also declined during this period.

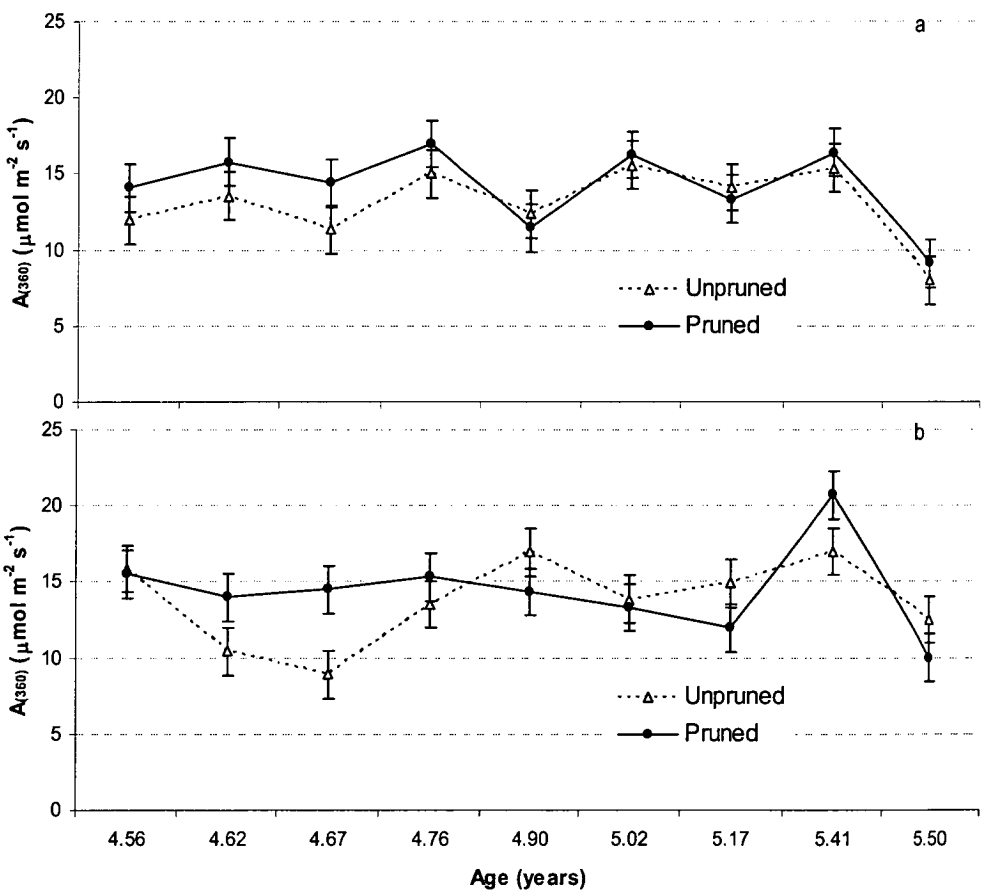


Figure 5.4. The CO_2 assimilation rate (A) for *E. globulus* subject to two fertiliser treatments (a = N0 – 0 kg N ha^{-1} and b = N5 - 500 kg N ha^{-1}) and two pruning treatments (unpruned and pruned - 60 % green crown removal). Second-lift pruning was carried out immediately after the first measurement period at age 4.56 yr

As for A_{360}, g_s in pruned and unpruned trees in the N0 treatment did not diverge, whereas significant differences were apparent between pruned and unpruned trees in the N5 treatment. Initially g_s declined in both pruned and unpruned trees in the N5 treatment. This decline was not evident in the N0 treatment. By 0.1 yr post pruning, pruned N5 trees had significantly greater (45%) g_s in comparison to unpruned trees. After rising, between 0.1 and 0.19 yr after pruning, g_s stabilized in unpruned trees, but rose in pruned trees within the N5 treatment. 0.33 yr post pruning, pruned N5 trees had values of g_s 60% higher than unpruned trees.

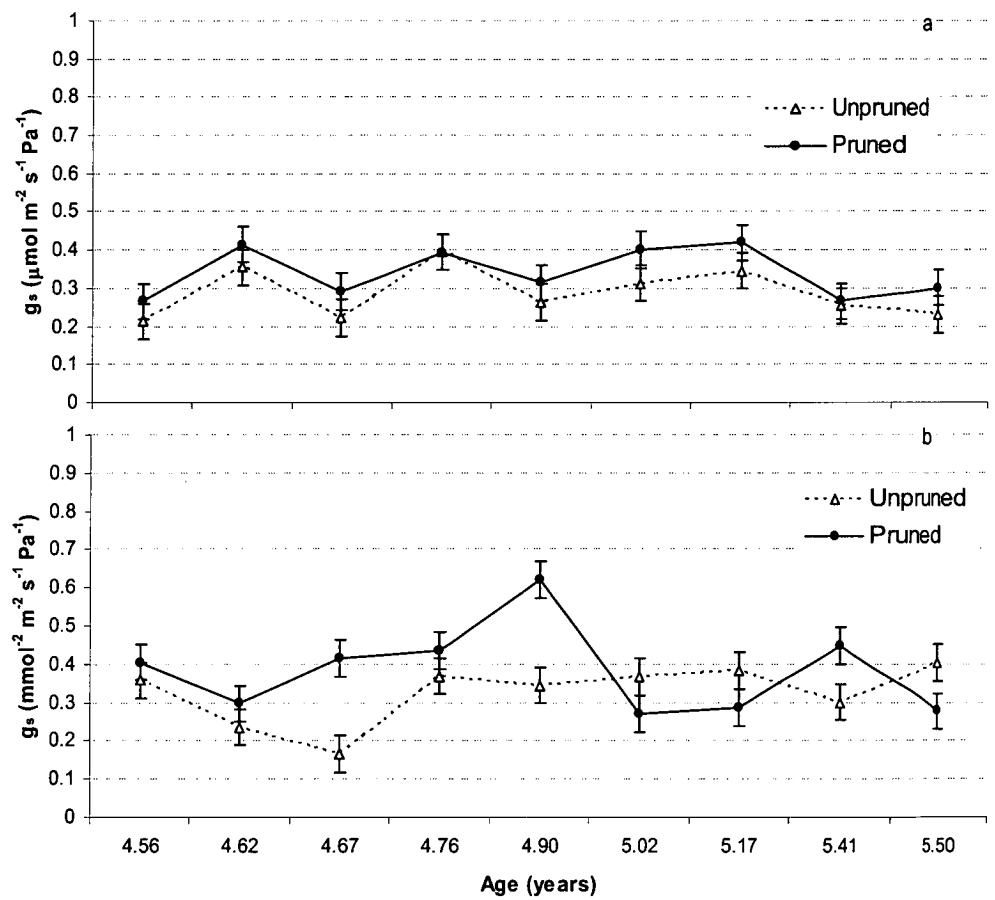


Figure 5.5. Stomatal conductance (g_s) for *E. globulus* subject to two fertiliser treatments (a = N0 – 0 kg N ha^{-1} and b = N5 - 500 kg N ha^{-1}) and two pruning treatments (unpruned and pruned - 60 % green crown

5.3.4 A/C_I curves

In the N0 treatment, the maximum rate of RuBP carboxylation (V_{CMAX}) did not vary significantly between pruned and unpruned trees, although V_{CMAX} was generally higher in pruned trees (3.8-13%) (Figure 5.6a). V_{CMAX} did vary significantly between pruned and unpruned trees in the N5 treatment; V_{CMAX} increased in pruned trees in response to pruning and decreased in unpruned treatments (Figure 5.6b). V_{MAX} was 27-28% higher in pruned N5 trees 0.05 yr post pruning and 0.33 yr post pruning.

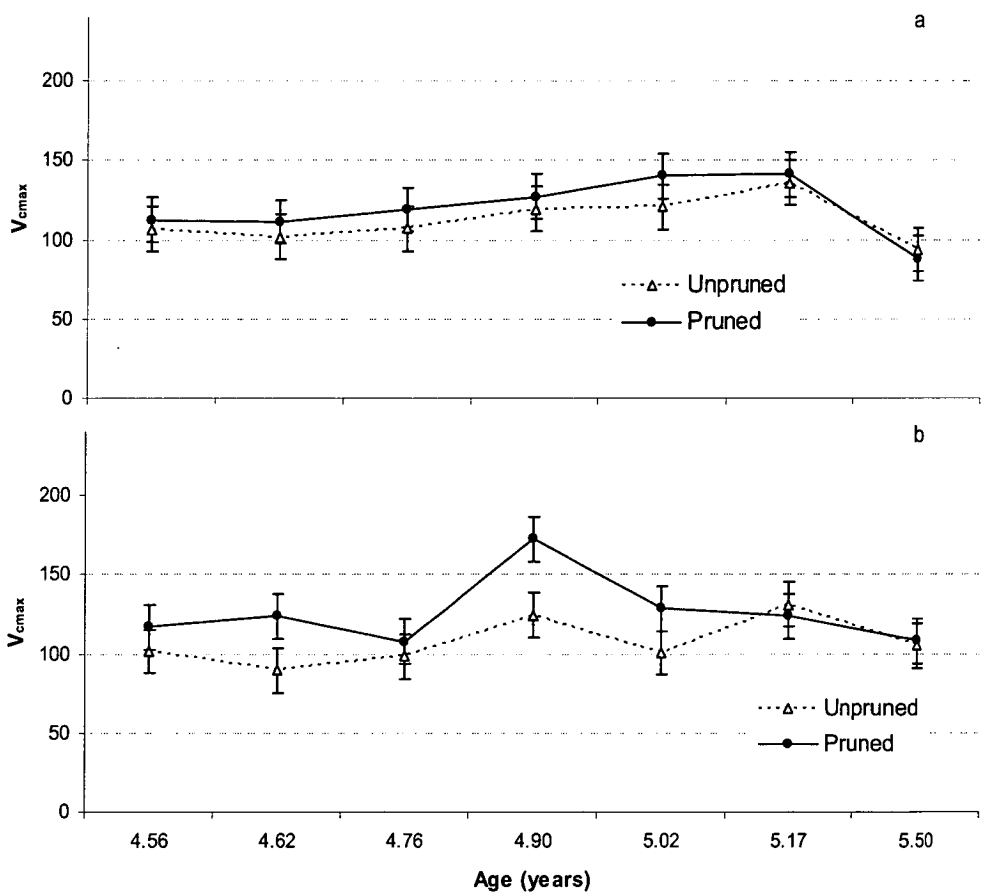


Figure 5.6. V_{CMAX} (maximum carboxylation rate limited by Rubisco) for *E. globulus* subject to two fertiliser treatments (a = N0 – 0 kg N ha^{-1} and b = N5 - 500 kg N ha^{-1}) and two pruning treatments (pruned and pruned - 60 % green crown removal). Second-lift pruning was carried out immediately after the first measurement period at age 4.56 yr

The results for the rate of photosynthetic electron transport (J) were similar to V_{CMAX} in that there were no significant differences between pruning treatments in the N0 treatment, but there were in the N5 treatment (Figure 5.7a). J remained fairly constant in response to pruning in the N5 pruned trees, but decreased in the N5 unpruned trees leading to significant differences between J for the two measurement periods immediately post pruning (27% and 29% respectively) (Fig 5.7b). J showed increased seasonal variation in N0 trees in comparison to N5 trees.

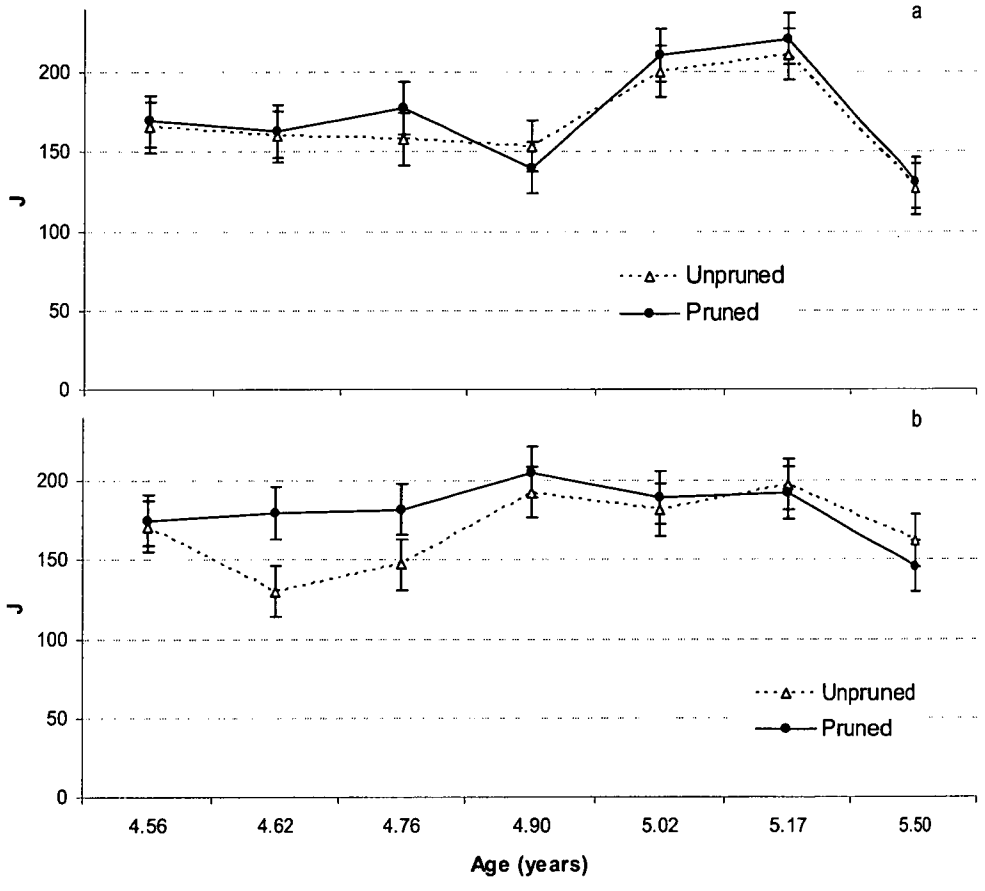


Figure 5.7. J (rate of photosynthetic electron transport) for *E. globulus* subject to two fertiliser treatments (a = N0 – 0 kg N ha^{-1} and b = N5 - 500 kg N ha^{-1}) and two pruning treatments (pruned and pruned - 60 % green crown removal). Second lift pruning was carried out immediately after the first measurement period at age 4.56 yr

5.3.5 Leaf area distribution

Prior to experimental treatments being imposed (at age 3.7 yr), leaf area was proportionally greater in zone 2 (Figure 5.8). At the end of the experiment (age 5.7 yr), leaf area was more evenly distributed between zones, but preferentially distributed towards zones 2 and 3 (Figure 5.8). Unpruned trees in the N5 treatment retained significantly greater leaf area in zone 1 in comparison to unpruned trees in the N0 treatment (Figure 5.8). Pruned trees in the N5 treatment had proportionally more leaf area in zone 2 than zone 3 while the reverse was true for unpruned trees in the N5 treatment (Figure 5.8).

Average total leaf area was unpruned N5 (45.3 m^2), pruned N5 (38.4 m^2), unpruned N0 (25.4 m^2). In all cases the treatment differences were significant. Leaf area was not determined for pruned trees in the N0 treatment.

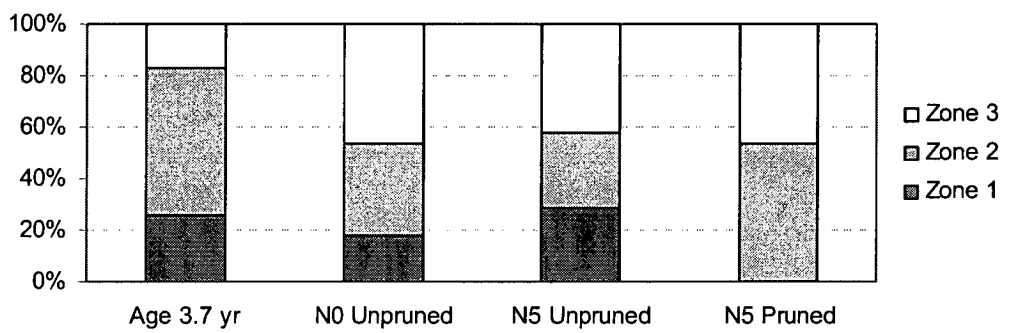


Figure 5.8. Leaf area by zone at age 3.7 yr (before the treatments were applied), in comparison to age 5.5 yr (0.93 yr post 2nd lift pruning pruning and 1.8 yr post fertiliser application and 1st lift pruning). Results for unpruned *E. globulus* (N0 – 0 kg N ha^{-1}) and pruned and unpruned *E. globulus* (N5 – 500 kg N ha^{-1}). Pruning removed 60% of leaf area

5.4 Discussion

Stimulation of leaf area production due to improved N nutrition appears to be the main factor in preventing growth suppression due to pruning in this trial. The expected up-regulation of photosynthetic rates and activity did not occur when N was not applied. There was no physiological response to pruning in N0 trees. In the N5 treatment, significant differences in photosynthetic rates and activity were observed, but these were due to a decline in unpruned trees rather than an increase in pruned trees.

The application of fertilizer N can improve site productivity. The ability of trees to recover from defoliation due to pests and disease (Stone 2001) or pruning (Pinkard 2003) is less on poor productivity sites. Results from the larger trial area (see chapter 4) and other trials

examining the effects of N nutrition on defoliation within a site have demonstrated the advantages of the application of fertilizer N on recovery from defoliation (Pinkard, Baillie *et al.* 2006a; Pinkard, Baillie *et al.* 2006b). Pruning trials comparing sites of differing quality have found that growth suppression from pruning 70% of the green crown was less pronounced on a high than on a low quality site (Pinkard and Beadle 1998b). Using a physiological approach, Pinkard and Beadle (2000) demonstrated that the growth response to pruning can be related to the effect of pruning on leaf area. Trees can maintain leaf area at levels in excess of the optimum for 95% light interception (Jarvis and Leverenz 1983), and the shaded lower crowns may contribute little to biomass production. The application of fertiliser N can result in increased leaf area (Smethurst, Baillie *et al.* 2003) and retention of existing leaves for an extended period, particularly in the lower canopy (Wiseman, Smethurst *et al.* 2006) as an adequate supply of N reduces the tree's need to translocate N from lower shaded leaves for use in the well-lit upper canopy (Dell, Malajckzuk *et al.* 2001; Field and Mooney 1983). In the N5 treatment in this experiment, there was evidence of both greater overall leaf area, as well as greater retention of leaves in the lower canopy compared to the N0 treatment. Therefore, removal of leaf area in the N5 treatment was less likely to reduce remaining leaf area to sub optimal levels. N0 trees reduced the proportion of leaf area invested in the lower canopy and had proportionally more leaf area in zones 2 and 3. This may explain why pruned and unpruned trees behaved similarly in terms of physiological parameters in this treatment.

Nitrogen is preferentially located in the upper canopy in order to maximize a tree's photosynthetic rate, making the upper canopy sensitive to changes in N concentration (Stockhoff 1994). Little change in soluble N concentrations was observed in response to pruning indicating that differences between pruned and unpruned trees in A_{360} was not the result of re-allocation of N. Instead, results from biomass sampling in this trial indicated N application stimulated the production of leaf area rather than increasing leaf N concentration. The evidence suggests that the improved ability of trees receiving fertilizer N to recover from pruning is a partly due to their ability to replace lost leaf area.

Chlorophyll concentrations and nitrogen concentrations declined from the first measurement period through to the end of summer and the decline was most pronounced in the pruned trees. Initial declines, in response to pruning are in contrast with a similar study (Pinkard, Battaglia *et al.* 2007). As water limitation has a negative effect on chlorophyll content

(Shimada, Kokubun *et al.* 1992), the low water availablility post pruning may have mitigated the effect that pruning wouldhave had on chlorophyll content. Most nitrogen is found in photosynthetic enzymes (Evans 1989), and a decline in chlorophyll could be associated with a decline in photosynthetic enzymes (Trumble, Kolodnyhirsch *et al.* 1993).

The physiological responses to pruning were complex and there was an interaction between the effects of N on leaf area and physiological parameters. An increase in the photosynthetic rate has been observed in response to defoliation in *E. globulus* (Pinkard 2003) (Turnbull, Adams *et al.* 2007) and other tree species (Hoogesteger and Karlsson 1992; Pinkard and Beadle 1998c) and this has been attributed to enhanced stomatal conductance (g_s) (Reich, Walters *et al.* 1993) and enhanced nitrogen allocation to remaining leaves (Ozaki, Saito *et al.* 2004). Pruning did not lead to an increase in A_{360} in comparison with unpruned trees as was expected from previous trials (Pinkard and Beadle 1998c; Pinkard, Mohammed *et al.* 2004; Turnbull, Adams *et al.* 2007). Where N was limiting pruning had no significant effect on any of the physiological parameters measured. Where N was supplied all physiological parameters showed significant differences 0.05 and/or 0.1 yr post pruning, but this was due to sharp declines in A_{360}, J and g_s in unpruned trees rather than up-regulation in pruned trees. This is in contrast to other studies of *E. globulus* which found increased photosynthetic activity in response to pruning (Pinkard 2003; Turnbull, Adams *et al.* 2007). The summer in which the trees were pruned was exceptionally dry and this may have restricted the trees ability to increase assimilation rates. Quentin (2010) found differences in the response of A to defoliation with irrigated trees responding, while non-irrigated trees did not. While in this case there was not an increase on pre-pruning rates, nevertheless the rate in pruned trees was significantly higher than unpruned trees. Multiple studies have demonstrated the dependence of defoliation response to resource availability (Fahnestock and Detling 1999; Maschinki and Whitham 1989; McGraw, Gottschalk *et al.* 1990; Yang and Midmore 2004). At times of low water availability, water stress has been shown to be greater in *E. globulus* supplied with fertiliser N (White, Crombie *et al.* 2009), due to the effect of additional leaf area on transpiration rates. Defoliation reduced water stress in N5 trees as evidenced by increasing g_s in the pruned trees. Several studies have found that defoliation of water limited plants increased photosynthetic capacity (McGraw, Gottschalk *et al.* 1990; Shimada 1991) and increased leaf water potential and stomatal conductance (g_s) (Shimada 1991). In this case photosynthetic rates were prevented from declining, rather than increased, but were still significantly higher. In conclusion, the results of this trial support the theory that resource

availability strongly influences the response to defoliation. Increased leaf area as a result of N application improved a tree's ability to recover from pruning, but probably induced water stress in unpruned trees. Where N was limiting, the pruned trees were unable to up-regulate photosynthesis in response to defoliation. Differences between N0 and N5 trees in their response to defoliation by pruning at a time of water stress indicates an effect of N on the way trees respond to defoliation in times of water stress. Implications of these results for management are discussed in Chapter 6.

CHAPTER SIX

General discussion and conclusions

6.1 Background to research

The expansion of the plantation timber industry is limited by the availability of suitable land at lease or purchase prices which make the production of timber (often on rotations of 20 – 50 years) economic. For these reasons plantations are often located on marginal land and so production can be limited by resource availability. Most of the expansion in the hardwood plantation industry in recent years has been driven by managed investment schemes (MIS). These schemes seek to provide a return to investors, and so require high production and reduced rotation lengths.

One way to improve the economics of timber plantations is to optimise growth in order that, either the volume of merchantable timber produced per hectare is as high as possible, or the rotation length is reduced. Alternatively, input costs can be reduced. There are many costs involved in producing solid wood from plantations, and so each tree represents a significant investment which needs to be maximised. The tools available to plantation managers in Australia to maximise growth are effective weed control (eg. Baker & Battaglia 2007, Adams, Beadle *et al.* 2003, Wilkinson & Neilsen 1990) application of fertiliser (eg. Xu, Dell 2002, Judd, Bennet *et* al. 1996, Bennett, Weston 1996,. Comer, Smethurst 1995) and optimal scheduling of pruning eg. (Pinkard & Beadle et al. 1998) and thinning (eg. Gerrand, Medhurst et al. 1997) operations. We looked at two of these options, fertiliser nitrogen and pruning.

In a simple pulpwood plantation, managers seek to keep the costs of fertiliser applications as low as possible while ensuring that sufficient fertiliser is applied to maintain maximum growth rates. In solid wood plantations, additional objectives come in to play. Early applications of fertiliser can ensure trees are vigorous, but may also increase the size of the knotty core. We considered the interaction that fertiliser may have with pruning in terms of two of the major concerns in solid wood plantations in Tasmania, tree growth and pruning associated decay.

6.2 Interaction of fertiliser, branch size and decay in respect to plantation management

Eucalyptus globulus and *E. nitens* do not effectively shed branches when grown in plantations. When grown for high value wood products these species must be pruned and pruned before branches senesce and die. Without pruning retained branch stubs will result in excessive knots and may cause up to 75% of recovered volume to be downgraded. When branches are pruned whilst alive clean, tight knots are produced. Pruned dead branches on the other hand can exude large amounts of kino, slowing stub occlusion, and increasing the size of the knotty core (Chapters 2 and 3). Stub ends can also become trapped in the bark and be dragged outward as the tree grows (Chapters 2 and 3). This results in a kino filled void which will run outwards from the knotty core through the clear wood.

For these reasons, managing crown lift, (whereby lower branches senesce and the height of the green crown rises) and the timing of pruning operations is vital to successfully producing high quality sawlogs (Beadle , Volker et al. 2008). There are three factors which can accelerate crown lift; Water limitation, nutrient limitation (Chapter 2 and 5) and, high stocking rates (Neilsen and Gerrand 1999). When water, nutrients or sunlight are limiting, trees will redirect resources such as nitrogen from less productive lower leaves to the more productive upper canopy (Ueda, Mizumuchi 2009). The upper canopy is more productive than the lower branches as it is exposed to more sunlight. When water is limiting, the tree can increase the amount of water available to the upper canopy by allowing the lower leaves to senesce (Muenne-Bosch & Allegre 2004). This allows the upper leaves to keep their stomata open longer, increasing the period of time which they can photosynthesise. Similarly when nitrogen, potassium or phosphorus are limiting the tree is able to re-allocate nutrients from lower leaves to developing leaves in the upper canopy (Attiwell & Adams 1993). High stocking rates hasten the onset of canopy closure at which time lower branches receive limited sunlight and so become a net drain, rather than supplier of carbon. Controlling water availability is usually not in the plantation managers' control, so this leaves the manipulation of stocking through thinning and nutrient management (Chapter 2 and 4) as the tools available to plantation managers to influence the rate of crown lift.

While live branch pruning is a necessity, pruning associated decay is almost exclusively the result of pruning living branches (Mohammed, Barry et al. 2000b, Chapter 2 and 4). The larger the diameter of the pruned branch, the higher the risk the branch will be infected by

wood decay fungi (Mohammed, Barry et al. 2000b, Chapter 2 and 4). By examining pruning decay risk in terms of branch status (living, dead or senescent at the time of pruning) and branch size we found that pruning a living branch greater than 20 mm in diameter will result in a decay infection more than 50% of the time (Chapter 2). Pruning dead and senescent branches did not result in decay, but did result in the defects such as kino trace defect (Chapter 2).

Early applications of fertiliser nitrogen and phosphorus caused trees to retain living branches for longer, delaying crown lift (Chapter 2 and 4). The retained branches increased in size, so trees which received fertiliser early had a higher proportion of large branches and associated decay infections (Chapter 2). The number of pruned branches with kino associated defects was also less in the trees which received fertiliser as they had less pruned dead branches (Chapter 2). Early fertiliser application also caused a higher incidence of multiple leaders (Beadle, Tunbull *et al.* 1994, Chapter 2). Large branches and multiple leaders were found predominantly in the most vigorous trees (Chapter 2). The most vigorous or dominant trees are also targeted for pruning as volume is the primary determinant of log value. Also selection of dominant trees is important to ensure that pruned trees do not become suppressed by surrounding trees. The positive effects of early fertiliser application in slowing crown lift must be weighed against the possibility of deterioration in form in the most vigorous trees and increased incidence of pruning associated decay. Plantation managers should therefore err on the side of caution when prescribing fertiliser in the early stages of the rotation.

Further research has found that pruning associated decay is confined to the knotty core for at least 6 years post pruning (Barry, Davies *et al.* 2003) and there is evidence that this is still the case in pruned 26 year old *E. globulus* and *E. nitens* (Wardlaw, Glen *et al.* 2007). As more information is gained from long term studies into decay spread over time, it may become apparent that decay is largely confined to the knotty core for the length of the rotation. At that time pruning specifications may be revised. Until that time the relationship between decay risk and pruned branch size can be used to minimise the incidence of decay and so risk (Chapter 2).

Branch size was related to tree diameter at breast height (Chapter 2). Therefore, tree diameter, an easily measured variable, can be used to schedule pruning operations to ensure that branch size thresholds are not exceeded. This relationship was similar between sites, with

each centimetre increase in tree diameter leading to an increase of 0.54-0.64 mm in average branch diameter. Where early fertiliser was applied the ratio changed to an increase of 0.7-0.75 mm for each centimetre increase in tree diameter. Therefore, plantations which are given early applications of fertiliser will require pruning earlier.

Branch diameter was also found to increase with tree height, as does the number of living branches. This means the risk of pruning associated decay will be higher in second and subsequent lifts than in the first pruning lift (Chapter 4). This result emphasises the need to ensure subsequent pruning lifts contain the knotty core to a diameter at or below that established in the first lift prune (Todoroki 2003). If not there is a very high risk of pruning associated decay spreading down into clearwood produced after first lift pruning although Wardlaw, Glen *et al.* (2007) found no evidence of this in 26 year old *E. nitens* that had been high pruned.

The use of genetic variation is a possible management tool that has been considered to reduce fungal decay incidence and spread. In *E. nitens*, family and progeny trials have shown that the incidence of heart rot and decay infections via wounds is under moderately strong genetic control (heritabilities 0.27 to 0.4 and 0.6, respectively; Kube 2004; D. Wiseman, unpublished data) and easily assessed during routine sampling for wood properties. Susceptibility to decay spread in sapwood however appears not to be under wide genetic control although southern races of *E. nitens* are more susceptible to sapwood decay (D. Wiseman, unpublished data).

6.3 Nitrogen nutrition, pruning and tree growth

Nutrient requirements within a plantation follow a trend of increasing demand from establishment through to a peak just prior to canopy closure (May, Smethurst et al. 2009). Response to fertiliser application during this initial phase is common (. For solid wood production, wood produced prior to first lift pruning will be invested in the knotty core and will not result in increased returns unless the response is sustained for the entire rotation. Post canopy closure, requirements for mobile nutrients such as N, P and K are largely met through re-distribution within the canopy. Management events such as thinning or pruning disturb this cycle and responses to fertiliser are more common after thinning than in an undisturbed stand.

Application of fertiliser N just prior to first lift pruning had a positive effect on pruned branch occlusion and tree growth (Chapter 5). The effect was still apparent after second lift pruning. Increasing applications of fertiliser N up to 300 kg N ha^{-1} resulted in increased tree growth, while the application of 500 kg N ha^{-1} did not significantly increase growth any further (Chapter 5). Diameter growth post pruning is the most important factor in branch occlusion, clearwood production and hence optimising the value of the pruned stem (Chapter 3).

We found that second lift pruning, removing 40 % of green crown height suppressed growth. By applying fertiliser N we were able to stimulate growth in pruned trees such that they had significantly greater volume than unpruned, unfertilised trees (Chapter 5). Therefore it is recommended that fertiliser N be applied just prior to pruning.

6.4 The mechanism by which nitrogen promotes recovery from pruning

There was some indication that applications of N in excess of that which significantly increased growth improved recovery from defoliation in *E. globulus*. Similar results were found by Pinkard, Baillie *et al.* (2006b), indicating that even sites which are not N deficient may respond to N after a defoliation event. N is a valuable tool for promoting crown recovery post defoliation and can be used to promote quick recovery and recapture pre-defoliation growth rates.

Investigation into the method by which fertiliser N influenced recovery from pruning defoliation found that the effect was primarily due to the stimulatory effect on leaf area. Trees which received fertiliser N were able to replace lost leaf area within 11 months of pruning. In the highest N application rate, pruned trees had significantly more leaf area 11 months after pruning than unpruned trees which had no fertiliser N, despite having had 60% of their leaf area removed in the second lift. The effect on N on replacement of leaf area is a rapid and effective way to promote recovery from defoliation.

In this study the period after pruning was a remarkably dry summer, and photosynthetic rates were restricted by water availability. A common response to defoliation is an up-regulation in photosynthetic activity, and this is considered a compensation mechanism for the loss of leaf area. While evidence from other studies showed an increase in photosynthetic activity in response to pruning or defoliation (Pinkard 2003), we found this may be mitigated in

resource limited environments (N and water limited) (Chapter 5). The combination of improving N availability and the effect of defoliation on stomatal conductance combined to assist trees to recover from pruning (Chapter 5). We know that site quality can influence recovery from defoliation, with poor quality sites less able to recover from defoliation. The application of fertiliser N may be used to help promote recovery from defoliation on poor quality sites.

The effect of fertiliser N on leaf area is a useful tool to mitigate growth suppression due to defoliation and so can be harnessed by plantation managers to optimise clearwood production. Production of clearwood, is primarily determined by diameter growth post pruning. Branch stub length and kino exudation also have an effect (Chapter 3). Kino exudation is controlled by pruning before branches are dead and stub length is controlled by good pruning technique. Clearwood production can be maximised by ensuring thinning and nutrition are optimised post pruning and the interaction and optimisation of these practices is recommended for further study.

Silvicultural recommendations for plantations managed for solid wood stemming from this work are:

I. Unless it is confirmed that decay is largely confined to the knotty core for the length of the rotation in species pruned for solid wood production pruning branches greater than 20 mm in diameter is not recommended as this operation is associated with a higher risk of decay infection.

II. Early (establishment and age 1-2 years) applications of fertiliser N and P should be conservative to avoid a deterioration in tree form and an increase the incidence of pruning decay associated with larger branches.

III. To ensure rapid branch occlusion, schedule pruning operations to precede crown lift and ensure stub length is minimised.

IV. The optimal time to apply fertiliser N is immediately prior to pruning. This will promote recovery from pruning defoliation, stimulate growth and direct growth into valuable clearwood.

REFERENCES

Adams PR, Beadle CL, Mendham NJ, Smethust PJ (2003) The impact of timing and duration of grass control on growth of a young *Eucalyptus globulus* Labill plantation. *New Forests.* **26**, 147-165.

Alcorn PJ, Bauhus J, Smith RGB, Thomas D, James R, Nicotra A (2008) Growth response following green crown pruning in plantation-grown *Eucalyptus pilularis* and *Eucalyptus cloeziana. Canadian Journal of Forest Research* **38**, 770-781.

Attiwell PM & Adams MA (1993). Tansley Review No. 50 Nutrient cycling in forests. *New Phytoogisstl.* **124,** 561-582.

Australian Government: Bureau of Meteorology (2003) Summer – hotter and drier than normal. *Available at* http://www.bom.gov.au/announcements/media_releases/tas/20030228.shtml

Baker T, Battaglia M (2007) Long-term growth responses of *Eucalyptus globulus* to soil ripping, weed control and fertiliser application at establsihment on a former agricultural site in South-eastern Australia. Proceedings IUFRO Working Group 2.08.03 'Eucalypts and Diversity: Balancing Productivity and Sustainability'. 22-26 October 2007. Duban, South Afirca.

Barry KM, Davies NW, Mohammed CL (2001a) Identification of hydrolysable tannins in the reaction zone of *Eucalyptus nitens* wood by high performance liquid chromatography–electrospray ionisation mass spectrometry *Phytochemical Analysis* **12**, 120 - 127.

Barry KM, Pearce RB, Evans SD, Hall LD, Mohammed CM (2001b) Initial defence responses in sapwood of *Eucalyptus nitens* (Maiden) following wounding and fungal inoculation. *Physiological and Molecular Plant Pathology* **58**, 63 - 72.

Barry KM, Davies NW, Mohammed CL (2002) A Chemical Comparison of Two Types of Antifungal Defence: Reaction Zones and Branch Protective Zones in *Eucalyptus globulus*. In 'Proceedings of the 7th International Mycological Congress'. Oslo, Norway pp. 242

Barry KM, Davies NW, Mohammed CL, Beadle CL (2003) Post-harvest chemical staining in blackwood (*Acacia melanoxylon* R. Br.). *Holzforschung* **57**, 230-236.

Barry KM, Hall MF, Mohammed CL (2005) The effect of time and site on pruning-related decay in plantation-grown *Eucalyptus nitens. Canadian Journal of Forest Research* **35**, 495-502.

Barry KM, Pearce RB, Evans SD, Hall LD, Mohammed CM (2001) Initial defence responses in sapwood of *Eucalyptus nitens* (Maiden) following wounding and fungal inoculation. *Physiological and Molecular Plant Pathology* **58**, 63 - 72.

Battaglia M, Beadle CL, Loughhead S (1996) Photosynthetic temperature responses of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiology* **16**, 81-89.

Beadle CL, Turnbull CRA, McLeod R (1994) An assessment of growth and form for pruning to six metres in Eucalyptus nitens plantations. *Tasforests* **6**, 1-6.

Beadle CL, Volker P, Mohammed C, Barry K, Pinkard, E, Harwood C, Nolan G. (2008) Solid wood production from temperate eucalypt plantations: a Tasmanian case study. *Southern Forests* **70**, 45-57.

Bennett LT, Weston CJ, Attiwill PM (1997) Biomass, nutrient content and growth response to fertilisers of six-year-old Eucalyptus globulus plantations at three contrasting sites in Gippsland, Victoria. *Australian Journal of Botany* **45**, 103-121.

Bredenkamp BV, Malan FS, Conradie WE (1980) Some effects of pruning on growth and timber quality of *Eucalyptus grandis* in Zululand. *South African Forestry Journal* **114**, 29-34.

BRS (2010) 'Australia's forests at a glance 2010.' Bureau of Rural Sciences, Department of Agriculture, Fisheries and Forestry. www.daff.gov.au/forestsaustralia

Bryant JP, Chapin FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* **40**, 357-368.

Caemmerer Sv, Farquhar GD (1984) Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced p(CO2) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. *Planta* **160**, 320-329.

Candy SG (1997) Growth and yield models for *Eucalyptus nitens* plantations in Tasmania and New Zealand. *Tasforests* **9**, 165-196.

Chandrashekara UM (2007) Effects of pruning on radial growth and biomass increment of trees growing in homegardens of Kerala, India. *Agroforestry Systems* **69**, 231-237.

Chiu C-M, Lo-Cho C-N, Suen M-Y (2002) Pruning method and knot wound analysis of taiwan selkova (*Zelkova serrata* hay.) plantations. *Taiwan Journal of Forest Science* **17**, 503-513.

Cromer RN, Balodis V, Cameron D, Garland CP, Rance S, Ryan P (1998) *Eucalyptus grandis* fertiliser trials: growth, wood properties and kraft pulp yield. *Appita* **51**, 45-49.

Cromer RN, Cameron DM, Rance SJ, Ryan PA, Brown M (1993) Response to nutrients in *Eucalyptus grandis*. 2. Nitrogen accumulation. *Forest Ecology and Management* **62**, 231-243.

Cromer RN, Turnbull CRA, LaSala AV, Smethurst PJ, Mitchell AD (2002) Eucalyptus growth in relation to combined nitrogen and phosphorus fertiliser and soil chemistry in Tasmania. *Australian Forestry* **65**, 256-264.

Dai KH, Richter DD (2000) A re-examination of exchangeable acidity as extracted by potassium chloride and potassium flouride. *Communications in Soil Science and Plant Analysis* **31**, 115-139.

Deadman H, Calderon S (1988) Pruning Eucalypts in New Zealand. In 'AFRI International Forestry Coference for Australian Bicentenary'. Albury, NSW, Australia

Dell B, Malajckzuk N, Xu D, Grove TS (2001) 'Nutrient disorders in plantation eucalypts. 2nd edition.' ACIAR Monograph No. 74, Canberra, Australia 188 pp pp.

Duchesne LC, Hubbes M, Jeng RS (1992) Biochemistry and molecular biology of defense reactions in the xylem of angiosperm trees. In 'Defense Mechanisms of Woody Plants Against Fungi'. (Eds RA Blanchette and AR Biggs). pp. 133-146. (Springer-Verlag: Berlin, Germany)

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* **78**, 9-19.

Eyles A, Mohammed CL (2003) Kino vein formation in *Eucalyptus globulus* and *E. nitens*. *Australian Forestry* **66**, 206-212.

Eyles A, Pinkard EA, Mohammed CL (2009a) Shifts in biomass and resource allocation patterns following defoliation in *Eucalyptus globulus* growing with varying water and nutrient supplies. *Tree Physiology* **29**, 753-764.

Eyles A, Pinkard EA, O'Grady AP, Worledge D, Warren CR (2009b) Role of corticular photosynthesis following defoliation in *Eucalyptus globulus*. *Plant Cell and Environment* **32**, 1004-1014.

Fahnestock JT, Detling JK (1999) Plant responses to defoliation and resource supplementation in the Pryor Mountains. *Journal of Range Management* **52**, 263-270.

Field C, Mooney HA (1983) Leaf age and seasonal effects on light, water and nitrogen use efficiency in a California shrub. *Oecologia* **56**, 348-355.

Florence RG (2000) Growth habits and silviculture of eucalypts. In 'Diseases and Pathogens of Eucalypts'. (Eds PJ Keane, GA Kile, FD Podger and BN Brown). pp. 35-46. (CSIRO Publishing: Collingwood, Victoria)

Gadgil PD, Bawden AD (1981) Infection of wounds in *Eucalyptus Delegatensis*. *New Zealand Journal of forestry Science* **11**, 262 - 270.

Gerrand AM, Medhurst JL, Neilsen WA (1997) 'Research results for thinning and pruning eucalypt plantations for sawlog production in Tasmania.' Forestry Tasmania, Hobart

Gerrand AM, Neilsen WA (2000) Comparing square and rectangular spacings in *Eucalyptus nitens* using a Scotch plaid design. *Forest Ecology and Management* **129**, 1-6.

Gerrand AM, Neilsen WA, Medhurst JL (1997) Thinning and pruning eucalypt plantations for sawlog production in Tasmania. *Tasforests* **9**, 15-34.

Glass BP, McKenzie H, Griffith JA (1989) Decay distribution in relation to pruning and growth stress in plantation-grown Eucalyptus regnans in New Zealand. *Special issue: Workshop on forest health in the South Pacific, Rotorua* **19**, 2-3.

Hallam PM, Reid JB, Beadle CL (1989) Frost hardiness of six potential plantation *Eucalyptus* species. *Canadian Journal of Forest Research* **19**, 1235-1239.

Hawkins S, Boudet A (1996) Wound-induced lignin and suberin deposition in a woody angiosperm (Eucalyptus gunnii Hook.): histochemistry of early changes in young plants. *Protoplasma* **191**, 96-104.

Hooda N, Weston CJ (1999) Influence of site and fertiliser addition on nutrient cycling in *Eucalyptus globulus* plantations in Gippsland, southeastern Australia I. Foliage and litter quality. *Australian Journal of Botany* **47**, 189-206.

Hoogesteger J, Karlsson PS (1992) Effects of defoliation on radial stem growth and photosynthesis in the Mountain Birch (*Betula pubescens* spp. *Tortuosa*). *Functional Ecology* **6**, 317-323.

Isbell RF (1996) 'The Australian Soil Classification.' CSIRO Publishing, Melbourne, Australia

Jarvis PG, Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In 'Encyclopedia of Plant Pathology vol 12D. Physiological Plant Ecology: Productivity and Ecosystem Processes' pp. 234-280. (Springer-Verlag: Berlin, Germany)

Jenkin BM, Tomkins B (2006) The use of chemical pesticides by the Australian Plantation Forest Industry. FWPRDC Project no: PN06.4016. http://www.plantations2020.com.au/assets/acrobat/FWPpestreport.pdf

Judd TS, Bennett LT, Weston CJ, Attiwill PM, Whiteman PH (1996) The response of growth and foliar nutrients to fertilizers in young Eucalyptus globulus (Labill.) plantations in Gippsland, southeastern Australia. *Forest Ecology and Management* **82**, 87-101.

Kube PD, (2004) Genetic improvement of the wood properties of *Eucalyptus nitens*: Breeding to improve solid wood and pulp properties, Ph.D. thesis, University of Tasmania, Hobart, Australia,

Lowther JR (1980) Use of a single sulphuric acid / hydrogen peroxide digest for the analysis of *Pinus radiata* needles. *Communications in Soil Science and Plant Analysis* **11**, 175-188.

Mackensen J, Bauhus J, Webber E (2003) Decomposition rates of coarse woody debris—a review with particular emphasis on Australian tree species. *Australian Journal of Botany* **51**, 27-37.

Marks GC, Incoll WD, Long IR (1986) Effects of Crown Development, Branch Shed and Competition on Wood Defect in *Eucalyptus regnans* and *E. sieberi*. *Australian Forest Research* **16**, 117 - 129.

Maschinki J, Whitham TG (1989) The continuum of plant responses to herbivory: The influence of plant association, nutrient availability and timing. *American Naturalist* **134**, 1-19.

May B, Smethurst P, Carlyle C, Mendham D, Bruce J, Baillie CC (2009) 'Review of fertiliser use in Australian forestry.' Forest & Wood Products Australia, Hobart 113 pp pp.

McGraw JB, Gottschalk KW, Vavrek MC, Chester AL (1990) Interactive effects of resource availabilities and defoliation on photosynthesis, growth and mortality of red oak seedings. *Tree Physiology* **7**, 247-254.

Medhurst JL (2000) Growth and physiology of *E. nitens* in plantations following thinning. Doctor of Philosophy. University of Tasmania.

Mercer D, Underwood A (2002) Australian timber plantations: national vision, local response. *Land Use Policy* **19**, 107-122.

Metzler B (1997) Quantitative assessment of fungal colonization in Norway spruce after green pruning. 1-10.

Misra RK, Turnbull CRA, Cromer RN, Gibbons AK, LaSala AV, Ballard LM (1998) Below- and above-ground growth of *Eucalyptus nitens* in a young plantation. *Forest Ecology and Management* **106**, 295-306.

Mohammed C, Barry K, Battaglia M, Beadle C, Eyles A, Mollon A, Pinkard E (2000a) Pruning-Associated Stem Defects in Plantation *E. nitens* and *E. globulus* Grown for Sawlog and Veneer in Tasmania, Australia. In 'The Future of eucalypts for wood production : proceedings, Country Club Casino, Launceston, Tasmania, Australia, 19-24th March 2000.'. Country Club Casino, Launceston, Tasmania, Australia pp. 357-364. (Hobart, Tas. : Conference Secretariat, Conference Design)

Mohammed CL, Barry K, Battaglia M, Beadle CL, Eyles A, Mollon A, Pinkard EA (2000b) Pruning-associated stem defects in plantation *E. nitens* and *E. globulus* grown for sawlog and veneer in Tasmania, Australia. In 'The Future of Eucalypts for Wood Production : Proceedings'. Country Club Casino, Launceston, Tasmania, Australia pp. 357-364. (Hobart, Tasmania : Conference Secretariat, Conference Design)

Moore RW, Siemon GR, Eckersley P, Hingston RA (1996) Sawlogs from 13-year-old *Eucalyptus globulus*. In 'Investing in the Future: Proceedings of teh Australian Forest Growers Conference'. Mt. Gambier, South Australia pp. 219-231

Moroni MT, Smethurst PJ, Holz GK (2002) Nitrogen fluxes in surface soils of young *Eucalyptus nitens* plantations is Tasmania. *Australian Journal of Soil Research* **40**, 543-553.

Munné-Bosch S, Alegre L (2004) Die and let live: leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology* **31**, 203-216.

Neilsen WA (1996) Response of Eucalyptus nitens and Eucalyptus regnans seedlings to application of various fertilisers at planting or soon after planting. *New Zealand Journal of Forestry Science* **26**, 355-369.

Neilsen WA, Gerrand AM (1999) Growth and branching habit of *Eucalyptus nitens* at different spacing and the effect on final crop selection. *Forest Ecology and Management* **123**, 217-229.

Nielsen WA, Pinkard EA (2003) Effects of green pruning on growth of *Pinus radiata*. *Canadian Journal of Forest Research* **33**, 2067-2073.

Nolan G, Greaves B, Washusen R, Parsons M, Jennings S (2005) 'Eucalypt plantations for solid wood products – a review.' Forest and Wood Products Research and Development Corporation, Melbourne, Australia 130 pp.

O'Hara KL, Buckland PA (1996) Prediction of pruning wound occlusion and defect core size in ponderosa pine. *Western Journal of Applied Forestry* **11**, 40-43.

Ozaki K, Saito H, Yamamuro K (2004) Compensatory photosynthesis as a response to partial debudding in ezo spruce, *Picea jezoensis* seedlings. *Ecological Research* **19**, 225-231.

Pearce RB (1996) Tansley Review No. 87. Antimicrobial Defences in the Wood of Living Trees. *New Phytologist* **132**, 203 - 233.

Petruncio M, Briggs D, Barbour RJ (1997) Predicting pruned branch stub occlusion in young, coastal douglas-fir. *Canadian Journal of Forest Research* **27**, 1074-1082.

Pinkard EA (2002a) Effects of pattern and severity of pruning on growth and branch development of pre-canopy closure *Eucalyptus nitens*. *Forest Ecology and Management* **157**, 217-230.

Pinkard EA (2002b) Effects of pattern and severity of pruning on growth and branch development of pre-canopy closure *Eucalyptus nitens*. *Forest Ecology and Management* **157**, 217-230.

Pinkard EA (2003) Physiological and growth responses related to pattern and severity of green pruning in young *Eucalyptus globulus*. *Forest Ecology and Management* **182**, 231-245.

Pinkard EA, Baillie CC, Patel V, Battaglia M, Smethurst PJ, Mohammed CL, Wardlaw TJ, Stone C (2006a) Growth responses of *Eucalyptus globulus* Labill. to nitrogen application and severity, pattern and frequency of artificial defoliation. *Forest Ecology and Management* **229**, 378-387.

Pinkard EA, Baillie CC, Patel V, Mohammed CL (2006b) Effects of fertilising with nitrogen and phosphorus on growth and crown condition of *Eucalytpus globulus* Labill. experiencing insect defoliation. *Forest Ecology and Management* **231**, 131-137.

Pinkard EA, Battaglia M, Mohammed CL (2007) Defoliation and nitrogen effects on photosynthesis and growth of *Eucalyptus globulus*. *Tree Physiology* **27**, 1053-1063.

Pinkard EA, Beadle CL (1998a) Above-ground biomass partitioning and crown architecture of *Eucalyptus nitens* following green pruning. *Canadian Journal of Forest Research* **28**, 1419 - 1428.

Pinkard EA, Beadle CL (1998b) Effects of green pruning on growth and stem shape of *Eucalyptus nitens* (Deane and Maiden) Maiden. *New Forests* **15**, 107-126.

Pinkard EA, Beadle CL (1998c) Regulation of photosynthesis in *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning *Trees* **12**, 366 - 376.

Pinkard EA, Beadle CL (2000) A physiological approach to silvicultural pruning. *International Forestry Review* **2**, 295-305.

Pinkard EA, Beadle CL, Davidson NJ, Battaglia M (1998) Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning *Trees* **12**, 119 - 129.

Pinkard EA, Mohammed CL, Beadle CL, Hall MR, Worledge D, Mollon A (2004) Growth responses, physiology and decay associated with pruning plantation-grown *Eucalyptus globulus* Labill. and *E. nitens* (Deane and Maiden) Maiden. *Forest Ecology and Management* **200**, 263-277.

Quentin A (2010) Growth and physiological responses of *Eucalyptus globulus* Labilladière following defoliation. Doctor of Philosophy, School of Agricultural Science, University of Tasmania.

Rayment GE, Higginson FR (1992) 'Australian laboratory handbook of soil and water chemical methods.' (Inkata Press: Melbourne, Australia)

Raymond CA, Muneri A (2000) Effect of fertilizer on wood properties of *Eucalyptus globulus*. *Canadian Journal of Forest Research* **30**, 136-144.

Reich PB, Ellsworth DS, Walters MB (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology* **12**, 948-958.

Reich PB, Walters MB, Krause SC, Vanderklein DW, Raffa KF, Tabone T (1993) Growth, nutrition and gas-exchange of *Pinus resinosa* following artificial defoliation. *Trees: Structure and Function* **7**, 67-77.

Reis GG, Pulrolnik K, Reis MGF, Silva EAM, Lima APL (2004) Wound closure in pruned Eucalyptus grandis. In 'Eucalypts in a Changing World. Proceedings of International Union of Forestry Research Organisations Conference'. Aveiro, Portugal. (Eds NMG Borrahlo, JS Pereira, C Marques, J Coutinho, M Madeira and M Tomé). pp. 11-15

Schirmer J, Parsons C, Charalambou C, Gavran M (2005) Socio-economic impacts of plantation forestry in the Great Southern region of WA, 1991-2004. FWPRDC Project No: PN04.4007.
http://www.daff.gov.au/__data/assets/pdf_file/0008/87362/36009_GSR_Text.pdf

Schupe TF, Yang ET (1995) The effects of silvicultural treatments on the chemical composition of plantation-grown loblolly pine wood. *Wood Fibre Science* **28**, 295-300.

Sharkey TD, Bernacchi CJ, Farquhar GD, Singsaas EL (2007) Fitting photosynthetic carbon dioxide response curves for C-3 leaves. *Plant Cell and Environment* **30**, 1035-1040.

Shimada A (1991) Fundamentos de nutricion animal comparativa. In 'Sistema de Educacion Continua en Produccion Animal en Mexico' pp. 375 pp: Mexico)

Shimada S, Kokubun M, Shibata H, Matsui S (1992) Effect of water supply and defoliation on photsynthesis, transpiration and yield of soybean. Japanese Journal of Crop Science. **61**, 264-270.

Smethurst PJ, Baillie CC, Cherry M, Holz G (2003) Fertilizer effects on LAI and growth of four *Eucalyptus nitens* plantations. *Forest Ecology and Management* **176**, 531-542.

Smethurst PJ, Holz G, Moroni M, Baillie CC (2004) Nitrogen management in *Eucalyputs nitens* plantations. *Forest Ecology and Management* **193**, 63-80.

Solomon DS, Blum BM (1976) Closure rates of yellow birch pruning wounds. *Canadian Journal of Forest Research* **7**, 120-124.

Stockhoff BA (1994) Maximization of daily canopy photosynthesis - effects of herbivory on optimal nitrogen distribution. *Journal of Theoretical Biology* **169**, 209-220.

Stone C (2001) Reducing the impact of insect herbivory in eucalypt plantations through management of extrinsic influences on tree vigour. *Austral Ecology* **26**, 482-488.

TAPPI (1989) Basic density and moisture content of pulpwood. *TAPPI No. T258 om-98.*

Todoroki CL (2003) Importance of maintaining defect cores. *New Zealand Journal of Forestry Science* **33**, 25-34.

Trumble JT, Kolodnyhirsch DM, Ting IP (1993) Plant compensation for Arthropod herbivory. *Annual Review of Entomology* **38**, 93-119.

Turnbull CRA, Beadle CL, West PW, Cromer RN (1994) Copper deficiency a probable cause of stem deformity in fertilised *Eucalyptus nitens*. *Canadian Journal of Forest Research* **24**, 1434-1439.

Turnbull TL, Adams MA, Warren CR (2007) Increased photosynthesis following partial defoliation of field-grown *Eucalyptus globulus* seedlings is not caused by increased leaf nitrogen. *Tree Physiology* **27**, 1481-1492.

Ueda MU, Mizumuchi E, Tokuchi N (2009) Allocation of nitrogen within the crown during leaf expansion in *Quercus serrata* saplings. **29**, 913-919.

Wardlaw TJ, Glen M, Mohammed CL (2007) Rotation-length spread of decay from branches in pruned *E. nitens*: Implications for pruning specifications. In 'Back to Basics:

Managing Plant Disease. Proceedings of 16th Biennial Australasian Plant Pathology Society Conference'. Adelaide, Australia pp. 213

Wardlaw TJ, Neilsen WA (1999) Decay and other defects associated with pruned branches of *Eucalyptus nitens*. *Tasforests* **11**, 49-57.

Washusen R, Reid R (1996) Agroforestry and farm forestry: productive trees for shelter and land protection in North East Victoria. *Agroforestry and farm forestry: productive trees for shelter and land protection in North East Victoria.*, 188 pp.

Washusen R, Waugh G, Hudson I (1998) 'Wood products from low-rainfall farm forestry.' Forest and Wood Products Research and Development Corporation project report (PN 007.96) FWPRDC, Melbourne, Australia 75 pp pp.

Washusen R, Waugh G, Hudson I, Vinden P (2000) Appearance product potential of plantation hardwoods from medium rainfall areas of the southern Murray-Darling Basin. Green product recovery. *Australian Forestry* **63**, 66-71.

Waugh G, Rozsa A (1991) Sawn products from regrowth *Eucalyptus regnans*. *The Young Eucalypt Report - some management options for Australia's regrowth forest*, 178-209.

Waugh G, Yang JL (1994) Opportunities for Sawn Poducts from Tasmanian Plantation Eucalypts. In 'Proceedings of the Biennial Conference of the Australian Forest Growers'. Launceston, Australia pp. 215-221

Waugh G, Yang JL, Ozarska B (1997) Wood properties of eucalypts for timber. In 'Environmentally Friendly Tree Products and their Processing Technology' pp. 42-50. (Forest and Forest Products Research Institute)

White DA, Beadle CL, Worledge D (1996) Leaf water relations of *Eucalyptus globulus* ssp. *globulus* and *E. nitens*: seasonal, drought and species effects. *Tree Physiology* **16**, 469-476.

White DA, Crombie DS, Kinal J, Battaglia M, McGrath JF, Mendham DS, Walker SN (2009) Managing productivity and drought risk in *Eucalyptus globulus* plantations in south-western Australia. *Forest Ecology and Management* **259**, 33-44.

White DA, Kile GA (1994) Breakdown of barrier zones and prediction of the spread of discolouration and decay resulting from stem wounds in Eucalyptus regnans and E. obliqua. *European Journal of Forest Pathology* **24**, 71-78.

White DA, Raymond CA, Kile GA, Hall MF (1999) Are there genetic differences in susceptibility of Eucalyptus nitens and E. regnans stems to defect and decay? *Australian Forestry* **62**, 368-374.

Wilkinson GR, Neilsen WA (1990) Effect of herbicides on woody weed control and growth of plantation eucalypt seedlings. *Australian Forestry*. **53**, 69-78.

Wiseman D, Smethurst PJ, Pinkard EA, Wardlaw TJ, Beadle CL, Hall M, Baillie CC, Mohammed CL (2006) Pruning and fertiliser effects on branch size and decay in two *Eucalyptus nitens* plantations. *Forest Ecology and Management* **225**, 123-133.

Wong AHH, Wilkes J, Heather WA (1983) Influence of wood density and extractives content on the decay resistance of the heartwood of *Eucalyptus delegatensis* R.T. Baker. *Journal of the Institute of Wood Sciences* **54**, 261-263.

Xu D, Dell B (2002) Nutrient management of eucalypt plantations in South China. *In: International Symposium on Eucalypt Plantations, Guangdong, PR China. Papers and Abstracts*, pp. 139-159.

Yang JL, Waugh G (1996) Potential of plantation-grown eucalypts for stuctural sawn products. II. *Eucalyptus nitens* (Dean & Maiden) Maiden and *E. regnans* F. Muell. *Australian Forestry* **59**, 99-107.

Yang Z, Midmore DJ (2004) Experimental assessment of the impact of defoliation on growth and production of water-stressed maize and cotton plants. *Experimental Agriculture* **40**, 189-199.

/