



An Australian Government Initiative



Silvicultural management of blackwood

Growth, form and quality

**A report for the RIRDC/Land & Water
Australia/FWPRDC/MDBC
Joint Venture Agroforestry Program**

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Foreword

The blackwood industry is relatively small but one of the most important and valuable in Australia that supports the furniture manufacturing and craft industries. However, it is reliant on an old growth resource that is likely to be phased out in a few decades. Planting of blackwood in both industrial plantations and farm forestry has been in place for the last decade or so.

Lack of management guidelines to define silvicultural regimes to maximise growth and optimise stem form is a major impediment to the successful production of high quality wood from this developing resource. The Joint Venture Agroforestry program (RIRDC/LWRRDC/FWPRDC) commissioned this project to develop such guidelines for nurse-crop systems that are currently in use and to investigate alternatives to these systems

This report is a summary of three years of research that has examined the silviculture of blackwood in plantations. It is the first time a physiological approach has been taken to examine how blackwood grows and responds to silvicultural treatment. An important advance is a proper definition of how to manipulate pruning and thinning commercial blackwood plantations grown with commercial nurse-crops so that adequate growth rates are maintained without prejudicing form. In addition the foundation has been laid for determining the efficacy of alternative nurse-crops to those used at present that are more suited to the development of good form in blackwood during the crucial early years following planting. This has included a better definition of the requirements for sidelight suppression.

In addition to these advances, the current knowledge base on the silviculture of blackwood has been brought up to date.

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This report, a new addition to RIRDC's diverse range of over 1000 research publications, forms part of our Agroforestry and Farm Forestry R&D program, which aims to integrate sustainable and productive agroforestry within Australian farming systems.

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Forestry Tasmania were generous in their provision of two field sites, one in an existing commercial plantation, the second a cleared native forest site for the testing of alternative nurse-crops. Thanks also to Forestry Tasmania, the Forests and Forest Industry Council of Tasmania and Britton Bros Pty Ltd for cash support and Private Forests Tasmania, the Centre for Forest Tree Technology and the University of Melbourne for in-kind support. We thank also Sven Ladiges, Alex Bradley, Gordon MacGillivray, Sven Myer, Maria Cherry, Ray McLeod, Rod Lewis, Geoff Downes, Ann Wilkinson, Phillip Pennington, Stephen Paterson and Martin Moroni for their willingness to provide technical support as required.

Abbreviations

Above sea level	asl	m
Diameter at breast height	DBH	cm
Total tree foliage area	F	m ²
Stem basal area	B	cm ²
Branch foliage area	f	m ²
Branch cross-sectional area	b	cm ²
Light-saturated net CO ₂ assimilation	A_{max}	$\mu\text{mol m}^{-2} \text{s}^{-1}$
Stomatal conductance	g_s	$\text{mol m}^{-2} \text{s}^{-1}$
Specific phyllode area	SPA	m ² kg ⁻¹
Nitrogen	N	
Phosphorus	P	
Mean foliar nitrogen concentration	N_{mass}	mmol N g ⁻¹
Mean foliar nitrogen content	N_{area}	mmol N m ⁻²
Mean foliar phosphorus concentration	P_{mass}	mmol P g ⁻¹
Mean foliar phosphorus content	P_{area}	mmol P m ⁻²
Instantaneous water-use efficiency (A_{max}/g_s)	WUE	$\mu\text{mol CO}_2 \text{ mol}^{-1} \text{H}_2\text{O s}^{-1}$
Instantaneous nitrogen-use efficiency (A_{max}/N_{area})	NUE	mmol CO ₂ mol ⁻¹ N s ⁻¹
Instantaneous phosphorus-use efficiency (A_{max}/P_{area})	PUE	mmol CO ₂ mol ⁻¹ P s ⁻¹
Net primary production (NPP)	G	kg _{DM} m ⁻² yr ⁻¹
Leaf area index (LAI)	L	m _{leaf} ² m _{ground} ⁻²
Light-use efficiency	ϵ	kg _{DM} MJ ⁻¹
Respiration	Y	kg _{DM} m ⁻² s ⁻¹
Canopy extinction coefficient	k	
Radiation incident on canopy	Q_0	MJ m ⁻² yr ⁻¹
Root biomass partitioning	η_R	
Foliage:stem biomass partitioning	η_{FS}	
Bark and branch biomass partitioning	η_{BB}	
Leaf litterfall	γ_F	
Root turnover rate	γ_R	
Ratio of height:diameter growth rates	η_{HD}	
Pruning response	P	
Generic symbol for ϵ , η_{FS} or γ_F	τ	
Per cent change in τ due to pruning	P_τ	
Incident radiation at top of canopy:top of nurse-crop	Λ	

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Executive Summary

In Australia, blackwood is logged from native forest stands. The limited size of this resource and its capacity to meet the demand for blackwood timber in the longer term, has resulted recently in the establishment of plantations in Australia. A major problem in plantation establishment is that blackwood has poor apical dominance, producing large numbers of branches and trees of poor form when grown under high light conditions.

Blackwood has two types of foliage, bipinnate compound leaves and vertically-oriented phyllodes. A phase change from leaves to phyllodes occurs although this is reversible. Changes in foliage type can be a useful indicator of the prevailing light conditions. Apical dominance is associated with conditions of low light and shade also reduces the extent of branch development, encouraging good form. Blackwood is susceptible to frost and defoliation by pests though both are a function of foliage type. Leaves are more efficient than phyllodes at producing photosynthate per unit carbon invested in foliage though both foliage types appear reasonably well adapted to a range of light environments.

Application of phosphorus fertiliser at planting is generally associated with improved early growth and this may be associated with increased numbers of root nodules. Addition of nitrogen fertiliser appears unnecessary in the absence of N deficiency. Whether grown in pure or mixed stands, form pruning is necessary to produce good stem form, and lift pruning of live branches to produce clearwood. Various approaches to form pruning have been used but each is designed to prevent the development of large branches. Crown shape, which is variable in blackwood, can determine whether lift pruning reduces subsequent growth. Establishment at high stockings and thinning to a final crop of between 100 and 250 stems ha⁻¹ is used commercially. The use of nurse-crops to induce good form and to minimise the requirement for form pruning has been used, particularly in Tasmania. This has met with mixed success as the use of eucalypts or *Pinus radiata* has led to overtopping and suppression of the blackwood.

A study investigated the feasibility of silvicultural intervention in blackwood plantations grown with a *Pinus radiata* nurse crop, to improve stem form and growth rate. The objective was to evaluate silvicultural options for managing the nurse crop to avoid suppression but improve stem form of blackwood. Using a five-year-old blackwood – *P. radiata* plantation, various levels of form pruning of the blackwood were tested by removing prescribed proportions of leaf area from treatment trees, either 25 or 50 per cent of tree foliage throughout individual tree crowns. In addition, a range of thinning treatments was imposed on the nurse crop. The effects of these treatments on blackwood growth rate, stem form, rate of crown development, and canopy light environment were assessed. Altering the canopy structure of the plantations by thinning the *P. radiata* nurse crop had a positive effect on diameter growth of blackwood. However less desirable changes were also evident following the thinning, such as reduced height increment, loss of dominance and a greater incidence of large branches in blackwood trees. Appreciable changes in the light environment of the blackwood crowns occurred only after more than 50 per cent of *P. radiata* trees were removed. Crowns of blackwood trees pruned of 50 per cent of their foliage area took 12 months to recover to pre-pruning levels of foliage area. Form pruning of blackwood significantly reduced growth when 50% of foliage area was removed.

Improvements in form by pruning were transient in nature, highlighting the need for on-going, low-intensity form pruning to establish good stem form. The rapid deterioration in form after heavy thinning of the nurse-crop indicated the need to establish form before reducing nurse-crop competition.

In a parallel study in the same plantation, the photosynthetic responses of the blackwood to the form pruning treatments were examined. Photosynthetic capacity, expressed as light-saturated photosynthetic rate (A_{max}), was measured periodically over a twelve-month period.

An increase in photosynthetic capacity was observed immediately after pruning in the 50 per cent pruning treatment, although this increase was confined to the upper two-thirds of the crown. Relative to the A_{max} measured prior to pruning, the greatest increase in A_{max} occurred in the middle crown zone of both the 25 and 50 per cent pruning treatments and the increase was limited to the first month post-treatment.

While maximum stomatal conductance values were generally higher following 50 per cent pruning, there were no pruning-induced changes in photosynthetic water-use efficiency. Foliar nutrient content was not altered by pruning treatment. Crown position had a significant influence on foliar nutrient content, photosynthetic water-use efficiency and photosynthetic nitrogen-use efficiency. Form pruning that removes foliage from upper crown positions will have the greatest impact on physiological functioning.

The role nurse-crops play in producing good stem form in blackwood, and the planting designs required to establish good form from an early age were examined in a 1- to 2-year old plantation. Within the plantation, an experiment using artificial shading quantified the link between light environment across a range of treatments and blackwood stem form.

The importance of the nurse-crop in providing an environment required for good form was becoming evident even at two years of age. While few differences in blackwood growth rate were observed at this early age, the different growth patterns of nurse-crop species and their planting in relation to the blackwood were already influencing blackwood stem form. Blackwood stem form was good in nurse-crop systems where the height of the blackwood was less than that of the nurse-crop, highlighting the importance of a 'lightwell' for good blackwood form. For commercial nurse-crop species, closer spacing than conventional is producing better blackwood form. However, there is also a tendency for slower blackwood growth, meaning that management of blackwood under systems such as the five-row nurse treatment must be vigilant to avoid blackwood growth suppression. The manipulation of sidelight using shade cloth showed that sidelight (defined as the daily light conditions measured at mid-stem height) was not significantly reduced unless the shade cloth height was the same height as the blackwood, or taller, at a distance of 50 cm from the blackwood. The sidelight suppression achieved with this treatment was matched with improved stem form.

It was concluded that fast-growing nurse-crop species, planted at close spacing, provide the earliest substantial sidelight suppression for blackwood. Height growth of slower-growing species planted at a similar distance from the blackwood was not suppressing sidelight sufficiently at this stage of the rotation. It is too early to evaluate the effectiveness of the lightwell system in producing good blackwood form. Ongoing measurement of blackwood and nurse-crop growth and form in this experimental plantation would provide valuable information for developing planting systems and management prescriptions for blackwood nurse-crop plantings.

A simple model based on plausible assumptions governing light interception, biomass partitioning, canopy development, and stem height and diameter growth was developed to model the growth of blackwood in response to form pruning and nurse-crop thinning. The response to form pruning postulates a pruning response that decays with time and affects one or more of light-use efficiency, ratio of foliage:stem biomass partitioning, and leaf litterfall. A model for partitioning intercepted radiation in a multi-species canopy takes into account effects of the nurse-crop. The basic elements of the model are summarised, and its qualitative behaviour compared to observed growth data from both blue gum (*Eucalyptus globulus*) and blackwood.

Chapter 1: Introduction

In Australia, blackwood (*Acacia melanoxylon* R. Br.) is used principally to support a furniture manufacturing and craft industry and is generally associated with the production of up-market products. To date, logging has been exclusively from native forest. The major part of this industry (about two-thirds) is located in north-west Tasmania where the species is observed to develop its full potential both in terms of growth and wood quality. A smaller part of the industry is based in Western Victoria.

Harvesting currently is exclusively from old-growth native forest, and in recent years up to 16 000 m³ per annum has been harvested in Tasmania from public and private lands. While it is anticipated that this source can be managed for some time to meet current demand for blackwood, it is likely that logging in old growth forest will be phased out in approximately 30 years. Regrowth forests (that replace old growth) are primarily managed for eucalypt production. They have an unknown blackwood component and cannot be relied on for a long-term blackwood supply.

It is widely recognised that the longer-term maintenance and expansion of the industry is dependent on the success of silvicultural systems based on plantations and farm forestry. Currently, plantations and more open-grown stands on farms are being established throughout Tasmania and Victoria.

Lack of management guidelines to define silvicultural regimes to maximise growth and optimise stem form is a major impediment to the successful production of blackwood in plantations and farm forestry in Australia. The production of high quality blackwood from plantations requires green pruning, as well as either a nurse-crop or manipulation of stand density for sidelight suppression, to improve apical dominance and stem form. These treatments reduce growth if inappropriately applied, and suppression of blackwood by nurse-crops is commonly encountered in plantations in Australia. There is little understanding of how to manipulate these treatments to optimise stem form, or of variation in response related to site or environmental conditions.

This project was developed specifically to address the appropriate management of nurse-crops that are currently used in commercial blackwood plantations in Australia and to investigate the use of alternative nurse-crops that have the potential to better influence the development of form than those used currently. There were three main components:

- Various levels and types of form pruning and nurse-crop thinning were used to investigate their effects on growth and form in a five to six-year old commercial blackwood plantation grown with *Pinus radiata* as nurse-crop.
- Novel nurse-crop systems were developed in an experimental plantation established as part of this project. Sidelight suppression and its potential for imposing good form during the early phase of growth was investigated
- A prototype decision support system was developed to determine the optimal timing for thinning the nurse-crop and pruning the blackwood to maximise growth and form of the blackwood.

The report begins with a review of our current understanding of blackwood silviculture. During the project, a workshop was convened by the Blackwood Industry Group (BIG) on this theme. A report on this workshop 'Silvicultural Management of Blackwood' appeared as RIRDC Publication No 01/176 in December 2001. The Blackwood Industry Group was convened after an earlier workshop at Lorne, Victoria in November 1996. The group publishes a Newsletter that has been managed through this project. Two Newsletters have appeared and were distributed to members of BIG.

Chapter 2: A review¹

Introduction

Blackwood (*Acacia melanoxylon* R. Br.) is one of Australia's native ornamental timber species (Boland et al. 1984). It is much sought after by the furniture manufacturing and craft industries (Britton 1996) because of its wood properties, including colour (Harris and Young 1988). Blackwood grows between 6 and 35 m tall, and occurs naturally throughout the eastern seaboard as far north as southern Queensland in areas with an annual rainfall of greater than 600 mm (Costermans 1981). Its best development, in terms of superior growth and form, is found in cool temperate environments with deep soils, especially in tall forests in Tasmania and Victoria (Boland et al. 1984).

Native forest logging in Tasmania and western Victoria is the predominant source of blackwood, although small quantities come from plantation-based resources in New Zealand, South Africa and Brazil (Nicholas 1981; de Zwaan 1982). Across its natural distribution, there are three forest types - swamp, wet sclerophyll and riverine - that support the production of high quality timber (Jennings 1998; Searle 2000). This is primarily because the structure of the forest encourages apical dominance and height growth, and restricts development of large branches (Allen 1992). Thus each type is characterised by the co-occurrence of blackwood with other species that restrict available sidelight during early growth, while allowing the upper crown to remain well lit. In swamp forests, close-spaced *Leptospermum* and *Melaleuca* species growing at the same rate as the blackwood result in the development of branch-free boles >15 m. In wet sclerophyll forests, the co-occurring species are *Pomaderris apetala* Labill. and eucalypts, mainly *Eucalyptus obliqua* L'Herit. and *Eucalyptus regnans* F. Muell. The length of the branch-free bole is noticeably shorter (but >5 m) because of the limited height of *P. apetala* which provides the majority of the sidelight suppression. Some thinning of the eucalypts is required in this forest type to maximise blackwood production (Jennings 1998). In riverine forests, blackwoods emerge through "light wells" into existing rainforest. These wells provide similar light conditions for growth and form as are found in swamps.

It is unlikely that the limited native forest resource can be managed sustainably to meet the current, as well as potential increases in, demand for blackwood timber (Allen 1992). Hence there is growing interest in Australia in the establishment of blackwood plantations. To date, approximately 800 ha have been established in Tasmania, the State with most potential for growing blackwood in plantations (Nielsen and Brown 1996). Conditions in plantations differ considerably from natural environments in which blackwood thrives. At planting, there is no sidelight suppression and no shelter. In addition, intensive silviculture generally is required in order to produce high quality logs (Pinkard and Beadle 2001). However the blackwood industry is small, and relatively little research has occurred into suitable management regimes for plantations.

The objective of this paper is to summarise current knowledge of blackwood plantation silviculture. The variables that are known to affect the growth and physiological behaviour of blackwood are first explored, including a consideration of wood properties and environment. Silvicultural practices to improve growth and form in plantations are then discussed.

Growth

As blackwood is considered to be a minor timber species, it is not surprising that existing knowledge about how quickly this species grows and what drives that growth is at best basic. On high productivity, sheltered sites in New Zealand, height and diameter growth rates of approximately 1 m year⁻¹ and 1.5 cm year⁻¹, respectively have been reported for plantations during the first 10–11 years of growth (Nicholas 1988, 2001). On equivalent sites, similar results for height growth have been reported in Japan and Tasmania (Waki 1984; Nielsen and Brown 1996). This may drop to as little as 0.3 m year⁻¹ on exposed or drought-susceptible sites (Nielsen and Brown 1996). More rapid growth

¹ Based on a manuscript developed by E.A. Pinkard and C.L. Beadle and published in *Australian Forestry* 65:7-13

rates have been achieved in South Africa, with 2 m year⁻¹ in height growth reported over the first four years of growth (de Zwaan 1980).

Heteroblasty, expressed by having foliage of different kinds, and poor apical dominance are characteristics of blackwood that have captured researchers' attention. In addition problems associated with unfavourable climatic conditions, particularly frost, and pests have been issues associated with plantation establishment. The consequences of crown shape and foliage distribution in relation to stem growth also have been investigated. These factors are now considered in more detail.

Light, foliage type and apical dominance

Blackwood has two types of foliage that can be described in broad terms as juvenile and adult. After germination, bipinnate compound leaves are produced. Later, expansion of the petiole results in vertically-oriented phyllodes (Costermans 1981). The leaves are mesomorphic, with thin cuticles and little structural thickening. Virtually all tissues are photosynthetic (Brodrribb 1992). In contrast, the phyllodes have a more elaborate structure, with very thick cuticles and substantial lignification. About half the tissue is photosynthetic, the rest serving support and storage functions (Brodrribb 1992).

High light conditions lead to an earlier change from leaves to phyllodes. In pot experiments phyllodes appeared within four to eight months on seedlings grown in full sunlight, whereas those grown at 20% full sunlight had only leaves until at least twelve months of age (Milton 1982; Brodrribb 1992). Under some conditions this phase change may not occur or is reversed. Thus under prolonged shade, the leaves may persist for several years (E.A. Pinkard, unpublished data) while there may be a reversion to leaves following a change from exposed to shaded conditions. The production of leaves may be associated with environments (eg. low light conditions) that favour apical growth (Borchert 1965; Carr and Burdon 1975). Factors other than light intensity may also trigger phase change. Brodrribb and Hill (1993) hypothesised that photoperiod and temperature may play a role and Farrell and Ashton (1978) suggested that phyllode initiation was inversely correlated with annual rainfall.

Leaves may be an adaptation to deal with low or variable light conditions, or to maximise height growth in environments where there is competition for light. Farrell (1973) suggested that leaves were shade adapted and phyllodes were sun adapted. This argument was supported by Milton (1982) who found that blackwood grown in shade had greater total foliage area, and greater height growth, than plants grown in sun. In addition, seedlings compensated for low light conditions by retaining leaves for longer and producing larger and more horizontal leaves.

Blackwood has poor apical dominance when grown under high light conditions (Barton 1993; Nicholas and Gifford 1995; Neilsen and Brown 1996). This results in large numbers of branches and relatively short trees. Apical dominance is strengthened by good growing conditions combined with adjacent vegetation that offers sidelight suppression, particularly during the early phase of growth (Brown 1997). Exposure to browsing, strong winds and frost can reduce apical dominance (Neilsen and Brown 1996; Brown 1997).

Thus both apical dominance and height growth increase under low light conditions (Milton 1982). Although height growth increased under shade, shoot dry mass did not differ between plants grown in sun or shade (Milton 1982). The ratio of shoot:root dry mass was also substantially greater in plants grown under shade than those in a high light environment. Blackwood seedlings grown in the shade allocated less biomass to branch development, although total leaf area could be as great as or greater than that of seedlings growing under high light (Milton 1982). These changes in biomass partitioning allow shaded blackwood to maintain height growth and produce trees of good form where sidelight suppression is adequate.

Frost

Phyllodes have greater frost resistance than leaves, probably as a result of the thicker cuticle and greater cell wall thickening (Brodribb and Hill 1993). In a comparative study of several *Acacia* species, including blackwood, Pollock et al. (1986) observed seasonal increases in frost tolerance of up to 4°C in winter. Blackwood was one of the more frost resistant species. However provenance trials have demonstrated inter- and intra-provenance variation in frost susceptibility (Franklin 1987; Brodribb 1992; Neilsen and Brown 1996). Neilsen and Brown (1996) found that high altitude provenances were less affected by frost than low altitude or coastal provenances, but were also slower growing. Within these generalisations, it is important to recognise that microenvironment and ambient conditions during hardening and dehardening are important determinants of the ability of any species to survive a frost (Greer and Stanley 1985; Hallam et al. 1989). A study of blackwood in China found that frost injury was most related to cold air pooling associated with topography and terrain rather than to altitude (Yang et al. 1992).

Pests

Blackwood foliage contains up to 16% protein content, and is a desirable food for many browsing animals (de Zwaan 1982; Neilsen and Brown 1996). Neilsen and Brown (1996) found that mammal browsing significantly reduced height growth over the three years following planting, with little height increment if seedlings were left unprotected from browsing. As pointed out above, browsing can lead to poor apical dominance. Another study using insecticides concluded that insect defoliation was not the major cause of poor apical dominance at one site in New Zealand (Nicholas and Hay 1990).

As phyllodes are less palatable than leaves to browsing animals and phosphorus (P) increases the proportion of phyllodes to leaves in the nursery, sound P nutrition may contribute to the survival of outplanted stock (Knight 1986).

Crown characteristics and stem growth

Stem growth rate may vary with crown shape and hence with patterns of foliage distribution through the crown. de Zwaan (1981a) found that trees with conical (largest branches in lower crown) or diamond-shaped (largest branches in mid-crown) crowns grew faster than those with poplar-shaped (long and narrow) crowns. Differences in crown shape appeared to be related to foliage area. The proportion of phyllodes present in the crown also may affect height growth. de Zwaan (1982) determined that growth rate decreased as the proportion of phyllodes increased, and Brodribb and Hill (1993) observed that slower growing provenances of blackwood generally produced phyllodes earlier than did faster growing provenances. This may also be an adaptation to deal with prolonged frost susceptibility associated with slower growth rates.

Physiological characteristics

Brodribb (1992) demonstrated that, while photosynthetic rates per unit leaf area were similar between leaves and phyllodes, leaves had greater photosynthetic rates per unit dry weight at most light intensities than did phyllodes. This means that a leaf is more efficient than a similar-sized phyllode at producing photosynthate per unit of carbon invested in foliage. The reduced investment of carbon required for leaf production results in a greater potential for rapid development of shoots and roots early in the life cycle (Brodribb 1992). Brodribb (1992) also found that increases in photosynthetic rates with increasing light levels of leaves and phyllodes were similar under conditions favourable for plant growth. A high degree of between-leaf/phyllode variability in these response curves suggests that foliage of either type has the capacity to adapt to a range of light environments (Brodribb 1992).

Brodribb (1992) observed that under water-stressed conditions, phyllodes had a higher water-use efficiency ($\text{g CO}_2 \text{ g}^{-1} \text{ H}_2\text{O}$) than leaves (Brodribb 1992). At soil water potentials below -2.8 MPa leaves had lower water-use efficiency than phyllodes, irrespective of relative humidity. Leaves were

damaged beyond recovery at these water potentials, whereas phyllodes recovered fully from water potentials as low as -5.5 MPa. These findings support the belief that phyllodes are an adaptation to drought (Givnish 1978).

Like many legumes, blackwood forms a symbiotic relationship with a nitrogen (N)-fixing bacterium that induces nodule formation on blackwood roots. The bacteria provide N to the plant in return for carbohydrate (Fogg 1966). However, little is known of the physiology of blackwood root nodules, although light environment, nutrition and water availability all may affect nodulation (Davey and Wollum 1984). Milton (1982) found that, while number and size of nodules on 15-month-old seedlings were reduced under low compared to high light conditions, nodule dry mass per unit root dry mass was greater for the shaded than the exposed plants. Nodule dry mass per unit whole plant dry mass was the same for sun and shade plants.

The effect of water stress on blackwood root nodules is unknown. However, water stress has been reported to reduce both N fixation and nodule development in a number of species (Mrema et al. 1997; Gonzalez et al. 1998). In *Leucaena leucocephala* seedlings inoculated with *Rhizobium* bacteria the combined effect of water stress and N addition resulted in cessation of N fixation, although the presence of root nodules in plants not receiving N increased tolerance to water stress (Mrema et al. 1997).

Wood properties

Blackwood is a medium density hardwood. Its basic density ranges between 465 and 671 kg m⁻³ (Harris and Young 1988; Clark et al. 1992). Basic density generally increases with age, although there is a large between-tree variation (Harris and Young 1988). A strong negative relationship has been found between basic density and rainfall in *Eucalyptus globulus* Labill. (Raymond and Muneri 2000): the effects of environment on basic density of blackwood have not been investigated. Streaks of tension wood are common in blackwood, and tend to become very gummy in the heartwood. This gives rise to dark coloured wood (Harris and Young 1988). Blackwood with poor form (ie poor apical dominance) has a tendency for severe cross-grain which makes processing difficult (Haslett 1986).

Heartwood development is greatest on moist but well-drained deep organic soils. Wetter, more organic soils seem to produce finer grain, and high rainfall may promote heartwood darkness (Harrison 1975b). The number of rain days may be more important than total annual rainfall in determining darkness, and a dormant growth season may maximise the brown pigment that is important in determining heartwood darkness (Harrison 1975b). In a study of genetic and environmental effects on timber quality, Harrison (1975a) found no correlation between timber and foliage characteristics.

Silvicultural practices to improve growth and form

Silviculture in blackwood plantations aims to improve growth rates and apical dominance, thereby producing tall, straight stems with small branches. The most valued products are veneer quality logs and timber suitable for furniture manufacturing and craft (Britton 1996). In most instances intensive silvicultural management is required in order to produce high quality blackwood in plantations over rotations of around 45 years (Searle 1996). To date only limited research has been undertaken, and this is summarised below.

Fertiliser application

As nitrogen-fixing bacteria provide N to the plant, it is commonly considered that N fertilisation is unnecessary in blackwood plantations. Waki (1984) found that large applications of N to established *Acacia mearnsii* did not improve growth, while growth was improved through phosphorus (P) application. Similar results were observed in a field study of blackwood (E.A. Pinkard, unpublished data). Large growth responses of blackwood to P but not to N or potassium (K) in South Africa (de

Zwaan 1982) support this finding. In a study using potted seedlings, Knight (1986) showed that a substantial and similar requirement for sulphur (S) and P were required to maximise seedling height and dry mass. Vigorous growth was associated with foliar N:P:S of 2.7%:0.23%:0.16% and he concluded that superphosphate (10% P:11% S) was a suitable fertiliser source for both nutrients.

Applications of N are important to early growth of *A. mearnsii* (Waki 1984). In blackwood, Brodribb (1992) found that N deficiency significantly depressed photosynthetic rates of leaves, although phyllodes with similar levels of N were unaffected, suggesting that N nutrition may be an important determinant of growth during the juvenile phase.

Fertilising four-year-old trees with P doubled the number of root nodules, but applications of N had no significant effect on nodulation at a site in Tasmania (E.A. Pinkard, unpublished data). Waki (1984) also found that applications of P improved root nodulation in *A. mearnsii*, while N application had no effect. Large positive responses of blackwood to P addition have been reported in a number of studies (eg. de Zwaan 1982; Nicholas 1988). This has led to the general recommendation that P fertiliser be applied routinely at establishment of blackwood plantations (Nicholas 1988; Neilsen and Brown 1996). However at one New Zealand site with poor soils and summer drought, a negative linear relationship between diameter increment and application rate of superphosphate was observed. This was partly related to increased weed competition following the fertiliser application (Fairweather and McNeil 1997). Fertiliser responses will depend on soil type, water availability, competition from surrounding vegetation, and the presence and activity of root nodules.

Pruning

The primary objective of growing blackwood in plantations is the production of clearwood (knot-free timber). The characteristic lack of apical dominance exhibited by blackwood growing in high light environments, and its propensity to produce large branches, means that pruning may be necessary to produce clearwood. Two types of pruning are used: form pruning where selected branches are removed from throughout the crown; and clearwood pruning where all branches are removed from the lower crown to a predetermined height above ground.

Form pruning has been found to improve stem form and increase the number of trees that can be selected for clearwood pruning (Nicholas and Gifford 1995). Form pruning removes large (>3 cm diameter) branches and/or competing leaders. In New Zealand an experiment investigated annual and triennial form pruning, and annual form pruning to remove all branches >3 cm diameter. The treatments improved tree form by 15 – 18%, where form is judged on stem straightness, presence or absence of multiple leaders and number of large or competing limbs. The annual pruning that only removed branches >3 cm diameter removed the least number of branches over a four-year period (6.9 tree⁻¹), while the annual form pruning removed 11.3 branches tree⁻¹. Diameter and height increment were not affected by these treatments four years after pruning (Nicholas and Gifford 1995). Both treatments improved the ease of clearwood pruning because they reduced the number and size of branches to be removed in that operation.

Tip pruning has been suggested as an alternative to form pruning for open-grown trees (Barton 1993; Brown 1997). It involves removing about a third of the length of all competing shoots, and has been found to improve stem form. A similar method, known as segmental pruning, reduces stem malformation and development of large branches. Segmental pruning removes competing shoots, and reduces any remaining vertical shoots to half their original length (Brown 1997). Both tip and segmental pruning start about six months after planting, and must be carried out at the beginning and end of each summer in order to be successful. Hence they are expensive options for large-scale plantations.

Clearwood pruning removes live branches and is usually done in a number of stages known as lifts. In studies with species other than blackwood (eg. Helms 1964; Heichel and Turner 1983; Pinkard and Beadle 1998), the effects of pruning on growth were related to the amount of leaf area removed

and physiological characteristics such as foliage distribution throughout the crown, photosynthetic responses and rates of leaf development following pruning. Much of this information is not known for blackwood. However in South Africa it was demonstrated that crown shape (ie foliage distribution) affects responses to first lift pruning. Trees with poplar or diamond shaped crowns showed little change in stem growth following pruning, because little foliage was removed by the removal of 40% of green crown length. There was a significant reduction in stem diameter of trees with cone and bullet shaped crowns following pruning, although growth rates recovered in the longer term (de Zwaan 1981a). Nicholas and Gifford (1995) recommended removing a maximum of 50% of crown length to minimise growth losses following pruning. In Tasmania the recommended pruning regime involves removal of 40% of crown length (Neilsen and Brown 1996).

Pruning creates a cut surface that is a potential portal for the entry of pathogens causing disease and decay. Pruning wounds heal fastest when small (1–2 cm diameter) and when cuts are vertical (Nicholas et al. 1994). Large wounds (> 4 cm diameter) may take more than four years to occlude, increasing the risk of decay entry. There has been little study of microbial infection of pruning wounds in blackwood (Nicholas and Hay 1990; Swanson 2001), although serious problems may be encountered in eucalypts (Wardlaw 1996; Mohammed et al. 1998). Nicholas and Gifford (1995) recommended that form pruning should commence before four years of age to reduce the incidence of large pruning wounds.

Thinning

Thinning is required in blackwood plantations to ensure good diameter growth of pruned stems (Nicholas 1988). In New Zealand crown diameter ratios were used to determine that a final stocking of 100 stems ha⁻¹, while not maximising volume production of the stand, would allow maximum diameter growth of crop trees during a rotation of 40 years (Nicholas 1988). The recommended regime involves three thinning operations, from an initial stocking of 1500 stems ha⁻¹ to 1000 stems ha⁻¹ at age three, then to 150 stems ha⁻¹ at age 10, and to the final stocking of 100 stems ha⁻¹ at age 13 years (Nicholas 1988).

A progressive thinning to a final stocking of between 300 and 400 stems ha⁻¹ at age 17 years maximised the volume of utilisable timber at age 34 years in South Africa (de Zwaan 1982). Thinning to 173 stems ha⁻¹ was too severe, and to 445 stems ha⁻¹ may have been too light in terms of maximising both stand and individual tree volume.

The optimum stocking in natural stands in swamp forest in Tasmania is about 200 stems ha⁻¹ (Allen 1992). The Tasmanian blackwood plantation regime recommends thinning to a final stocking of 250 stems ha⁻¹ in one operation (Neilsen and Brown 1996).

Using nurse-crops to improve form and early growth

In native forests that include a blackwood component, the surrounding vegetation suppresses sidelight and offers buffering from high and low temperatures and wind, thereby promoting apical dominance (Jennings 1998). Nurse-crops are used in plantations to induce these effects. The main species that have been used to date are *Pinus radiata* L., *Eucalyptus nitens* (Deane and Maiden) Maiden or *E. globulus* (Neilsen and Brown 1996), although rainforest species such as *P. apetala* and *Melaleuca ericifolia* Sm. have been used on a small scale in experimental trials (S. Jennings, Forestry Tasmania, pers. comm.). Inter-planting blackwood with a nurse-crop species can improve blackwood form in some instances (Neilsen and Brown 1996). However, in New Zealand, there was little improvement in form when mixed blackwood/*P. radiata* plantings were compared with pure blackwood stands, and this led to the recommendation that pure blackwood stands be established. The success of the nurse-crop species in providing sidelight suppression and protection from wind and temperature extremes will depend on the density at which the nurse-crop is planted, the species used and the relative growth rates of the blackwood and the nurse-crop. In Tasmania, alternate rows of blackwood and the nurse-crop are spaced at 2.5 m to 4.0 m intervals. This system results in little

early ‘nursing’ of the blackwood and means that pruning must be combined with the nurse-crop system.

Nurse-crops may be ineffective in protecting blackwood from wind and frost damage. Franklin (1987) found that an *E. nitens* nurse-crop established with blackwood had little effect on frost-induced damage of blackwood, even when the eucalypts were 4–5 m tall. Most of the frost damage appeared to be caused by ponding of air and freezing fogs rather than radiation frosts. Where blackwood was planted under an existing cover of eucalypts, however, frost damage was negligible. Neilsen and Brown (1996) similarly found that there was greater frost damage and reduced height growth of blackwood grown near a windbreak than in the open, which they attributed to poor cold air drainage. This suggests that row orientation may be important in determining the effectiveness of a nurse-crop if ponding of cold air is likely to be a problem. In frost-prone areas establishing the nurse-crop before the blackwood may offer greater protection from frost damage.

Eucalypt species and *P. radiata* remain the favoured nurse-crop species (de Zwaan 1981b; Nicholas 1988; Neilsen and Brown 1996) and, as they generally have a much faster growth rate than does blackwood, it is possible to get effective early nursing if the *P. radiata* is spaced appropriately. However overtopping and eventual suppression of the blackwood can then be a problem (de Zwaan 1981b). For example at age five years, the average height of the blackwood and *P. radiata* nurse-crop was 7.2 m and 5.4 m, respectively (Medhurst and Worledge 2001). Thinning of the nurse-crop is therefore required. Removal of 66% of the *P. radiata* nurse-crop at age five years resulted in a significant increase in diameter growth of the blackwood (Medhurst and Worledge 2001) although this was accompanied by some deterioration of stem form of the blackwood (J.L. Medhurst, unpublished data).

There is little information comparing direct versus progressive thinning regimes for blackwood/nurse-crop systems. Direct regimes are favoured in large-scale plantations in Tasmania except where the aim is to produce clearwood from selected nurse-crop trees as well as the blackwood (Neilsen and Brown 1996). Windthrow can occur if the nurse-crop is thinned too late or too severely as blackwood growing in low light environments has a greater shoot: root ratio than do open-grown trees (Milton 1982). However factors influencing windthrow, including timing and severity of thinning, have not been examined in detail. When the nurse-crop is much taller than the blackwood, the potential for damaging the blackwood stems during thinning also requires consideration.

An alternative to thinning was tried in South Africa. It involved lopping the tops of the nurse-crop trees. However, it was done once the nurse-crop was too large for thinning, and it proved impractical (de Zwaan 1981b).

Conclusions and implications for management

Blackwood has proven to be a species that is not easy to grow in plantations without a substantial amount of intervention. This must include some level of form pruning and lift pruning to produce clearwood (Barr 1987; Barton 1993). Thinning schedules have also been developed. However, there may be opportunities to use nurse-crops more effectively than at present. While nurse-crops like eucalypts and *Pinus radiata* may improve form and reduce branch size (Neilsen and Brown 1996), there is little evidence that they provide much ‘nursing’ of the blackwood early in the rotation. Later, if managed inappropriately, nurse-crops can result in suppression of the blackwood and damage to blackwood stems during thinning operations. As nurse-crops remain an attractive option for inducing form in industrial plantations, more effective management of the species used at present or the possible use of alternative nurse-crops requires some attention.

The response of blackwood to fertiliser and the role of root nodules in its nutrition remain poorly understood. There is a positive response to phosphorus application (de Zwaan 1982; Nicholas 1988) and apparently no response to nitrogen application. However fertiliser responses are anticipated to

vary with site conditions such as soil fertility, moisture availability and level of weed competition, a level of detail that still requires more insight.

As blackwood has considerable within- and between-provenance and between-tree variation in growth, timing of phyllode initiation, crown shape and wood properties of blackwood (Harrison 1975a; de Zwaan 1982; Brodribb 1992), there may be potential for tree improvement through provenance selection and genetic manipulation (Searle 2000).

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Chapter 3: Growth¹

Introduction

Acacia melanoxylon R. Br., commonly referred to as blackwood, is a versatile and highly adaptive tree species that occurs naturally across a wide range of Australian forest ecosystems (see Searle 2000). This success is in part due to the ability of *A. melanoxylon* to tolerate a wide range of shade conditions. *A. melanoxylon* exhibits weak apical dominance (Nicholas et al. 1994) which enables a rapid crown response to changes in the directions of direct sunlight through the forest canopy. As a consequence, *A. melanoxylon* grown in open conditions with little or no competition for light typically displays poor form with short stems and a wide crown characterised by heavy lateral branches (Unwin et al. 2001). In contrast, *A. melanoxylon* growing as an understory species in wet sclerophyll forest or in pure stands of high stand density generally receives direct sunlight only from above. This tends to produce trees with straight stems free of lateral branching.

When stems have desirable form, *A. melanoxylon* is a highly valued timber species used for furniture, veneer and cabinet-making (Searle 2000). A potential increase in the demand for timber combined with restrictions on the logging of native forest will result in shortfalls in the supply of *A. melanoxylon* timber from natural forests in Tasmania (Forestry Tasmania 1999). An option for meeting the predicted supply shortage is the growing of *A. melanoxylon* in commercial plantations. Since the early 1990s, *A. melanoxylon* plantations have been established in Tasmania (Neilsen and Brown 1997) to meet the minimum area of 1200 ha of *A. melanoxylon* plantations recommended by Allen (1992).

The major challenge facing growers of *A. melanoxylon*, once the plantations are established, is the manipulation of form to produce acceptable sawlogs (Allen 1992). In most instances this requires active management of the light environment, in particular minimising the amount of sidelight reaching individual crowns. Industrial plantations of *A. melanoxylon* in Tasmania aim to achieve sidelight suppression by cultivating the *A. melanoxylon* with other tree species that act as nurse-crops. Nurse-crops produce a “light well” with direct light available only from above, and thus growth of the *A. melanoxylon* is directed upwards, producing small branches and good stem form (Neilsen and Brown 1997).

The main nurse-crop species used in Tasmania are *Pinus radiata* D. Don, *Eucalyptus globulus* Labill. and *Eucalyptus nitens* (Deane & Maiden) Maiden. Current spacings at planting (2.5 – 4 m) result in minimal sidelight suppression of *A. melanoxylon* early in the rotation, which increases the potential for the development of poor stem form. In addition, the faster initial growth rate of the *Eucalyptus* species (and to a lesser extent, *P. radiata*) can result in suppression of the *A. melanoxylon* due to overtopping and resultant low light conditions (Neilsen and Brown 1997).

The conflicting response of growth rate and form to an improvement in light conditions makes management of *A. melanoxylon* plantations difficult. Managing the light conditions in a nurse-crop system so as to maintain adequate growth of *A. melanoxylon* without loss of characteristics commensurate with desirable form requires the use of silvicultural treatments such as form pruning and nurse-crop thinning.

This study applied a range of levels of form pruning to *A. melanoxylon* in combination with a range of nurse-crop thinning intensities to a young *A. melanoxylon* – *P. radiata* plantation. The aims of the study were to quantify the changes in growth and form of *A. melanoxylon* in response to treatment; to relate these to crown dynamics of *A. melanoxylon* and changes in the light environment following treatment; and to identify appropriate pruning and thinning practices for *A. melanoxylon* growing with a nurse-crop.

¹ Based on a manuscript developed by J.L. Medhurst, E.A. Pinkard, C.L. Beadle and D. Worledge and accepted by Forest Ecology and Management

Materials and Methods

Site description

The Beulah thinning and pruning experiment was located in a plantation in northern Tasmania (41° 28' S 146° 21' E). The plantation was established on a site previously carrying *Eucalyptus obliqua* L'Herit native forest. The soils consisted of clay loam overlying light clay subsoils derived from Cambrian sandstone/greywacke parent material (Grant et al. 1995). The area was logged, windrowed and burnt, and mound ploughed prior to planting. The site was planted in 1994 using open-rooted *A. melanoxylon* seedlings (seed from a local collection). *P. radiata* was planted as a nurse-crop at 5.0 x 2.5 m (800 trees ha⁻¹). *A. melanoxylon* was planted between every second row of *P. radiata* at 10.0 x 2.0 m (500 trees ha⁻¹). The plantation was fertilized at age five years with 70 kg ha⁻¹ of phosphorus. The plantation was at an altitude of 250 m above sea level (asl). The long-term mean annual rainfall, and mean daily maximum and minimum temperatures at the nearby township of Sheffield (at 280 m asl) were 1179 mm, 16 °C and 6 °C, respectively. As part of this study, a meteorological station was established in an open area 2 km from the trial site and at the same altitude. Instrumentation included a tipping-bucket rain gauge with a 0.2 mm bucket and a screened Vaisala probe to measure air temperature. A data logger (Campbell 21X, Campbell Scientific, Logan, Utah, USA) was programmed to record instantaneous climatic data every 5 minutes and store hourly totals. During the twelve months of the experiment, 1243 mm of rainfall was recorded and mean daily maximum and minimum temperatures were 16.9 °C and 5.6 °C, respectively.

Treatments and experimental design

The experiment was established in January 2000. It consisted of twelve plots in a randomised complete block design with three replicates of four nurse-crop thinning treatments. Each plot was laid out across two rows of *A. melanoxylon* with a buffer row of *A. melanoxylon* on each side. Plot length was approximately 60 m and plot size was approximately 0.12 hectares, incorporating 60 stems of *A. melanoxylon*. The thinning treatments were (i) 100 per cent of nurse-crop removed, (ii) 66 per cent of nurse-crop removed (*i.e.* two of every three *P. radiata* trees along row), (iii) 33 per cent of nurse-crop removed (*i.e.* one of every three *P. radiata* trees along row), and (iv) no thinning of nurse-crop. The *A. melanoxylon* form pruning treatments were (i) 25 per cent of leaf area removed, (ii) 50 per cent of leaf area removed, and (iii) an unpruned control. These treatments were applied to 18 trees per thinning plot in a split-plot experimental design. To mimic a selective pruning regime, the selected trees were of high vigour and flanked by two unpruned *A. melanoxylon* trees. Six replicates of each form pruning treatment were applied in each plot. Branches removed in the treatment were selected to produce the greatest improvement in form that the treatment level would allow. Form pruning treatments were randomly allocated within each plot.

The percentage of tree leaf area removal was estimated using allometric relationships between stem diameter and tree leaf area and branch diameter and branch leaf area. These relationships were developed from destructive sampling of ten trees of *A. melanoxylon* in the Beulah plantation at age five years (Pinkard, unpublished data).

Every one in three *P. radiata* trees was pruned to 2.7 m between March and June 2001 as part of standard plantation management.

Measurements

The stem diameter and total height of each treated *A. melanoxylon* in all plots was measured immediately before treatment, then at three-month intervals for the twelve months following treatment, and again two years after treatment.

Measurements of crown responses to form pruning were carried out in one plot treated with 66 per cent nurse-crop thinning. Within this plot, the form pruning treatments were imposed on three groups, each consisting of three adjacent *A. melanoxylon* trees. To mimic selective pruning, the central tree in each replicate was an unpruned control. The remaining treatments (25 and 50 percent leaf area removed) were randomly assigned to the trees on each side of the control. Three replicates were used. Scaffolding towers were constructed to a height of 6 m around the middle tree of each replicate. Platforms at 2 and 5 m height gave access throughout the crowns of each tree. Using measured green

crown length, the crown of each tree was divided into three vertical zones of equal length. Diameters of all branches of these nine trees were measured on seven occasions over a twelve-month period using digital callipers (Toledo, China). The allometric relationship between branch diameter and branch leaf area used to apply the form pruning treatments was also used to estimate the changes in tree foliage area following pruning.

The effects of nurse-crop thinning on levels of photosynthetically active radiation (PAR) were measured using twelve quantum light sensors. The sensors used were Delta-T QS1 and QS2 (Delta-T Devices Limited, Cambridge, UK) and Skye 210 PAR sensors (Skye Instruments Ltd., Wales, UK). All sensors were calibrated using a Skye 210 PAR sensor connected to a hand-held meter for direct instantaneous readout and the resulting calibration was used to convert the mV output of each sensor to $\mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$. In each plot, a group of three sensors was placed at a randomly allocated distances along each of the four *P. radiata* rows (Figure 3.1). Sensors were placed between the *P. radiata* and the *A. melanoxylon* rows at a height of 1.3 m. Each group of sensors was spaced along the row using the same spacing as the *P. radiata* trees (or stumps if trees removed during thinning). This system ensured that light conditions were measured on both the eastern and western sides of the north-south oriented rows. Data were collected by a CR21X logger, which was programmed to record every 12 minutes. The light conditions in each thinning treatment were measured for seven days. An additional sensor was placed at the top of one of the aforementioned scaffolding towers to measure incident light.

An assessment of stem form of all treated *A. melanoxylon* trees was carried out immediately after treatment and 12 months after treatment. On each occasion tree crown widths were measured using two perpendicular measurements along and across the row. Crown projection area was calculated using the average of these two crown width measurements. Stem lean, sweep and kink were assessed based on a discrete class system. The number of apical leaders per tree and the number of (large) branches greater than 30 mm diameter at 40 mm from the stem junction were also assessed. The numbers of apical leaders and large branches per tree were assessed again two years after treatment.

Data analysis

The effect of treatment on growth, the number of large branches and number of apical leaders was investigated using split-plot analysis of variance with three blocks, four thinning treatments and three pruning treatments. Pruning treatment was treated as a split-plot, with the block x thin interaction used as the error term (Venables and Ripley 1999). All statistical analyses of growth were carried out using S-Plus 4.5 software (Insightful Corporation, Seattle, WA, USA). Where treatment was statistically significant, between-treatment comparisons were made using Fisher's Least Significant Difference test. The effects of treatment on leaders and large branches were analysed by χ^2 analysis using the PROC FREQ module in SAS Ver. 8.02.

For each treatment, the mean instantaneous (per second) light level of each sensor was calculated for one clear day (incident light levels ranged from 15.8 to 16.6 MJ PAR day⁻¹ for the four treatments). This value was used to calculate the daily total light intensity measured by each sensor. This was expressed as a percentage of incident light and averaged for each thinning treatment. The lack of treatment replication in the light measurements precluded any statistical analysis of this data.

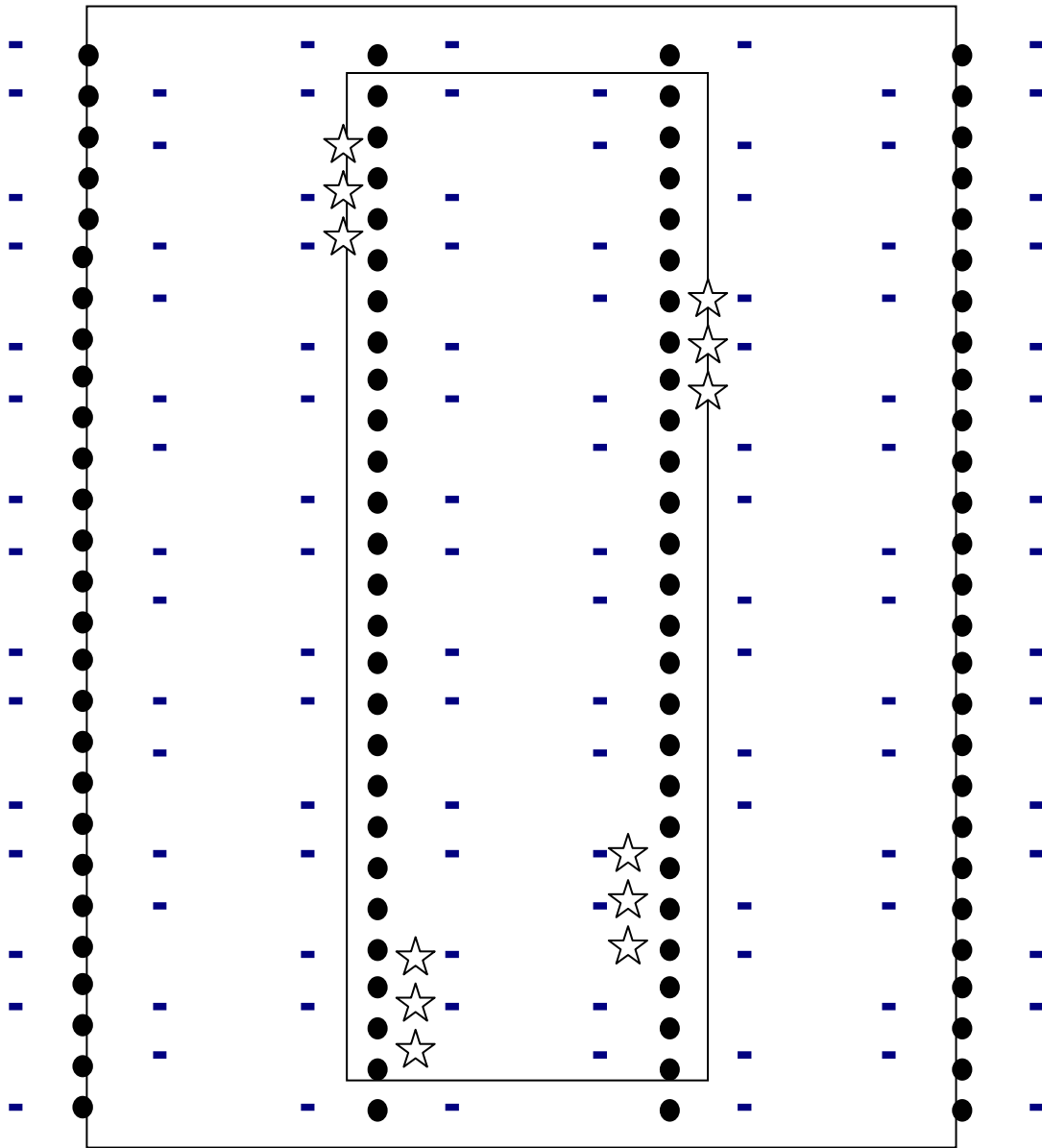


Figure 3.1. Schematic diagram of plot layout showing the measured inner plot and the outer buffer rows for a 66% nurse-crop thinning treatment. An example of quantum light sensor positions (☆) is shown in relation to the nurse-crop *P. radiata* (■) and blackwood (●) rows.

Results

Thinning effects on growth, form and light conditions

Tree height and diameter at breast height of *A. melanoxylon* averaged 5.4 m and 63 mm, respectively, prior to treatment. Mean nurse-crop (*P. radiata*) tree height and diameter at breast height at this time was 6.9 m (estimated using stem diameter-height regression from measurement of nurse-crop at Beulah outside experimental plots in August 2000; $r^2 = 0.85$, $p < 0.001$) and 112 mm, respectively.

Thinning and total removal of the nurse-crop had a positive effect on stem diameter growth of *A. melanoxylon*. A significant diameter growth response was measured in *A. melanoxylon* trees three months after removing either 66 per cent or all of the nurse-crop trees ($p < 0.05$; Figure 3.2a). This response was sustained during the two years following treatment. The diameter increment of *A. melanoxylon* in the 33 per cent thinning treatment was significantly greater than in the unthinned treatment after twelve months ($p < 0.05$). The mean diameter increment of *A. melanoxylon* was 14 and 23 mm yr^{-1} , respectively, for the unthinned and the 100 per cent nurse-crop removal treatments in the two years following treatment.

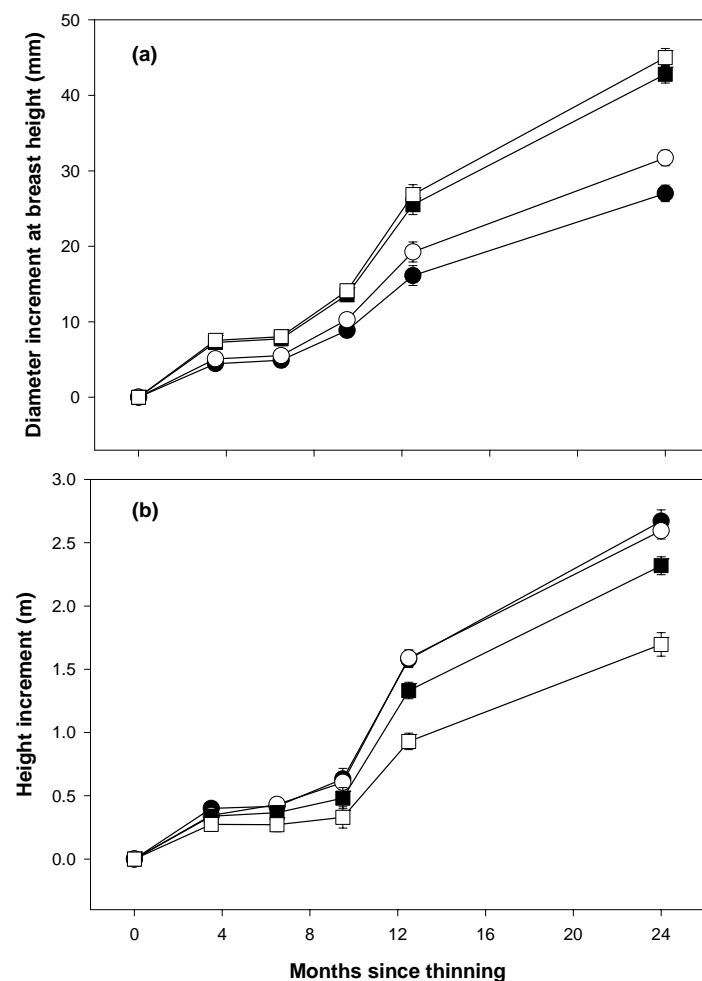


Figure 3.2. (a) Diameter and (b) height increment of *A. melanoxylon* after removal of *P. radiata* nurse-crop. (●=unthinned control, ○=33% of nurse-crop removed, ■=66% of nurse-crop removed, and □=100% of nurse-crop removed). Error bars show mean standard error.

The greatest height increment in the two years after treatment occurred in the unthinned and the 33 per cent thinning treatments (Figure 3.2b). *A. melanoxylon* trees in the 66 per cent thinning treatment had less height increment than the unthinned treatment ($p < 0.05$). Trees in the 100 per cent removal of the nurse-crop had the smallest height increment, significantly lower than in all other thinning treatments

($p < 0.05$). The mean height increment of *A. melanoxylon* was 1.34 and 0.85 m yr⁻¹, respectively, for the unthinned and the 100 per cent nurse-crop removal treatments.

Immediately following treatment, the incidence of large branches (*ie.* >30 mm diameter) and number of apical leaders was independent of thinning treatment (Table 3.1, $p > 0.05$). However, two years after thinning both form characteristics were significantly affected by treatment ($p < 0.05$). There was a notable deterioration in the form of *A. melanoxylon* in the heavily thinned treatments. After two years, the mean number of large branches per tree was 2.4, 2.9, 4.1, and 5.2, respectively, for the unthinned, 33 per cent, 66 per cent and 100 per cent thinned treatments. The mean number of apical leaders per tree was 1.6, 1.6, 1.8 and 2.1, respectively for the unthinned, 33 per cent, 66 per cent and 100 per cent thinned treatments. The mean crown projection area increased with thinning intensity ($p < 0.05$). At the time of treatment, the mean crown projection area was 4.61 m². The mean crown projection area twelve months after treatment was 6.2, 6.3, 7.0 and 7.5 m², respectively for the unthinned, 33 per cent, 66 per cent and 100 per cent thinned treatments.

Table 3.1. Proportion of *A. melanoxylon* stand by the number of large branches per stem and by the number of competing leaders per stem immediately and 24 months after pruning treatment. Mean standard errors are in parentheses.

Treatment	Mean number of leaders per tree	Mean number of branches >30 mm diameter per tree
Nurse-crop thinning ^a		
	<i>Immediately after treatment</i>	
0	1.91 (0.13)	1.19 (0.06)
33	1.69 (0.09)	1.15 (0.05)
66	1.80 (0.12)	1.37 (0.08)
100	2.04 (0.12)	1.30 (0.08)
	<i>24 months after treatment</i>	
0	1.59 (0.09)	2.37 (0.26)
33	1.61 (0.10)	2.91 (0.32)
66	1.80 (0.11)	4.07 (0.33)
100	2.11 (0.11)	5.17 (0.37)
Form pruning ^b		
	<i>Immediately after treatment</i>	
0	2.40 (0.10)	1.39 (0.08)
25	1.58 (0.09)	1.22 (0.05)
50	1.58 (0.09)	1.14 (0.05)
	<i>24 months after treatment</i>	
0	1.83 (0.09)	4.29 (0.33)
25	1.71 (0.09)	3.61 (0.31)
50	1.79 (0.09)	2.99 (0.25)

^aPercent of nurse-crop stand removed.

^bPercent of *A. melanoxylon* leaf area removed.

A non-linear relationship was found between the proportion of the *P. radiata* nurse-crop that was removed, and the light levels reaching the *A. melanoxylon* crowns at 1.3 m height (Figure 3.3). Based on this relationship, light levels did not show a major increase until more than 50 per cent of the *P. radiata* stand was removed. A large difference in light levels was found between the 66 and 100 per cent nurse-crop removal treatments (25 and 70 per cent of incident light, respectively), despite the similar growth rates of *A. melanoxylon* in these treatments (Figure 3.2a).

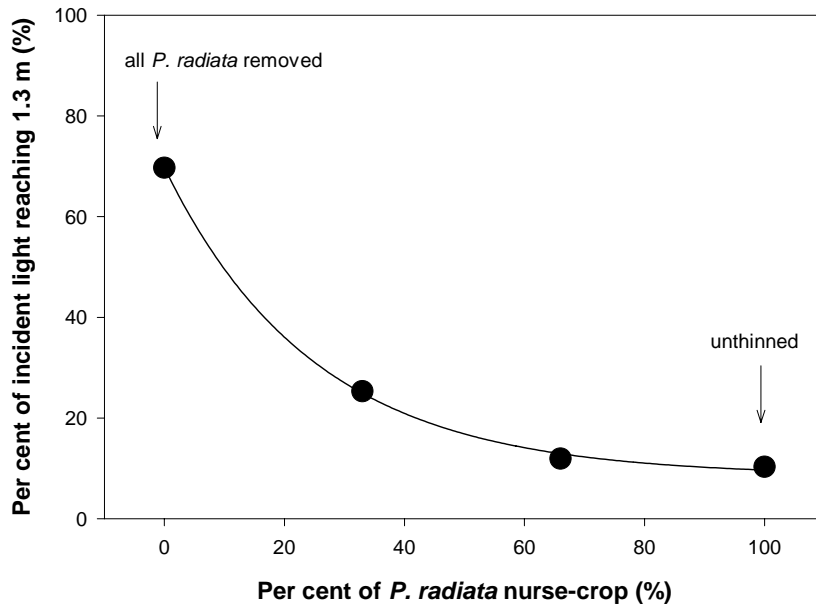


Figure 3.3. Changes in the level of light reaching 1.3 m with differing stocking of *P. radiata* nurse-crop.

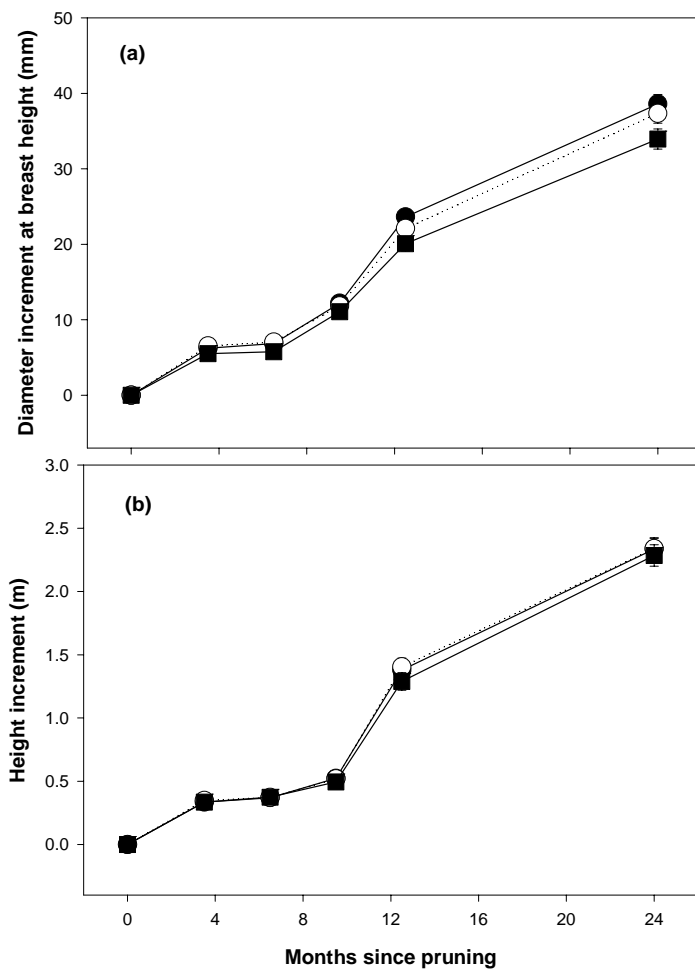


Figure 3.4. (a) Diameter and (b) height increment of *A. melanoxylon* after form pruning. Symbols are; ●=unpruned control, ○=25% of foliage area removed, and ■=50% of foliage area removed. Error bars show mean standard error.

Pruning effects on growth, form and rate of crown recovery

The diameter increment of trees in the 50 per cent pruning treatment was significantly lower than the other pruning treatments, two years after treatment ($p < 0.05$; Figure 4a). Pruning did not significantly reduce the diameter increment of the trees in the 25 per cent pruned *A. melanoxylon* ($p > 0.05$; Figure 3.4a). Pruning treatment had no significant effect on height increment ($p > 0.05$; Figure 3.4b).

Prior to pruning treatment, the form of the *A. melanoxylon* trees was poor. Of all the trees assessed, 41 per cent had a single main leader and 22 per cent had one or more branches greater than 30 mm diameter.

Immediately after treatment, form pruning significantly improved the number of trees with a single apical leader (Table 3.1, $p < 0.05$). The incidence of large branches declined with pruning treatment but this was not significant (Table 3.1, $p > 0.05$).

The effects of pruning were not evident two years after treatment. There was no significant difference between treatments in the incidence of multiple apical leaders or in the incidence of large branches (Table 3.1, $p > 0.05$).

Trees of *A. melanoxylon* pruned of 25 per cent of leaf area displayed a rapid rate of foliage area growth in the two months following form pruning. The rate of crown expansion/recovery was similar across all pruning treatments for the remainder of the measurement period (Figure 3.5). Trees in the 25 per cent pruning treatment recovered to pre-pruning foliage areas in less than two months. However, trees in the 50 per cent pruning treatment did not return to the pre-pruning foliage area level until more than ten months after pruning. Increases in foliage areas were greatest during the summer and negligible during the winter season.

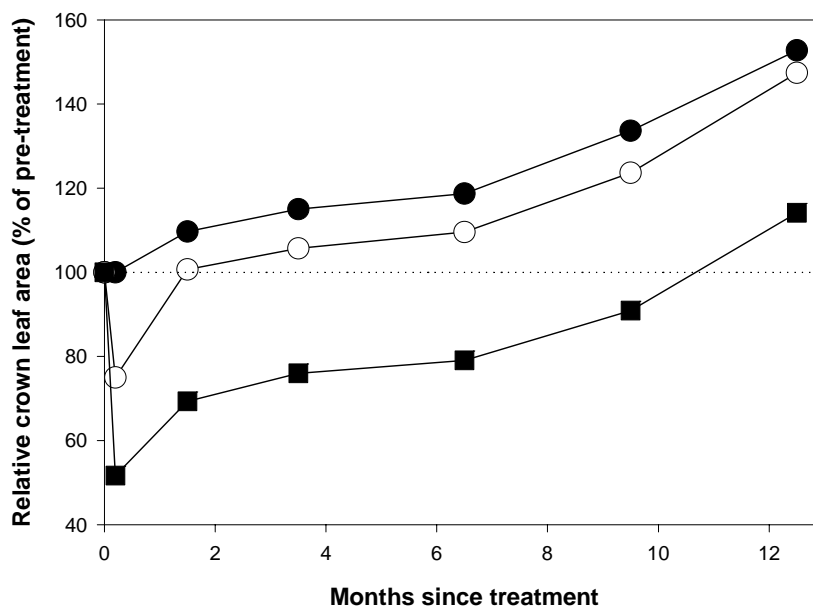


Figure 3.5. Changes in crown leaf area following form pruning, relative to pre-treatment leaf area. (●=unpruned control, ○=25% leaf area removed, ■=50% leaf area removed). The dotted line denotes the pre-pruning leaf area levels.

Discussion

Growth

Mixing *A. melanoxylon* with other tree species in plantations aims to grow straight, large diameter stems suitable for veneer and furniture-grade timber (Nielsen and Brown 1997). This study has demonstrated the need for timely silvicultural intervention in such nurse-crop systems in order to grow these products. Heavy thinning or total removal of the nurse-crop at an early stage of the rotation can

improve the diameter growth of *A. melanoxylon*. However, the accompanying deterioration in form and reduction in height growth make this an unsuitable approach to management unless it is combined with some kind of form pruning or the desired log length has already developed. Relatively little published data exists on growth rates of *A. melanoxylon*. Diameter growth rates reported in 7- to 21-year-old natural *A. melanoxylon* swamp forests range from 0.5 to 0.8 cm per year (Jennings et al. 2000). On productive sheltered sites diameter growth rates of up to 1 cm per year have been reported for *A. melanoxylon* plantations grown alone or with a nurse-crop (Waki 1984; Nicholas 1988; Neilsen and Brown 1997), with height growth of between one (Waki 1984; Neilsen and Brown 1997) and two metres (de Zwaan 1982). This is comparable with the current study where the stem diameter growth of 7-year-old *A. melanoxylon* with a full nurse-crop quota averaged 1.4 cm per year and height growth averaged 1.3 m per year over the period of the experiment. The improvement in stem diameter growth after thinning indicates that the potential growth rate of *A. melanoxylon* is greater than values previously reported.

Despite only a small improvement in light levels at 1.3 m (although greater increases probably occurred higher in the crowns), low intensity nurse-crop thinning produced a growth response in *A. melanoxylon*. *A. melanoxylon* has been described as a sub-canopy opportunist (Unwin et al. 2001) in terms of its ecology. It requires only 20% of full light for normal growth, and can survive (albeit with stunted growth) in 8% of full light (Milton 1982). Any improvement in light availability through thinning treatment is likely to produce a growth response. This is in contrast to other less shade-tolerant species such as *E. nitens* where prolonged competition can result in essentially irreversible suppression of growth in individual trees (Medhurst et al. 2001). The tolerance to shade exhibited by *A. melanoxylon* implies that the timing of nurse-crop thinning is not crucial. However, maintaining vigour of *A. melanoxylon* in these plantation systems is important from an economic perspective, and the relatively faster growth rate of *P. radiata* compared to *A. melanoxylon* (Neilsen and Brown 1996) means that there is a strong likelihood of the *P. radiata* suppressing the *A. melanoxylon* if timely thinning is not undertaken. Prolonged competition from the nurse-crop may also produce *A. melanoxylon* with small crowns and large height/diameter ratios, as well as greater shoot:root ratios (Milton 1982). Such trees are susceptible to windthrow after the eventual removal of the nurse-crop.

The reduction in growth following heavy form pruning and the transient nature of the improvement in form after form pruning highlights the need for a number of light form pruning operations, commencing from an early age. In common with studies undertaken in New Zealand (Nicholas and Gifford 1995), light form pruning did not reduce the growth of *A. melanoxylon*. The reduced stem growth in trees pruned to remove 50 per cent of foliage was probably due to the slow rate of crown recovery after this treatment. The effect of the 50 per cent pruning treatment on growth was greater in the low intensity compared to the high intensity thinning treatment (data not shown). This indicates that the crown responses to heavy form pruning may be even slower than those measured when thinning removes less than 66 per cent of the nurse-crop. The greater degree of shading provided by the nurse-crop in the low intensity thinning treatment may have restricted the rate of development of new foliage after pruning, although *A. melanoxylon* has the capacity to maintain levels of photosynthetic tissue in the shade by reverting from phyllodes to the more tissue-efficient bipinnate leaves (Milton 1982).

Form

The deterioration in stem form associated with heavy nurse-crop thinning, or total nurse-crop removal, makes these silvicultural options undesirable unless associated with frequent form pruning (Barr 1987; Nicholas et al. 1994; Nicholas and Gifford 1995). Nurse-crop thinning had a greater long-term effect on stem form of *A. melanoxylon* than did pruning. The opportunistic growth habit of *A. melanoxylon* means that form pruning is a 'corrective' rather than 'training' procedure and *A. melanoxylon* will maximise crown responses to the improvement in light levels following thinning. The lowest intensity thinning treatment in this experiment produced an improvement in diameter growth of *A. melanoxylon* without a marked deterioration in form. For this reason, a low intensity thinning of the nurse-crop early in the rotation is recommended.

The *A. melanoxylon* trees exhibited poor form prior to treatment. This can be attributed to the lack of sidelight suppression by the nurse-crop early in the rotation. The wide spacing between the nurse-crop trees and the *A. melanoxylon* (2.5 m) at establishment would also limit the level of protection of the *A. melanoxylon* from frost that was prevalent at the site, and wind. Frost in particular has been shown to have a negative impact on the form of planted seedlings of *A. melanoxylon* (Allen 1992; Neilsen and Brown 1997). As no correctional form pruning had been performed before the experiment commenced in the sixth year of growth, the *A. melanoxylon* was displaying the compounded effects of the lack of pruning as well as nursing from the *P. radiata*. The high incidence of multiple leaders and heavy branching was an indication of this. This highlights a deficiency of the current nurse-crop – *A. melanoxylon* system that provides no control of branch development in the early part of the rotation. The poor form that existed in this stand prior to treatment highlighted the need for early form pruning. An early commencement of form pruning in such stands (without nurse-crop thinning) should correct many of the form problems evident in young plantations and reduce the need for intensive remedial pruning treatments at a later age.

Form pruning has been found to improve stem form and increase the number of trees that can be selected for clearwood pruning (Nicholas et al. 1994). In this experiment, form pruning improved some of the form problems evident in the stand prior to treatment. In particular the number of large branches per tree was reduced with increasing pruning intensity. This is similar to the results of Nicholas et al. (1994). If pruning had been carried out earlier, a greater reduction in the number of apical leaders per tree may have been possible.

Conclusions

Are nurse-crop systems an effective method of growing *A. melanoxylon* to produce veneer and furniture-grade wood? This experiment has demonstrated that, with careful management, a nurse-crop system can be manipulated to improve growth and form of *A. melanoxylon*. However intensive management is required to maximise its growth and optimise stem form.

The improvement in form achieved by pruning was transient in nature and clearly a one-off pruning operation in these plantation systems will not produce the stem form required for solid-wood products. A study in New Zealand found that the greatest improvement in stem form occurred with annual form pruning (Nicholas et al. 1994) and in that country annual or biennial form pruning is commonly recommended (Barton, 1993; Nicholas and Gifford 1995; Brown, 1997). Form pruning needs to commence earlier than age six years on sites with reasonable growth rates in order to produce an acceptable improvement in form without disrupting growth. On such sites, form pruning may need to start from as early as two or three years of age in order to be effective. More frequent, less severe pruning operations may be preferable in terms of maintaining vigour of *A. melanoxylon*. Lighter form pruning from an early age may also have a greater effect on form than a similar intensity of pruning carried out at a later age, as branches can be removed before they become large. Identifying branching patterns that are likely to produce form problems at a later stage is a relatively simple procedure (Brown, 1997) if pruning is initiated early.

There was virtually no growth of *A. melanoxylon* crowns over the winter period followed by rapid crown growth during the spring-early summer period. The pattern of stem diameter growth was similar to that of foliage production. Scheduling pruning to precede the rapid rate of crown growth in the spring-early summer period will reduce the time required for crown recovery and minimise any effects on growth.

The early and strong response to heavy thinning of the nurse-crop indicates that by this early stage of the rotation the nurse-crop was beginning to suppress the *A. melanoxylon*. However, silvicultural management of *A. melanoxylon* – nurse-crop systems such as the one used in this experiment need to concentrate on producing good form as a priority over high growth rates. The clear incompatibility between these two goals, as demonstrated by the change in growth and form of *A. melanoxylon* without a nurse-crop, means that form in the first 6 m of the stem must be established before promoting growth. The vigour of *A. melanoxylon* can be maintained with a low intensity nurse-crop thinning at an early stage in the rotation.

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Chapter 4: Physiology

Introduction

Form pruning, the removal of live branches to correct problems with stem form, is a common silvicultural practice in stands of planted *Acacia melanoxylon* R. Br. (Nicholas et al. 1994; Neilsen and Brown 1997; Brown 2001). Defoliation can have a major effect on tree physiological processes, and the degree to which stem growth is reduced is a function of both the extent of foliage loss and the compensatory measures employed by the tree (Pinkard and Beadle 2000).

Removal of live foliage has been demonstrated to enhance the photosynthetic capacity of the remaining foliage in a range of tree species including *Eucalyptus nitens* (Deane and Maiden) Maiden (Pinkard et al. 1998), *Alnus glutinosa* L. Gaertn. (Singh and Thompson 1995) and *Abies balsamea* (L.) Mill. (Lavigne et al. 2001). However, the extent and period of response of such increases vary widely. In addition, other studies have reported either no change or a decrease in gas exchange (Troeng and Långström 1991) in response to artificial defoliation. Contradictory reports of the photosynthetic response to defoliation suggest that the growth environment plays a leading role in determining the response (McGraw et al. 1990).

The physiological mechanisms that drive changes in photosynthetic capacity following partial defoliation appear to vary widely between species. At the leaf level, there can be changes in rates of biochemical reactions associated with increased nitrogen availability or changes in partitioning of nitrogen within the leaf to increase levels of chlorophyll or ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) (eg. von Caemmerer and Farquhar 1984; Oesterheld and McNaughton 1991; Lavigne et al. 2001). Increased photosynthetic capacity can be associated simply with greater rates of translocation of photosynthate from the remaining foliage. Such an increase may be expressed by a positive relationship between the carbon assimilation rate of the foliage and its specific leaf area (Chatterton 1973; Thorne and Koller 1974). In some instances, the greater photosynthetic capacity of foliage following partial defoliation has been linked to improvement in tree water relations because of an increase in the root:shoot ratio (Singh and Thompson 1995), and greater maximum rates of stomatal conductance following pruning have been measured (Pinkard et al. 1998). However, changes in the intercellular rate of diffusion of carbon dioxide (mesophyll conductance) may be more important in controlling carbon assimilation rate after pruning (Farquhar and Sharkey 1982). At the plant-level, partial defoliation can alter the source:sink relationship for photosynthate and alter carbon partitioning between plant organs. Such changes are likely to be hormone-driven and indicate that the plant was not operating at maximum photosynthetic capacity prior to partial defoliation (Neales and Incoll 1968).

In its natural environment, *A. melanoxylon* often grows as an understorey forest species, but it has a capacity for rapid growth in response to positive changes in available resources (Jennings and Dawson 2001; Medhurst et al. see Chapter 3). Typical of most *Acacia* species, *A. melanoxylon* is capable of symbiotic N₂-fixation (Schortemeyer et al. 1999) and of tolerating high levels of water stress (Brodribb and Hill 1993). In a pruning study that removed selected branches from throughout the crown (form pruning) it was demonstrated that removing 50 per cent of foliage area of *A. melanoxylon* reduced stem growth rate and slowed the rate of recovery of foliage area while removing 25 per cent had no effect on growth (Medhurst et al. see Chapter 3). The present study was undertaken to (1) determine if the photosynthetic capacity of remaining foliage in these treatments was enhanced to offset foliage losses to form pruning, and; (2) identify the physiological mechanisms driving any photosynthetic changes.

Materials and Methods

Site description

The experiment was established in January 2000 in a plantation in northern Tasmania (41° 28' S 146° 21' E) that was planted on a site previously carrying *Eucalyptus obliqua* L'Herit native forest. The soil is a clay loam overlying a light clay subsoil derived from Cambrian sandstone/greywacke parent material (Grant 1995). The area was logged, windrowed and burnt, and mound ploughed prior to planting in 1994 using open-rooted *A. melanoxylon* seedlings (seeds from a local collection), with *P. radiata* as a nurse-crop at 5.0 x 2.5 m (800 trees ha⁻¹). The *A. melanoxylon* was planted between every second row of *P. radiata* at 10.0 x 2.0 m (500 trees ha⁻¹). The plantation was fertilised at age five years with 70 kg ha⁻¹ of phosphorus applied as superphosphate. The plantation is at an altitude of 250 m above sea level (asl). At the nearby township of Sheffield (at 280 m asl), the mean annual rainfall is 1179 mm and mean daily maximum and minimum temperatures are 16° C and 6° C, respectively.

Treatments and experimental design

The study was undertaken in an experimental area that was examining the growth responses of *A. melanoxylon* to thinning of the *P. radiata* nurse-crop and form pruning of the *A. melanoxylon* (see Medhurst et al. see Chapter 3). The present study was carried out in a 0.12 hectare area where the stand density of the nurse-crop had been reduced by 66 per cent and where selected *A. melanoxylon* had been pruned to remove either 0, 25 or 50 per cent of total foliage area. Pruning removed large branches and/or multiple leaders, and is referred to as form pruning.

Table 2. Mean diameter at breast height (DBH), tree height, tree foliage area, crown length, and mean number of branches removed from each crown zone of the six-year-old *A. melanoxylon* trees by pruning treatment.

	Pruning treatment (per cent of total foliage area removed)		
	0 per cent	25 per cent	50 per cent
Mean DBH (mm)	94.0	89.0	97.0
Mean tree height (m)	5.7	5.4	5.9
Mean total foliage area (m ²) ¹	20.8	15.0	15.5
Mean crown length (m)	5.3	5.0	5.2
Mean no. of branches removed from lower crown zone	0.0	2.7	6.3 ²
Mean no. of branches removed from middle crown zone	0.0	3.0	2.0
Mean no. of branches removed from upper crown zone	0.0	0.0	0.3

¹Prior to pruning treatment

²Includes the removal of leaders with foliage distributed throughout all crown zones

Nine trees were selected for physiological measurements. Three replicates of the form pruning treatments were imposed on adjacent trees. To mimic selective pruning (where only a proportion of the stand is pruned, with the remainder of stems removed with a mid-rotation thinning), the central tree in each replicate was an unpruned control. The remaining treatments (25 and 50 per cent leaf area removed) were randomly assigned to the trees on each side of the control. Scaffolding towers were constructed to a height of six metres around the middle tree of each replicate, and platforms at two and five metres height gave access throughout the crowns of the trees. Using measured green crown length at the time of pruning, the crowns of each tree were divided into three vertical zones (upper, middle and lower) of equal length. In each zone, foliage was divided into two age classes, current (fully expanded phyllodes less than 1-year-old) and old (phyllodes greater than 1-year-old).

Table 2 shows the growth characteristics of the nine physiology trees at time of treatment and the distribution of the pruning throughout the crown.

Pruning treatments were applied by using allometric relationships developed from destructive sampling of *A. melanoxylon* trees in the Beulah plantation (Pinkard, unpublished data). The total tree foliage area before pruning was estimated by;

$$\log_{10} F = -0.9224 + 1.1953(\log_{10} B) \quad (n=9, R^2=0.98, P < 0.001) \quad [1]$$

where B was stem basal area (cm²) at 10 cm height, and F was tree foliage area (m²).

The foliage area of each pruned branch was estimated by;

$$\log_{10} f = -0.5673 + 0.6578(\log_{10} b) \quad (n=90, R^2=0.66, P < 0.001) \quad [2]$$

where b was the cross-sectional area of the branch (cm²) at a distance of 30 mm from the main stem, and f was branch foliage area (m²).

Gas exchange

Gas exchange measurements were carried out using a CIRAS-1 Portable Photosynthesis System (PP Systems, Hitchin, Herts, UK). Measurements undertaken just before pruning (February 1, 2000 or 0 weeks) and on a further six occasions after the pruning treatments were applied on February 3, 2000. The dates of measurement were 16 February 2000, 16 March 2000, 17 May 2000, 17 August 2000, 8 November 2000 and 22 February 2001 (2, 6, 15, 28, 40 and 55 weeks after pruning, respectively). A Parkinson PLC-Broad leaf cuvette (area 2.5cm²) was used to enclose the leaves. Flow rate was 200 ml min⁻¹. Measurements of light-saturated net CO₂ assimilation (A_{max}) and stomatal conductance (g_s) were made under constant illumination using a lamp unit. The light intensity was 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with the power supplied by a 12 V 20 amp-hour car battery. The net gas-exchange of two phyllodes per foliage age class in each canopy zone of each tree was measured at ambient CO₂ (~360 $\mu\text{mol mol}^{-1}$) and water vapour concentrations. Leaf temperatures ranged between 15 and 25 °C. All measurements were carried out between 0900 and 1400 h Australian Eastern Standard Time (AEST). The order in which the towers were measured was randomly determined before each series of measurements.

An automatic weather station was used to measure air temperature, relative humidity, solar radiation, net radiation and rainfall for the day prior to gas exchange measurement and for the day of measurement. The station was located two kilometres from the trial and at a similar elevation. Measurements were recorded every five minutes using a datalogger (Campbell 21X, Campbell Scientific, Logan, Utah, USA) powered by a solar panel with voltage regulation through a 12 V gel cell battery. Hourly averages were recorded. Daily rainfall was also measured. Rainfall was measured using a tipping bucket rain gauge (0.2 mm), solar radiation with a pyranometer (LI-200s, Li-Cor Inc., Lincoln, NE, USA), and net radiation with a net radiometer (Model 3032, Qualimetrics, Sacramento, CA, USA). Vapour pressure deficit was calculated from a Vaisala temperature and humidity probe installed in a Stephenson screen at a height of 1.5 m.

Phyllode properties and nutrient concentrations

All phyllodes used for measurement of gas exchange were collected immediately following measurement in order to determine specific phyllode area (SPA), and nitrogen (N) and phosphorus (P) concentrations. The phyllodes from each foliage age class per canopy zone per tree were pooled for

nutrient analysis. Projected (one-sided) phyllode area was measured using a leaf area meter (Delta-T Devices Limited, Cambridge, UK). The phyllodes were subsequently dried at 80 °C for 48 h, cooled and weighed, and then ground in a hammer mill and dried for a further 24 h at 80 °C. Specific phyllode area was calculated as the ratio between fresh phyllode area and phyllode dry mass. The samples were prepared for analysis using a single acid-hydrogen peroxide technique (Lowther 1980). Analysis of total kjeldahl N and total P was carried out using a spectrophotometric flow injection analyzer (QuikChem 8000, Lachat Instruments, Milwaukee, WI, USA). The N and P concentrations were converted from a mass- to an area-basis using the calculated SPA values.

Data analysis

A multistratum model was used to analyse the differences in instantaneous rates of carbon assimilation (A_{max}), stomatal conductance (g_s), foliar nitrogen (N_{mass} and N_{area}), foliar phosphorus (P_{mass} and P_{area}), and SPA. Instantaneous water-use efficiency (A_{max}/g_s), instantaneous nitrogen-use efficiency (A_{max}/N_{area}) and instantaneous phosphorus-use efficiency (A_{max}/P_{area}) were calculated. Pruning treatments were allocated between trees (plot) while crown zone and foliage-age class were allocated within trees (split-split plot). The statistical software package S-Plus 4.5 (Venables and Ripley 1999) was used for the analyses. Treatment means and standard errors were calculated using the least squares method.

The relationships between the relative change in A_{max} with pruning treatment and the relative changes in SPA, foliar N, foliar P and g_s , respectively, were analysed using linear regression. The PROC GLM procedure in SAS (SAS Institute Inc., 1990) was used for the analysis.

Results

Gas exchange

When averaged over the whole crown, A_{max} of the 50 per cent pruning treatment was significantly greater than both the unpruned and 25 per cent pruning treatments, two weeks after pruning ($p < 0.05$). There was no significant difference in A_{max} of the 25 per cent pruning treatment and the unpruned treatment at this time.

Six weeks after pruning, the A_{max} of the upper and middle crown zones of the 50 per cent pruned treatment was 33 and 62 per cent higher, respectively, than that of the unpruned treatment ($p < 0.05$). At this time the overall effect of pruning treatment was significant at $p = 0.10$ (Table 3). Significantly higher A_{max} values were measured in the 50 per cent pruned treatment 40 weeks after pruning ($p < 0.05$) but there was no difference after 55 weeks.

Table 3. Analysis of variance of mean instantaneous CO₂ assimilation rates measured six weeks after pruning.

	df	SS	MS	F value	P
Block	2	2.71	1.36		
Prune	2	175.25	87.63	5.48	0.072
Zone	2	2836.07	1418.03	128.13	0.000
Age	1	166.38	166.38	15.03	0.0002
Zone*Age	2	35.28	17.64	1.59	0.209
Zone*Prune	4	82.83	20.71	1.87	0.123
Age*Prune	2	85.88	42.94	3.88	0.024
Zone*Age*Prune	4	42.82	10.71	0.97	0.430
Residuals	84	929.65	11.07		

A_{max} varied by crown zone (Figure 1a-c, Table 3) and foliage age class (data not shown, see also Table 3) throughout the measurement period ($p < 0.001$). For all pruning treatments, current foliage had

greater values of A_{max} than old foliage and the greatest and lowest values of A_{max} were found in the upper and lower crown zones, respectively.

The highest g_s values were measured in the 50 per cent pruning treatment in the upper and mid-crown on all except one of the measurement periods (Figure 1d-f). There were no significant differences between treatments in the lower crown except at the last measurement.

The mean values of g_s in the 50 per cent pruning treatment were greater than both the unpruned and 25 per cent pruning treatments at weeks 2 and 6 ($p < 0.05$).

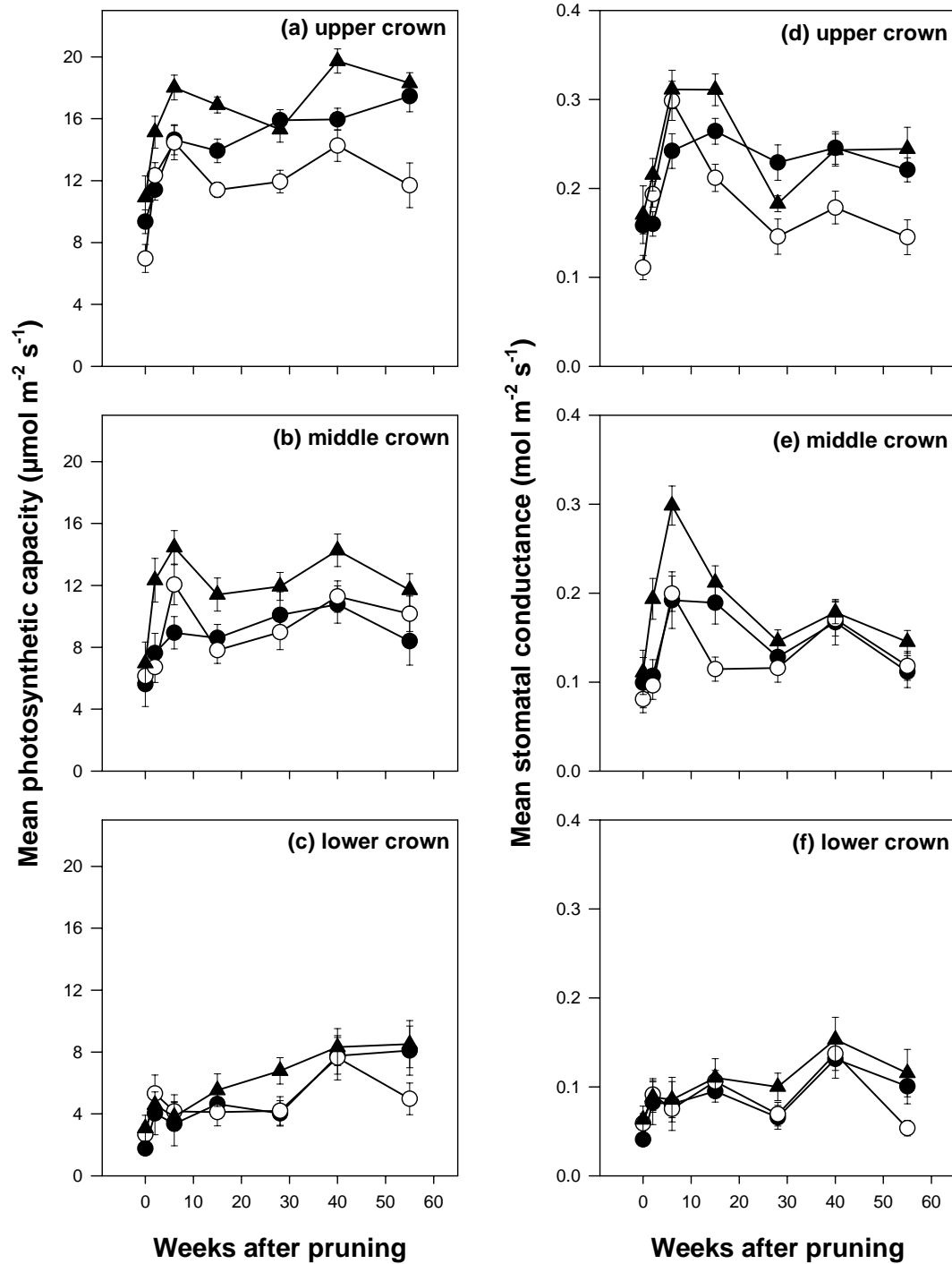


Figure 1. Mean light-saturated photosynthetic rate of (a) upper, (b) middle, and (c) lower crown zones and mean stomatal conductance of (d) upper, (e) middle, and (f) lower crown zones of pruned and unpruned trees during the experiment. Current and old foliage values were pooled. Error bars show mean standard errors for unpruned (●), 25 per cent pruned (○), and 50 per cent pruned (▲) treatments.

All measurements after pruning showed a linear increase in A_{max} with g_s for g_s values up to $0.25 \text{ mol m}^{-2} \text{ s}^{-1}$ ($p < 0.0001$; Figure 2). For g_s values greater than $0.25 \text{ mol m}^{-2} \text{ s}^{-1}$ there was no relationship between g_s and A_{max} . Pruning treatment had no significant effect on this relationship ($p > 0.05$) except for 40 weeks after pruning ($p < 0.05$). The minimum g_s values were similar across all pruning treatments ($0.01 \text{ mol m}^{-2} \text{ s}^{-1}$).

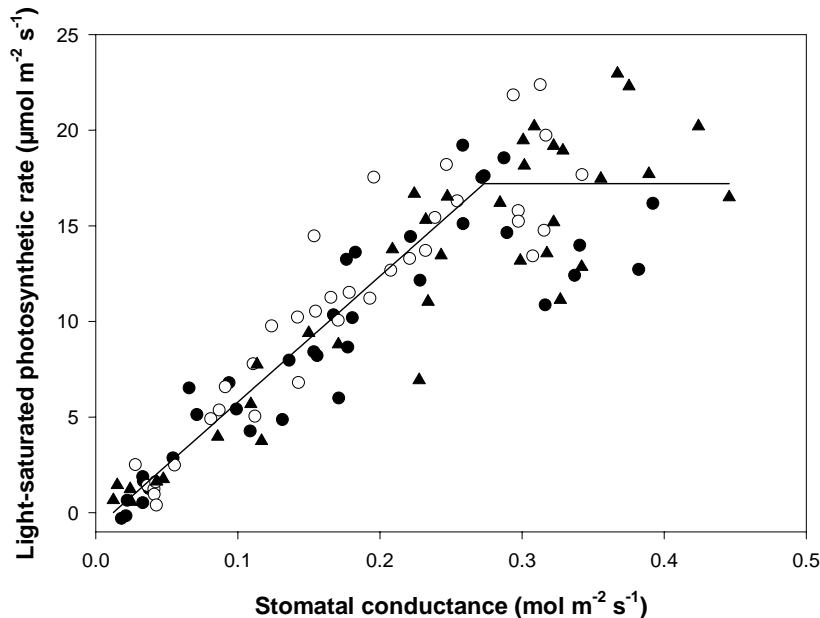


Figure 2. Relationship between stomatal conductance and light-saturated photosynthetic rate measured six weeks after pruning for the unpruned (●), 25 per cent pruned (○) and 50 per cent pruned (▲) treatments. Relationship for stomatal conductance values less than $0.25 \text{ mol m}^{-2} \text{ s}^{-1}$ is; $y = 64.82x - 0.72$ ($r^2 = 0.86$, $n = 71$). Mean light-saturated photosynthesis for stomatal conductance values greater than $0.25 \text{ mol m}^{-2} \text{ s}^{-1}$ was $16.8 \text{ μmol m}^{-2} \text{ s}^{-1}$

Specific phyllode area

There was no consistent pattern in specific phyllode area (SPA) with crown zone during the course of the experiment. Crown zone had a significant effect on SPA ($p < 0.05$) at weeks 6, 15, 40 and 55, but not at weeks 0, 2 and 28. Values of SPA were consistently greater in current foliage compared to the old foliage throughout the experiment ($p < 0.001$; Table 4). Pruning treatment had no significant effect on SPA.

Weak (R^2 range of 0.12-0.31) yet significant ($p < 0.01$) linear relationships were found between A_{max} and SPA during weeks 0, 2, 6, and 15. On each occasion, pruning treatment had no significant effect on the slope or intercept of the relationship.

Foliar nitrogen

The mean concentration of nitrogen in the phyllodes (N_{mass}) ranged between 1.44 and 2.09 mmol N g^{-1} (Table 4). Throughout the experiment, N_{mass} values were always least in the lower crown zone, and greatest in the upper crown zone ($p < 0.05$). Significant differences in N_{mass} were found across foliage-age classes throughout the experiment, with current foliage having greater N_{mass} than old foliage ($p < 0.05$). Pruning treatment had no significant effect on N_{mass} . Mean foliar nitrogen content (N_{area}) ranged between 286 and 378 mmol m^{-2} throughout the experiment (Table 4). Foliage age-class did not influence N_{area} , except during weeks 15 and 55 ($p < 0.05$). Significant differences in N_{area} across crown zones were found in weeks 2, 6, 15, 28, 40, and 55 ($p < 0.05$). The greatest N_{area} values were found in the upper crown zone and the lowest values were found in the lower crown zone. Pruning treatment did not affect N_{area} . Pruning treatment had no effect on mean instantaneous nitrogen-use efficiency

(NUE) but NUE increased with crown height ($p < 0.01$) and decreased with foliage age-class ($p < 0.01$) throughout the experiment. The ranges of mean NUE values for the upper and lower crowns across all pruning treatments were $3.7\text{-}4.7 \times 10^{-2}$ and $1.3\text{-}2.2 \times 10^{-2}$ mmol CO₂ mol⁻¹ N, respectively (Table 4).

Foliar phosphorus

The mean concentration of phosphorus in the phyllodes (P_{mass}) varied by crown zone throughout the experiment ($p < 0.001$) with the greatest P_{mass} values in the upper crown zone and the least in the lower crown (Table 4). Old phyllodes had lower P_{mass} than current phyllodes throughout the experiment ($p < 0.01$), except for week 40 where there was no significant difference between the foliage age-classes. While trees in the 50 per cent pruning treatment had greater P_{mass} values than the unpruned trees throughout the experiment, this difference was not significant.

Mean foliar phosphorus content (P_{area}) ranged between 4.2 and 8.4 mmol m⁻² throughout the experiment (Table 4). Foliage age-class did not influence P_{area} , except during weeks 15 and 40 ($p < 0.05$). Significant differences in P_{area} across crown zones were found throughout the experiment ($p < 0.001$). The greatest P_{area} values were found in the upper crown zone and the lowest values were found in the lower crown zone. Pruned trees had greater P_{area} values than unpruned trees throughout the measurement period but these differences were not significant ($p > 0.05$).

Pruning treatment had no effect on mean instantaneous phosphorus-use efficiency (PUE) but PUE increased with crown height during all measurements ($p < 0.01$) except week 2. There was no consistent difference in PUE with foliage age-class. The ranges of mean PUE values for the upper and lower crowns across all pruning treatments were 1.86-2.26 and 0.87-1.48 mmol CO₂ mol⁻¹ P, respectively (Table 4).

Water use efficiency

Mean instantaneous water-use efficiency (WUE) was not influenced by pruning treatment at any stage during the experiment. Mean WUE increased with crown height during all measurements ($p < 0.05$) except weeks 15 and 55. The WUE of current foliage was only greater than that of old foliage during weeks 15 and 28 ($p < 0.05$). Mean treatment values of WUE ranged between 51.4 and 72.9 μmol CO₂ mol⁻¹ H₂O (Table 4).

Table 4. Current and old phyllode characteristics in the upper, middle and lower crown of *A. melanoxylon* by pruning treatment. Values are means of all measurement data (\pm mean standard error). Different letters within rows indicate differences in values at $p < 0.05$ using least significant difference test of treatment means.

Parameter	Crown position	Unpruned		25 per cent pruned		50 per cent pruned		ANOVA statistic
		Current	Old	Current	Old	Current	Old	
SPA m ² kg ⁻¹	upper	5.84(0.18) ^a	5.40(0.13) ^{ab}	5.54(0.14) ^{ab}	5.31(0.12) ^b	5.72(0.18) ^{ab}	5.69(0.14) ^{ab}	prune n.s. age<0.0001 zone n.s. age*zone<0.0001
	middle	5.88(0.16) ^a	5.10(0.11) ^b	5.99(0.24) ^a	5.14(0.12) ^b	6.18(0.15) ^a	5.16(0.13) ^b	
	lower	6.35(0.24) ^a	4.99(0.15) ^b	6.29(0.35) ^a	4.99(0.20) ^b	6.11(0.30) ^a	4.89(0.21) ^b	
N _{mass} mmol N g ⁻¹	upper	2.05(0.06) ^a	1.93(0.06) ^b	2.07(0.05) ^a	1.95(0.06) ^{ab}	2.05(0.04) ^{ab}	2.05(0.04) ^{ab}	prune n.s. age<0.0001 zone<0.0001 age*zone<0.001
	middle	1.95(0.04) ^b	1.73(0.05) ^c	1.95(0.06) ^b	1.67(0.05) ^c	2.09(0.04) ^a	1.89(0.04) ^b	
	lower	1.80(0.05) ^a	1.50(0.05) ^c	1.75(0.08) ^{ab}	1.44(0.04) ^c	1.84(0.07) ^a	1.62(0.05) ^{bc}	
N _{area} mmol N m ⁻²	upper	357(15.2) ^a	360(12.0) ^a	378(12.9) ^a	372(15.8) ^a	366(13.2) ^a	364(10.9) ^a	prune n.s. age n.s. zone<0.0001 age*zone n.s.
	middle	337(10.8) ^b	342(11.0) ^b	330(10.3) ^b	325(8.6) ^b	343(11.4) ^{ab}	370(10.0) ^a	
	lower	286(7.0) ^b	306(12.8) ^b	286(11.2) ^b	296(11.2) ^b	306(8.2) ^b	337(10.6) ^a	
P _{mass} μmol P g ⁻¹	upper	44.2(2.9) ^a	37.1(1.6) ^b	44.7(2.2) ^a	38.5(1.6) ^b	47.7(2.7) ^a	41.7(1.6) ^{ab}	prune n.s. age<0.0001 zone<0.0001 age*zone n.s.
	middle	35.9(0.9) ^a	30.1(1.5) ^b	37.4(3.6) ^a	29.0(1.4) ^b	39.7(6.9) ^a	33.4(1.5) ^{ab}	
	lower	31.8(3.2) ^a	22.0(1.2) ^b	30.7(4.6) ^a	21.0(1.4) ^b	32.6(3.8) ^a	23.7(1.6) ^b	
P _{area} mmol P m ⁻²	upper	7.6(0.4) ^{abc}	6.9(0.3) ^c	8.1(0.4) ^{ab}	7.3(0.3) ^{bc}	8.4(0.4) ^a	7.4(0.3) ^{bc}	prune n.s. age<0.0001 zone<0.0001 age*zone<0.05
	middle	6.2(0.2) ^a	5.9(0.3) ^a	6.2(0.3) ^a	5.7(0.3) ^a	6.5(0.3) ^a	6.5(0.3) ^a	
	lower	4.9(0.3) ^{ab}	4.4(0.2) ^{ab}	4.7(0.4) ^{ab}	4.2(0.2) ^b	5.2(0.4) ^a	4.9(0.3) ^{ab}	
NUE mmol CO ₂ mol ⁻¹ N s ⁻¹	upper	0.042(0.003) ^{abc}	0.039(0.002) ^{bc}	0.039(0.002) ^{bc}	0.037(0.003) ^c	0.047(0.002) ^a	0.044(0.003) ^{ab}	prune n.s. age<0.0001 zone<0.0001 age*zone<0.0001
	middle	0.034(0.002) ^b	0.018(0.002) ^d	0.033(0.002) ^b	0.023(0.002) ^c	0.041(0.002) ^a	0.026(0.002) ^c	
	lower	0.021(0.003) ^a	0.013(0.002) ^b	0.021(0.003) ^a	0.014(0.002) ^b	0.022(0.003) ^a	0.015(0.002) ^b	
PUE mmol CO ₂ mol ⁻¹ P s ⁻¹	upper	2.05(0.16) ^a	2.07(0.15) ^a	1.86(0.12) ^a	1.92(0.15) ^a	2.13(0.16) ^a	2.26(0.16) ^a	prune n.s. age<0.0001 zone<0.0001 age*zone<0.0001
	middle	1.85(0.10) ^b	1.07(0.10) ^d	1.84(0.15) ^b	1.35(0.13) ^{cd}	2.26(0.17) ^a	1.55(0.13) ^{bc}	
	lower	1.21(0.18) ^{abc}	0.87(0.11) ^c	1.48(0.26) ^a	0.93(0.12) ^{bc}	1.30(0.14) ^{ab}	1.10(0.12) ^{abc}	
WUE μmol CO ₂ mol ⁻¹ H ₂ O s ⁻¹	upper	68.2(2.1) ^{ab}	65.3(2.0) ^b	75.1(3.3) ^a	75.6(3.2) ^a	72.9(2.5) ^{ab}	72.8(3.1) ^{ab}	prune n.s. age<0.01 zone<0.001 age*zone n.s.
	middle	68.8(3.2) ^{ab}	62.5(3.7) ^b	73.7(2.4) ^a	70.1(3.2) ^{ab}	70.7(2.9) ^a	66.5(2.9) ^{ab}	
	lower	58.2(3.9) ^{ab}	54.2(3.9) ^b	56.8(4.3) ^{ab}	51.4(4.5) ^b	63.2(3.6) ^a	55.4(4.3) ^b	

Discussion

Acacia melanoxylon is known to have plasticity in growth that allows it to respond to changes in environment and available resources (Pinkard and Beadle 2002). This is an important evolutionary strategy for a species that grows under a wide range of conditions (Boland, Brooker et al. 1994). One expression of this plasticity is the capacity to change rates of CO₂ assimilation that was demonstrated in this experiment. The increase in A_{max} observed in response to form pruning indicates that, under normal growth conditions, *A. melanoxylon* does not photosynthesise at maximum capacity (Myers et al. 1999). This photosynthetic compensation following loss of leaf area is considered generally to be a response that maintains a balance between zones of carbon uptake and utilisation (sources and sinks) and thereby minimising the effects of defoliation on biomass production (Neales and Incoll 1968; Reich, Walters et al. 1993). The rapid increase in A_{max} that was observed following pruning in this study suggests that the trees had low levels of reserve carbohydrates that they could draw on to moderate the abrupt change in source/sink ratio following pruning (Cannell and Dewar 1994). *A. melanoxylon* grows very little in winter, followed by a period of rapid growth in spring/early summer. Thus any carbohydrate reserves may have been used in producing new growth by the time the trees were pruned in January. Carbohydrate dynamics were not examined in this study. However a positive relationship between A_{max} and SPA soon after pruning provides evidence that the rate of carbohydrate translocation from remaining phyllodes increased as a result of pruning (Thorne and Koller 1974).

The magnitude of the increase in A_{max} was proportional to the severity of defoliation, and was similar to that reported for other species pruned to a comparable severity (Heichel and Turner 1983; Reich et al. 1993; Layne and Flore 1995). For example, the increase in A_{max} of mature foliage of *E. nitens* trees pruned to remove 50% of leaf area peaked at around 120%, but was generally less than 60% (Pinkard et al. 1998). However the duration of the increase was relatively short compared to other species (Heichel and Turner 1983; Reich et al. 1993). The increases in A_{max} recorded following pruning coincided with the period of time required to replace the lost foliage area (approximately six weeks following 25% pruning and 40 – 55 weeks following 50% pruning) (Medhurst et al. see Chapter 3). In contrast to other studies that have reported increased A_{max} throughout the crowns of defoliated trees (Pinkard et al. 1998), the increase in pruned *A. melanoxylon* was confined to the upper two thirds of the crown. Strong vertical stratification of N and P throughout the crown of *A. melanoxylon* may have contributed to this difference.

That WUE was not affected by form pruning suggests that the increases in A_{max} following pruning were not due to improved plant water relations. While an increase in plant water status following pruning has been observed for some species, eg. *Alnus glutinosa* (Singh and Thompson 1995), other studies have shown no discernable effect of pruning on plant water relations (Lavingne et al. 2001). *A. melanoxylon* phyllodes are characterised by a high photosynthetic water-use efficiency and are capable of recovering from soil water potentials as low as -5.5 MPa (Brodrribb and Hill 1993). We therefore expect that any improvement in plant water status as a result of removing transpiring foliage would have minimal effect on photosynthetic capacity.

It is possible that there were changes in the light environment of the crown as a result of form pruning, although this was not specifically investigated. The 50% pruning treatment in particular removed branches that had foliage distributed throughout the crown. However shading from the adjacent *P. radiata* nurse-crop may have offset any expected increases in incident light and hence CO₂ assimilation rates in the lower crown of *A. melanoxylon* (Medhurst et al. see Chapter 3).

The increases in A_{max} following pruning were not driven by changes in foliar nutrient levels. This is a common finding in defoliation studies (Lovett and Tobiessen 1993; Reich et al. 1993; Ögren 1994). However the fact that NUE did not increase suggests some relationship between A_{max} and foliar N and P content that requires further investigation. In addition, pruning-induced changes in the partitioning of N within phyllodes to increase chlorophyll or Rubisco content cannot be discounted (von Caemmerer and Farquhar 1984; Lavingne et al. 2001; Warren and Adams 2002).

Although there was a strong linear relationship between A_{max} and g_s , the plateauing of A_{max} at high values of g_s suggests that the increase in A_{max} following pruning was not a result of changes in g_s (Farquhar and Sharkey 1982). Many studies investigating the effects of source limitation on CO₂ uptake have concluded that changes in mesophyll conductance are more important in determining photosynthetic responses to defoliation (Hodgkinson 1974; Thorne and Koller 1974; Peet and Kramer 1980; Layne and Flore 1995).

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Chapter 5: Sidelight Suppression

Introduction

Acacia melanoxylon (blackwood) displays poor apical dominance when grown under open conditions with high light levels (Unwin et al. 2001, Medhurst et al. submitted). The stem form that arises from this poor apical dominance (large branches, multiple main leaders, relatively short trees and stem lean) is undesirable when blackwood stands are managed for solid wood production (Neilsen and Brown 1997).

Sidelight suppression is viewed as crucial for improving the form of planted blackwoods by creating a lightwell and encouraging apical growth. Planting blackwood in mixed species plantings ('nurse-crops') is generally undertaken to produce a "lightwell" effect and, in turn, produce good blackwood form. Nurse-crops provide a means of sidelight suppression but both the planting arrangement and growth rate of nurse-crops in relation to the blackwood are likely to be critical factors in determining successful sidelight suppression.

Experience to date with conventional nurse-crop plantings (ie. commercial nurse-crop species established at relatively wide spacing) has shown that such planting designs offer little sidelight suppression early in the rotation and the resultant form problems require corrective pruning treatment at a later age. Additionally, without careful plantation management, the faster growth rates of the traditional nurse-crop species (*Pinus radiata*, *Eucalyptus globulus* and *Eucalyptus nitens*) can lead to growth suppression in blackwood.

The key to producing good blackwood form in plantations may lie with the use of alternative planting arrangements and/or the use of nurse-crop species with growth rates similar to that of blackwood (Pinkard and Beadle 2001). Establishing effective sidelight suppression earlier in the rotation is likely to reduce the need for, or intensity of, later form pruning. This study was carried out in a young experimental blackwood plantation that uses alternative nurse-crop species and planting arrangements. The objectives of the study were to (1) determine the requirements for nurse-crop systems in order to promote early and effective sidelight suppression; (2) determine the role of sidelight suppression in developing good blackwood form; and (3) provide guidelines for managing sidelight suppression in blackwood plantings.

Site description

The Esperance experiment was established in southern Tasmania (43° 17' S 146° 55' E). The site previously carried *Eucalyptus obliqua* wet sclerophyll forest with a blackwood understorey. The site was prepared for planting by windrowing and burning. The plantation is at an altitude of 110 m above sea level. The mean annual rainfall measured at the nearby township of Dover is 888 mm.

Design and Treatments

Plot layout

The trial was established in October 1999 when open-rooted blackwood seedlings (Esperance provenance) were planted along with a range of nurse-crop species (see below for details). Three nurse-crop systems were used. They were;

1) Conventional nurse-crop system

This system was so-named as it is often adopted for large industrial blackwood plantations in Tasmania. Each row of blackwood was flanked by two rows of nurse-crop in a 'row-for-row' arrangement. The distance between each blackwood row and nurse-crop row was 4 metres and the distance between trees in each row was 2.5 metres. The nurse-crop species used in each plot were either *Eucalyptus nitens* (shining gum) or *Pinus radiata* (radiata pine). Plot size was 0.18 hectares (40 x 44 metres). The blackwood stand density at planting was 500 trees per hectare (trees ha⁻¹).

2) *Five-row nurse-crop system*

This system featured five rows of either *E. nitens* or *P. radiata* between each blackwood row. The distance between each row was 2 metres while within-row spacing was 1.5 metres. Sidelight suppression is likely to be achieved earlier with this system compared to the conventional nurse-crop system. Management of the five-row system requires progressive removal of the nurse-crop rows immediately adjacent to the blackwood rows once they suppress blackwood growth. The middle nurse-crop row will be retained and managed for sawlog production. Plot size was 0.22 hectares (48 x 46 metres). The blackwood stand density at planting was 555 trees ha⁻¹.

3) “*Sue Jennings*” system

This system mimics the growing conditions of young blackwood in natural regrowth forest by planting the blackwood in a closely-spaced arrangement with other understorey species from blackwood-rich regrowth forest. This system was first developed by Sue Jennings on her farm property in NW Tasmania. The nurse-crop species used in each plot were one of *Melaleuca ericifolia*, *Pomaderris apetala* or *Phebalium squameum*. In each plot the blackwood and nurse-crop were planted on a 1 x 1 metre grid so that each blackwood seedling was surrounded by eight nurse-crop seedlings. Plot size was 0.04 hectares (20 x 20 metres). The blackwood stand density at planting was 1111 trees ha⁻¹. In one set of Sue Jennings plots (ie. three plots, one of each nurse-crop species), the planting of blackwood was delayed by 12 months (planted October 2000) to examine the potential of creating a light-well prior to planting blackwood.

The plantation also included control plots, consisting only of blackwood (no nurse-crop). In addition, pure blackwood plots were also established for use in an artificial shading experiment (see description below). The blackwood rows in the control and artificial shading plots were spaced 4 metres apart and blackwoods were planted at 2.5 metre spacings within each row. Plot size was 0.18 hectares (40 x 44 metres). The blackwood stand density at planting was 1000 trees ha⁻¹.

In total, the experiment consisted of 30 plots in a randomised block design.

Hand-weeding (hoeing) was used during the first year after planting to remove herbaceous weeds and naturally-regenerated blackwood seedlings from around planted blackwood seedlings

At age one year (October 2000), 29 g tree⁻¹ of triplesuperphosphate was applied to all blackwood and nurse-crop trees in a 1 square metre area centred on each tree (equivalent to 60 kg ha⁻¹ as phosphorus).

Some re-planting of nurse-crop and blackwood was required after 3, 6 and 12 months due to drought losses.

Artificial shade experiment

Artificial shade was imposed on the blackwood seedlings in the three artificial shading plots between October 2000 and June 2001. Four blackwood rows were selected in each plot, and shading treatments were randomly assigned to each row. The shade treatments assigned randomly to the four rows (each comprising 6 trees) were;

- 1) no shade
- 2) shade height equal to 50 per cent of seedling height
- 3) shade height equal to 100 per cent of seedling height
- 4) shade height equal to 150 per cent of seedling height

Two wires were strung along each blackwood row at a height of 1.8 m for the 50 and 100 per cent shading treatments, and at 2.4 m for the 150 per cent shading treatment. The wires were supported by 2400 x 100 mm posts at the end of each row. The wire was strained along the row using steel pickets approximately two metres from the posts. The posts were stabilised so that the wire on each side of the row was 0.5 m from the blackwood saplings.

Wooden stakes (1800 or 2400 x 20 mm) were threaded onto the wire and spaced along the row so that each was equidistant between two blackwood saplings. Nominally this was 1.25 metres from each of the two blackwood saplings (2.5 m between stakes).

Black shadecloth (providing 80 per cent light reduction) was attached to the wooden stakes. The height of the shadecloth between each pair of stakes depended on the treatment assigned to the row and the height of each individual sapling within the row.

The height of the shadecloth was raised once (23 March 2001) during the course of the experiment in order to keep pace with the height growth of the blackwood saplings.

Measurements and assessment

The heights of blackwood and nurse-crop trees were measured at ages one and two years. Stem diameter at 15 cm height was measured at age two years. A form assessment of blackwood was carried out at ages one and two years. The form assessment examined the number of apical leaders, stem lean, sweep or kink, the number of forks, any stem damage, and tree health.

The light environment of the shaded seedlings in the artificial shading experiment was measured between 23 January 2001 and 16 February 2001. Two trees were randomly selected in each shading treatment and quantum light sensors were installed at 0, 50 and 100 per cent of tree height. Two dataloggers measured light conditions every 60 seconds and recorded 30-minute totals from each of the 24 quantum light sensors.

The effect of the shadecloth on temperatures was measured in one artificial shading plot from 22 December 2000 to 5 January 2001. Shielded and ventilated thermocouples were installed at heights of 30 and 80 cm close to similarly-sized blackwoods across all four treatments. Wind speed was measured at a height of 1.3 metres using a cup anemometer. A datalogger measured and recorded average temperatures and wind speed every 30 minutes.

Results and Discussion

Blackwood survival

Following re-planting of some trees after 3, 6 and 12 months due to drought losses, there were excellent rates of survival of blackwood across all treatments two years after planting. The overall survival rate was 98 %. The poorest survival rates were found in the “lightwell” plots (blackwood planted 12 months after nurse-crop) with blackwood survival rates of 96, 92 and 88 per cent for the *M. ericifolia*, *P. apetala*, and *P. squameum* lightwell plots, respectively at age one year.

Height & diameter growth

There were no significant differences in tree height between the blackwood trees in the control treatment (grown without a nurse-crop) and the blackwood trees in any of the other planting systems, two years after planting (Figure 5.1a). The one-year-old blackwood trees in the three lightwell plots were excluded from this analysis. The blackwoods grown in the Sue Jennings-*Phebalium* system were taller than the blackwoods grown with *E. nitens* in a five-row nurse system. Three of the four greatest treatment mean heights belonged to the Sue Jennings system (Figure 5.1a).

There were no significant differences in stem diameter between the blackwood trees in the control treatment (grown without a nurse-crop) and the blackwood trees in any of the other planting systems, two years after planting (Figure 5.1b). The poor growth and health of blackwoods in the lightwell plots at age one year meant that stem diameters were not measured. The stem diameters of blackwood in the Sue Jennings-*Phebalium* treatment were significantly greater than those in the conventional and five-row nurse *E. nitens* treatments. There were no other significant differences between treatments. The three Sue Jennings treatments (*Melaleuca*, *Pomaderris* and *Phebalium* nurse-crops) were the three treatments with the greatest blackwood stem diameter at age two years.

An exceptionally dry summer in the first year after planting resulted in slow growth rates in both blackwood and nurse-crop species (data not shown, but see Pinkard and Beadle 2001).

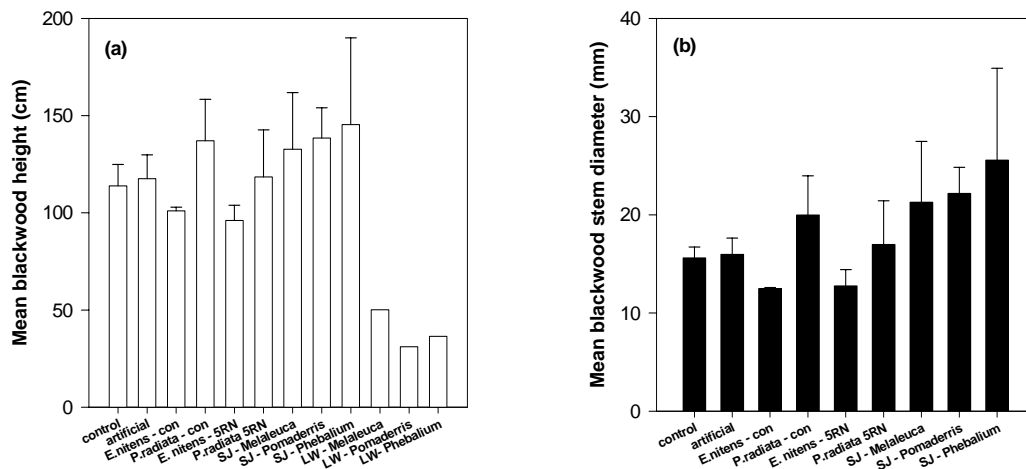


Figure 5.1. Mean blackwood height (a) and mean blackwood stem diameter at 0.15 m stem height (b) by nurse-crop system at age two years, Esperance. Error bars show mean standard error. CON = conventional system, 5RN = five-row nurse system, LW = lightwell planting. Blackwoods in the lightwell treatments (LW) are one-year-old.

Nurse-crop height growth differed greatly between species (Figure 5.2). *E. nitens* exhibited the greatest height growth, followed in magnitude by *P. radiata*, *M. ericifolia*, *P. apetala* and then *P. squameum*. The poor growth of the *P. squameum* may be due to the use of cuttings rather than seedlings at plantation establishment. However, there was no statistical difference between the heights of the three nurse-crop species used in the Sue Jennings system (Figure 5.2).

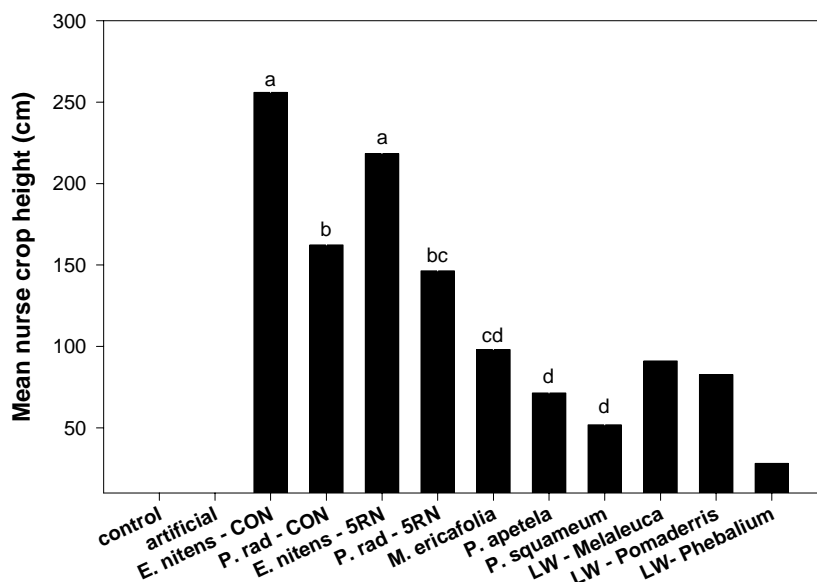


Figure 5.2. Mean nurse-crop height by nurse-crop system, age two years. Mean nurse-crop heights with the same letter are not statistically different (at $p < 0.05$; lightwell plots not included in this analysis). CON = conventional system, 5RN = five-row nurse system, LW = lightwell planting.

Height ratios

The blackwood height was less than that of the nurse-crop in all of the nurse-crop systems involving *E. nitens* and *P. radiata* (Figure 5.3). The poor growth of *P. squameum* produced high ratios in the Sue

Jennings system and the lightwell system that used this species. The ratios in the lightwell plantings were 0.55 and 0.38 for the *M. ericifolia* and *P. apetala*, respectively.

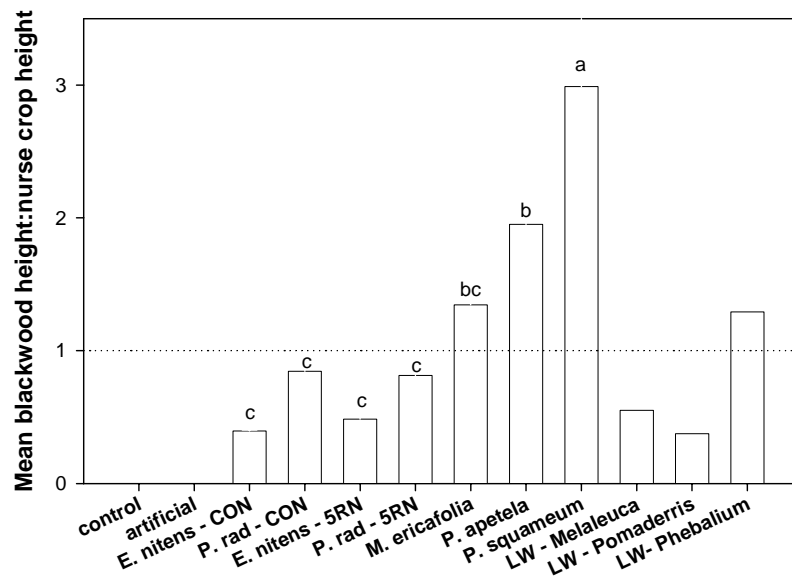


Figure 5.3. Ratio of mean blackwood height to mean nurse-crop height at age two years, Esperance. Dotted line shows height ratio equal to 1.0 (*i.e.* equal blackwood and nurse-crop heights). Height ratios with the same letter are not statistically different (at $p < 0.05$; lightwell plots not included in this analysis). CON = conventional system, 5RN = five-row nurse system, LW = lightwell planting.

Blackwood form

The nurse-crop systems which had the lowest incidence of straight, single-leader blackwood trees were the control and the Sue Jennings systems (Table). The best form was found in the lightwell *M. ericifolia* plot, however this was accompanied by very slow growth (see above). The blackwood in the other lightwell plots were not assessed for form at age one year.

The five-row nurse system tended to produce better blackwood form than the conventional system for both *E. nitens* and *P. radiata* (Table).

The incidence of stem lean increased with decreasing nurse-crop height in the Sue Jennings systems (the taller the nurse-crop, the straighter the blackwood).

In general, the best blackwood form was produced in nurse-crop systems where the blackwood height was less than the nurse-crop height (see Figure 5.3).

The incidence of good health of the blackwood trees was lowest in the control treatment (40 % of stand) and greatest in the Sue Jennings *P. apetala* treatment (63 % of stand). The high variability in soil quality and differences in slope (and subsequent cold air drainage and ponding) across the site makes it impossible to categorically state that treatment differences in blackwood health were due to the level of wind and frost protection given by the nurse-crop. However, the clear improvement in blackwood health after shading in the artificial shading experiment (see Figure 5.6) suggests that the nurse-crops are providing some protection at this site.

Table 5.1. Percentage of blackwood trees with single apical leader, straight stems, and both a single leader and straight stem by nurse-crop system, age two years.

Nurse-crop system	% of blackwood trees with single leader	% of blackwood trees with straight stem	% of blackwood trees with single leader and straight stem
control	25	32	22
artificial	42 [†]	26 [†]	26 [†]
<i>E. nitens</i> conventional	34	35	29
<i>P. radiata</i> conventional	36	29	26
<i>E. nitens</i> five-row nurse	33	45	33
<i>P. radiata</i> five-row nurse	44	45	33
Sue Jennings <i>M. ericifolia</i>	21	32	20
Sue Jennings <i>P. apetala</i>	28	28	20
Sue Jennings <i>P. squameum</i>	40	19	19
Lightwell <i>M. ericifolia</i> [‡]	40	40	40
Lightwell <i>P. apetala</i> [‡]	n/a	n/a	n/a
Lightwell <i>P. squameum</i> [‡]	n/a	n/a	n/a

[†]Includes effect of artificial shading treatment (see below).

[‡]Blackwoods are one-year-old in these treatments.

Sidelight suppression

Artificial shading

The light environment experienced by blackwood trees within each shading treatment was compared to that of blackwoods without shade cloth (Figure 5.4). Trees in the 50 % shade height treatment experienced significant shading only at the base of each tree with a 24 % reduction in light levels relative to the base of the unshaded trees.

The proportion of daily light reaching the base and mid-stem of trees in the 100 % shade height treatment was significantly less than that received by the unshaded trees. There was a 27 % and 15 % reduction in light levels for the base and mid-stem, respectively. There was no difference in the light environment of the 50 % shade height and 100 % shade height treatments at tree base, mid-stem, or tree top.

The 150 % shade height treatment produced the strongest shading effect, with significantly lower daily light levels at tree base, mid-stem and tree top compared with the unshaded trees. For this treatment, shading reduced the daily light received by the base, middle and top of the trees by 56 %, 46 % and 20 %, respectively. The light conditions at the top of the trees were similar for the 100 % and 150 % shade height treatments.

The shadecloth had a minimal effect on the temperatures experienced by the blackwood trees. On a day when the ambient temperature reached 32.4 °C at the Esperance site (3 January 2001) the temperatures within the shadecloth did not differ from ambient temperatures by more than 1.5 °C. The maximum windspeed measured near the shadecloth on this day was 13 kilometres per hour.

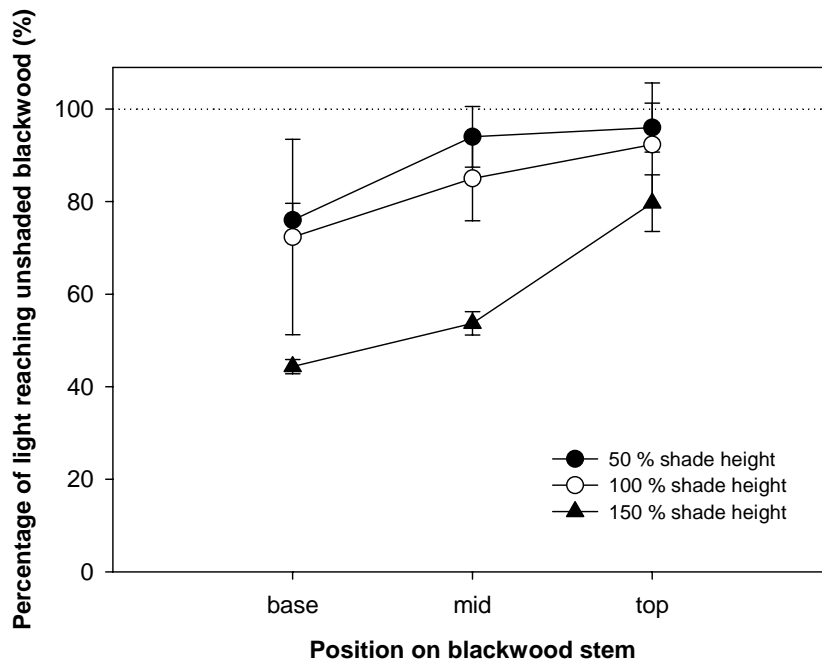


Figure 5.4. The mean proportion of daily light reaching the base, mid and top of blackwood trees by shading treatment, relative to the light reaching the base, mid and top of unshaded blackwoods, January 2001. Dotted line shows the relative light environment of unshaded blackwoods. Error bars show standard deviations.

Effect of shade on blackwood growth and form

The greatest relative height growth was found in the 150 % shade height treatment (Figure 5.5). Over twelve months the height of trees in the 150 % shade height treatment increased, on average, by 126 %. In comparison, the height of blackwood in the unshaded control treatment increased by 82 %. The height of trees in the 100 % and 50 % shade height treatments increased by 84 % and 118 %, respectively. Statistically however, there were no differences in the relative height growth of the shadecloth treatments.

Shade treatment improved the form of blackwood with a higher incidence of single-leadered trees, compared to trees in the unshaded control treatment (Figure 5.6). There was also a notable improvement in blackwood health with shading (Figure 5.6).

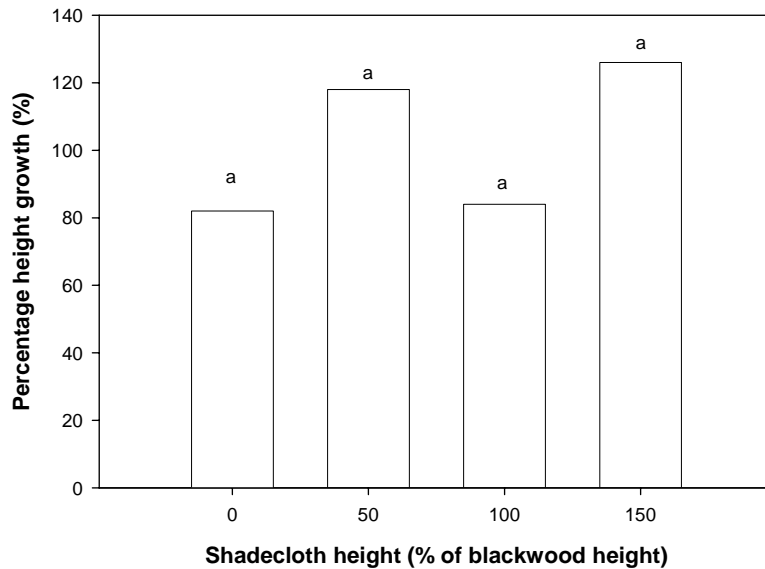


Figure 5.5. Percentage height growth from October 2000 to October 2001 by shading treatment, Esperance. Shadecloth height treatments with the same letter are not statistically different (at $p < 0.05$).

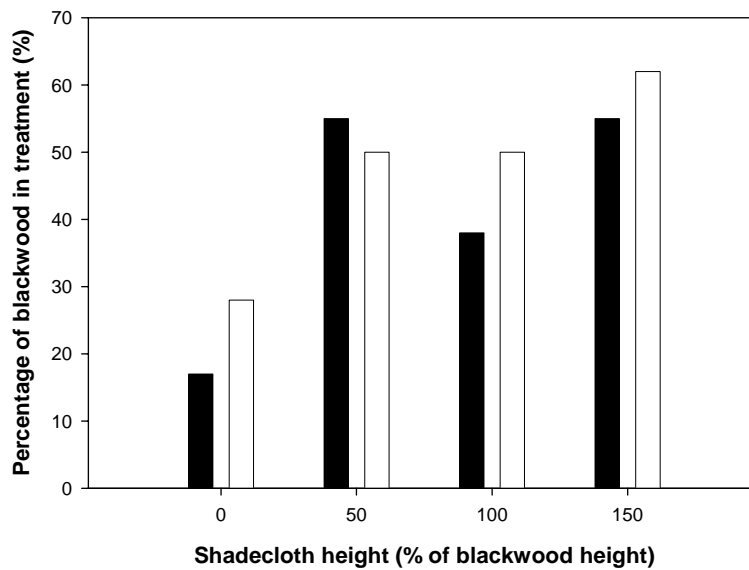


Figure 5.6. Solid bars show percentage of stand with single apical leader, open bars show percentage of stand in good health.

Conclusions

The influence of nurse-crops in providing an environment required for good blackwood form was becoming evident even at two years of age. While little differences in blackwood growth rate were observed, the different characteristics of nurse-crop species and their planting in relation to the blackwood is already influencing blackwood stem form.

Form improvement with the five-row nurse system indicates that early sidelight suppression is achieved with fast-growing nurse-crops planted close to blackwood trees (1 m in this system). Slower-growing nurse-crop species planted at a similar spacing (eg. Sue Jennings system) did not provide adequate sidelight suppression during the first two years of growth. However, the benefit of using

slower-growing nurse-crop species may become evident at a later age if the faster-growing nurse-crop species suppress blackwood growth.

Blackwood stem form was good in nurse-crop systems where the height of the blackwood was less than that of the nurse-crop, highlighting the importance of a 'lightwell' for good blackwood form. The artificial shade experiment demonstrated that shade height needs to be greater than 100% to have an appreciable effect on blackwood growth habit.

For commercial nurse-crop species, closer spacing than conventional is producing better blackwood form. But there is also a tendency for slower blackwood growth, meaning that management of blackwood under systems such as the five-row nurse must be vigilant from an early age to avoid the onset of blackwood growth suppression.

Chapter 6: Decision Support

Introduction

Experiments on how form pruning and nurse-crop thinning affect blackwood (*Acacia melanoxylon*) growth and physiology provide general qualitative guidelines for silvicultural management of blackwood (Medhurst *et al.*, 2002). However, much of this data came from experiments conducted under quite specific conditions. The actual response to an intervention will depend on factors such as stand age and site conditions. To provide support for management that is neither site- nor age-specific it is necessary to develop a model consistent with both general stand growth and specific physiological responses of blackwood. In this chapter, the basics of such a model are developed.

The stand growth model described by McMurtrie and Wolf (1983) was used as the starting point for such a model. Their model takes into account light interception and photosynthetic production, respiration, allocation to various biomass pools, and litterfall and root turnover. Each of these was represented by simple empirical relationships with constant parameters. The model used here has biomass pools for foliage, stem wood, branches and bark, and roots, in some instances based on generalised relationships in the original model. Relationships for the affects of form pruning on canopy growth and photosynthetic capacity, and for the affect of the nurse-crop on the radiation available to the blackwood, were added.

The emphasis is on simplicity, perhaps at the risk of over simplification, but detail can be readily added as needed. The assumptions of the simple model are described, and how a more rigorous approach could be adopted is indicated.

Effects of blackwood silviculture

Figure 6.1 summarises the observed effects of nurse-crop thinning and form-pruning on the growth and physiology of blackwood. This is based on data from experiments by Medhurst *et al.* (2002) at Beulah in NW Tasmania, which are typical of responses observed elsewhere and for other species. In Figure 6.1 factor A affects B *positively* if an increase in A leads to an increase in B, or *negatively* if an increase in A leads to a decrease in B. Figure 6.1 also differentiates responses observed directly from blackwood from those inferred from other experiments or generic responses.

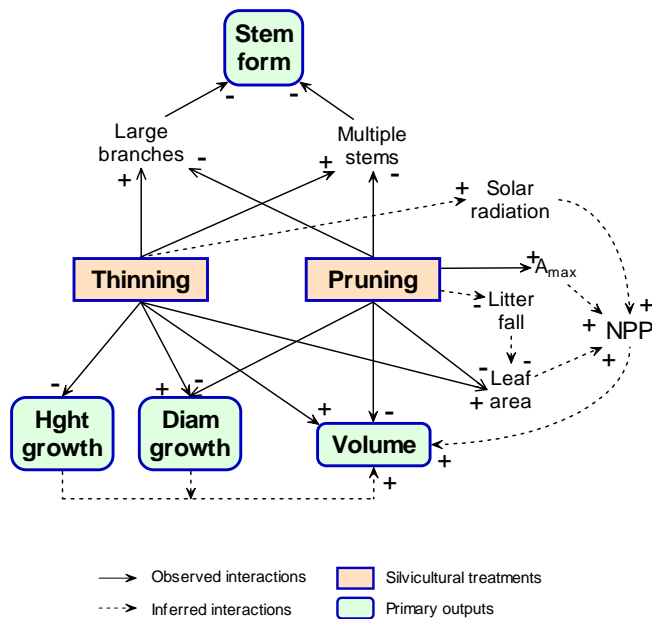


Figure 6.1. Influence of nurse-crop thinning and form-pruning on blackwood growth and stem-form.

For example, nurse-crop thinning increases the number of large branches and multiple stems in the blackwood. It also increases solar radiation impinging on the blackwood, and hence leads to an increase in NPP and volume. Blackwood form-pruning has been shown to increase photosynthetic rates, and as pruning is mainly from below it decreases litter fall. These two effects enhance the immediate recovery of the canopy.

Analyses such as those in Figure 6.1 are the basis for incorporating silvicultural effects into the growth model. For example, NPP (G , $\text{kg}_{\text{DM}} \text{m}^{-2} \text{yr}^{-1}$) is proportional to intercepted radiation, which is determined from canopy LAI (L , $\text{m}_{\text{leaf}}^2 \text{m}_{\text{ground}}^{-2}$) using Beer's Law, i.e.

$$G = \varepsilon Y (1 - e^{-kL}) Q_0$$

where ε ($\text{kg}_{\text{DM}} \text{MJ}^{-1}$) is a measure of the efficiency of conversion of light into dry matter (light-use efficiency), Y takes into account respiration, k is the canopy extinction coefficient, and Q_0 ($\text{MJ m}^{-2} \text{yr}^{-1}$) is the radiation incident on the canopy. Nurse-crop thinning

- immediately allows more light to reach the blackwood canopy, which increases Q_0 , and
- opens space for the blackwood canopy to develop, which allows L to increase.

The result is an increase in growth rate. (However, the improved light environment reduces height growth, and increases diameter growth, relative to an unthinned stand.) Form pruning immediately reduces L , and so reduces growth rate, but induces a pruning response that

- a) increases light-saturated photosynthetic rate A_{max} , and hence increases ε
- b) decreases leaf litter fall, and
- c) increases biomass partitioning to foliage at the expense of stemwood.

The result is an immediate increase in photosynthetic rate per unit leaf area, together with a recovery over time of L , but at the expense of stem diameter growth.

Modelling growth and silvicultural effects

Figure 6.2 is a schematic diagram of the full model. It shows the flow of carbon through the McMurtrie and Wolf (1983) model, and submodels for height and diameter growth, and for the effects of pruning and of nurse-crop thinning on blackwood growth. It also shows various influences and feedbacks. These components are discussed in more detail below.

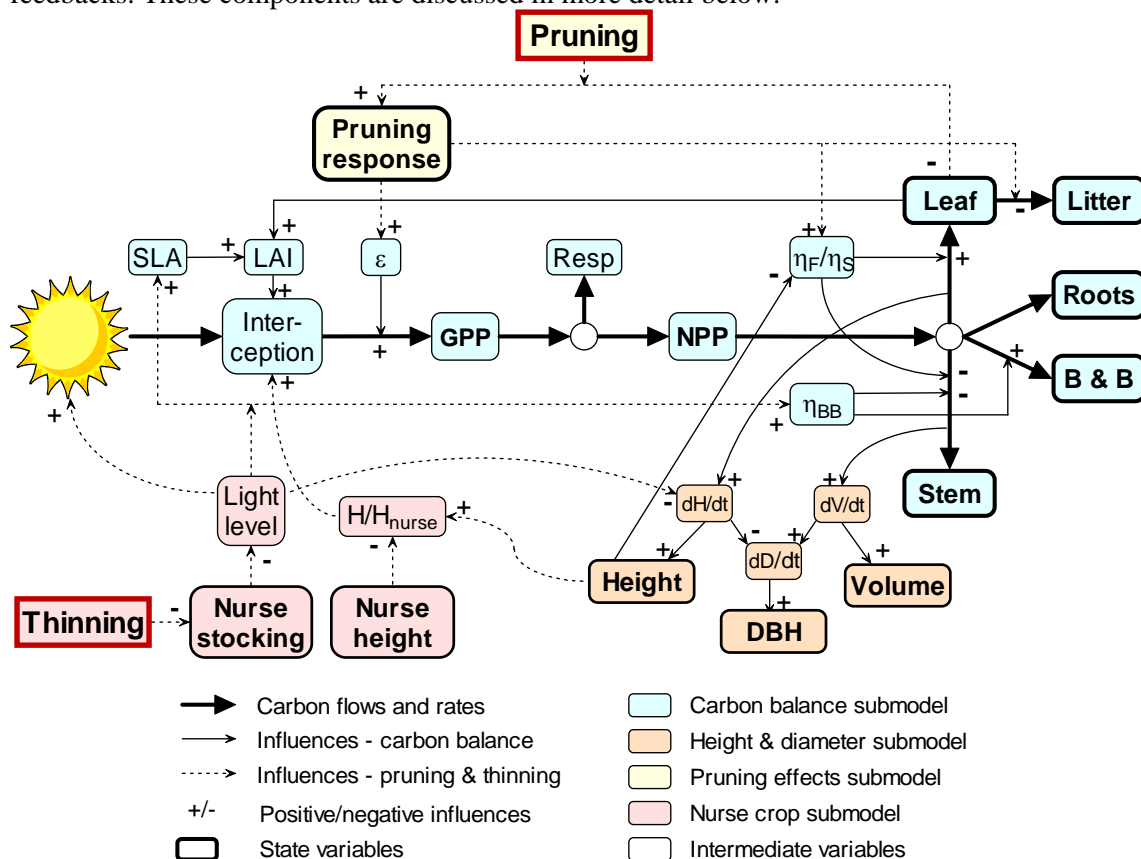


Figure 6.2. Schematic diagram of tree growth model including potential effects of a nurse crop and pruning.

Light interception, photosynthetic production, and respiration

Light interception by the canopy is determined using Beer's law and requires L . Total production is assumed to be proportional to intercepted solar radiation since above-ground dry matter production is observed to be so (e.g. Linder, 1985), and ϵ is the slope of this relationship.

The simplest way to take respiration into account is to assume that G is a fixed fraction ($Y \approx 47\%$) of gross production (e.g. Waring *et al.*, 1998).

Biomass allocation, litterfall, root turnover and mortality

In McMurtrie and Wolf (1983) the biomass partitioning ratios were constant parameters. It is assumed that: partitioning to roots is a constant parameter (η_R) with a higher value on nutrient poor or water-stressed sites, the ratio (η_{FS}) of foliage:stem biomass partitioning declines as stem height increases, and partitioning to branches and bark (η_{BB}) declines with age.

Leaf litterfall and root turnover rates (γ_F and γ_R) are assumed to be proportional to the current leaf and root biomass pools. Mortality assumes a constant death rate.

Height growth

It is assumed that tree canopies are ellipsoids with a uniform leaf area density, and that foliage is added at the top of the canopy and litterfall confined to the base. In a closed canopy the height growth rate is proportional to the rate of production of foliage and inversely proportional to canopy leaf area density, and the rate of canopy lift is determined by the litterfall rate.

Stem diameter growth

A conical stem with a constant shape factor is assumed, so increments in stem biomass, height and diameter are constrained by a simple volume formula. As biomass is added to the stem it increases stem volume, and this is accompanied by an increase in one or both of stem height or diameter. It is also assumed that the ratio (η_{HD}) of height and diameter growth rates is under environmental control; so, for example, nurse-crop thinning reduces competition for light, which reduces height growth.

Response to pruning

A simple mechanistic approach to represent the pruning response is used. Data from blackwood (e.g. Medhurst *et al.*, 2002) and for *E. nitens* (e.g. Pinkard *et al.*, 1998) show that responses in both growth and physiology were maintained over a significant period of time. For example, for several months following pruning, light-saturated photosynthetic rate A_{max} was higher than in unpruned trees, and canopy growth rate was enhanced.

It is assumed that pruning initiates a pruning response (P), which affects one or more of photosynthesis, partitioning to foliage, and litterfall. P is a dimensionless quantity whose value declines with time and reflects the current strength of the pruning response. At pruning P is set equal to the fraction of foliage biomass removed, but then declines exponentially with a time constant of the order of 6-12 months. No attempt is made to provide a physiological basis for P .

Pruning initiates an increase in the efficiency with which the remaining leaves produce assimilates, so A_{max} , and hence also the light-use efficiency ϵ , increase with P . It is assumed that the increase in the rate of canopy development is mediated by an increase in the ratio η_{FS} and/or a decrease γ_F . So ϵ and η_{FS} are modelled as increasing functions of P , and γ_F as a decreasing function of P . As P declines towards 0, these parameters return to their values in the absence of pruning. The strength of the response of these various parameters (say τ) is expressed as the per cent change (P_τ) in the parameter when $P=1$. Thus the change in τ induced by pruning depends both on the value of P_τ and the pruning intensity.

This simple model has a potentially rich repertoire of behaviour and can be parameterised from data on assimilation and stand development at several times following pruning.

Light interception in a mixed-species canopy

Since the blackwood/nurse-crop system is a two-species stand, light interception by each species is required to drive the tree-growth model. The ERIN model (Wallace & Verhoef, 2000) is used to partition intercepted light between the nurse-crop and blackwood. ERIN requires the heights and leaf areas of each canopy. Blackwood height and leaf area were predicted using the tree growth model. The nurse-crop top height was assumed to be 90% of mean dominant height predicted by a simple empirical model (Candy, 1989), and nurse-crop leaf area was assumed to be proportional to its canopy depth

In the ERIN model, a species is said to be *dominant* if its canopy completely overtops that of the second, or *suppressed* species if its canopy is completely below that of the second. In these cases, Beer's law applies to each canopy, and the light incident upon the suppressed canopy is that transmitted by the dominant canopy. If the canopies intermingle the light intercepted by one species is

a weighted average of interception assuming it is in turn dominant or suppressed, and the weighting factor is proportional to the square of the ratio of the canopy top heights.

Effect of a nurse crop

The nurse-crop reduces the radiation available to the blackwood for growth. This is quantified by the ratio Λ of radiation incident at the top of the blackwood canopy to that incident on the top of the nurse-crop, with $0 \leq \Lambda \leq 1$. High light levels ($\Lambda \rightarrow 1$) tend to increase branch production and reduce height growth, as demonstrated by the response to nurse-crop thinning (see Fig. 1). In the model I represent this by making partitioning to branch and bark (η_{BB}) an increasing function of Λ , and the height growth rate a decreasing function of Λ .

Application of the model

The full model on data from a nurse-crop/blackwood stand has not yet been rigorously tested, but its major elements have been verified in various ways as shown here.

Application of the tree growth model to blue gum

The tree-growth model was tested by applying it to a blue gum plantation that was neither water nor nutrient limited, and for which nine years of growth data were available. Some parameters were assigned values based on data from other blue gum stands, but a few were estimated by fitting model output to observed mean tree height, stem volume, and canopy L . This was not a rigorous validation, but Fig 6.3 shows the model can reproduce observed data and provide plausible long-term trends. Although the model is intended for use with real daily or monthly climatic data, it was applied here with no seasonal variation in radiation.

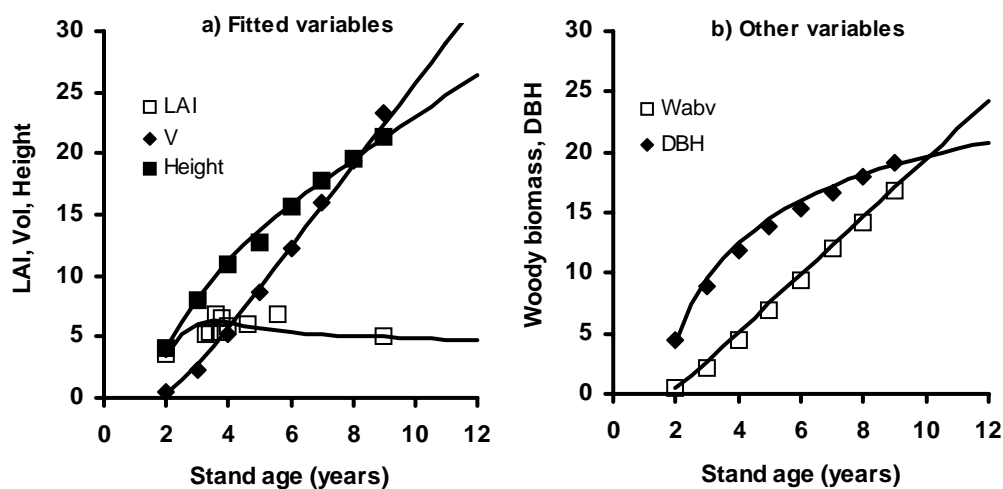


Figure 6.3. Comparison of observed stand development (symbols) of irrigated blue gum with predictions (lines) from the tree growth model.

Application to the pruning submodel

The ability of the pruning submodel to reproduce observed effects was tested by using it to prune a notional stand and then comparing the responses with those shown in Chapter 3. Figure 6.4 illustrates response of canopy L , stem height and DBH to two levels of pruning as predicted by the tree growth model with no pruning response (i.e. $P=0$). Over time the canopy recovers, but height and diameter always lag the unpruned stand.

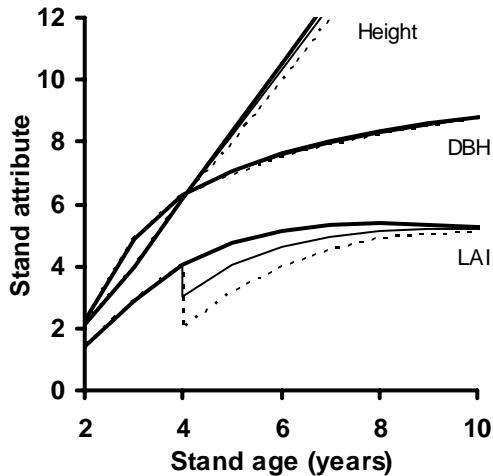


Figure 6.4 Effect of pruning at age 4 years on subsequent growth of a notional stand: unpruned (—), 25% pruned (—), 50% pruned (----).

A pruning response was then assumed such that

- P is initially the fraction of foliage removed and decays exponentially with a rate constant of 1 yr^{-1} ,
- γ_F is decreased, and ε and η_{FS} are increased by 50% for unit P (i.e. $P_{\tau}=50\%$). The magnitude of these effects is arbitrary.

Figure 6.5 shows post-pruning growth increments in L , DBH and height over a three-year period as predicted using the pruning submodel. Figure 6.5a shows the growth of L with and without the pruning response, and canopy recovery is enhanced by the pruning response. The qualitative nature of canopy recovery is consistent with Fig. 3.5. Figure 6.5b shows that DBH growth with the pruning response is qualitatively consistent with Figure 3.4a. Figure 3.5c shows the height growth with the pruning response. In this case the result obtained differs from that observed in blackwood as Figure 3.4b shows no effect of pruning on height growth.

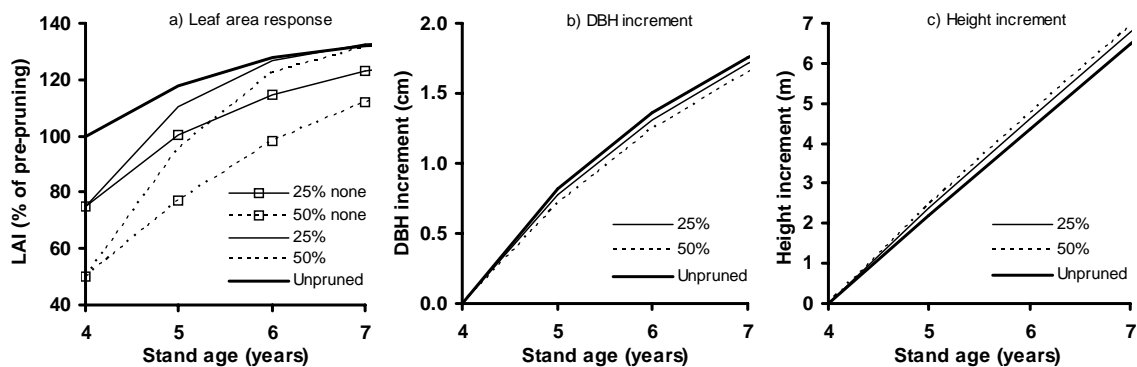


Figure 6.5. Post-pruning growth of (a) LAI, (b) DBH and (c) height of a notional stand: unpruned (—), 25% pruned (—), 50% pruned (----); symbols (\square) indicate growth in the absence of a pruning response ($P = 0$).

Application of ERIN model

Application of the ERIN model requires the top height and canopy L of the nurse-crop and of the blackwood. These were obtained for May 2000 and 2002 from the Beulah experiments (Medhurst *et al.*, 2002) and from unpublished data of Cherry and Worledge. Top heights had been measured directly, blackwood canopy leaf area was inferred from an allometric relationship between leaf area and stem diameter, and stand leaf areas were measured for the four thinning treatments at Beulah. It

is assumed that as canopy lift had not occurred for the nurse-crop, its L was proportional to tree height; it was found to be 5.5–5.6 m² leaf m⁻¹ height.

The light transmitted to breast height in the blackwood-nurse-crop stand in May 2000 was calculated using Beer's law and is compared in Figure 6.6a with observed data (see Figure 3.3) as a function of nurse-crop stem number. Figure 6.6b shows the fraction of incoming radiation intercepted by both the blackwood and the nurse-crop.

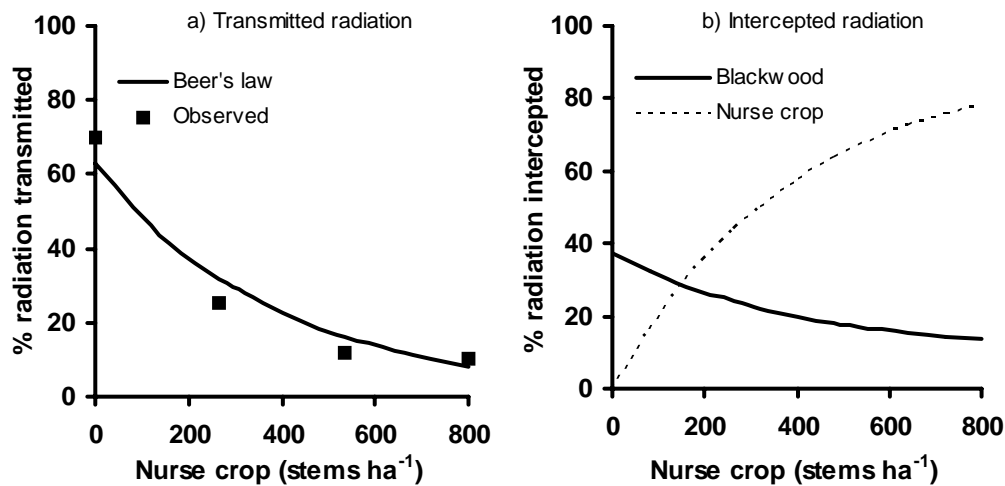


Figure 6.6. Transmitted (a) and intercepted (b) incoming solar radiation by a blackwood-nurse-crop stand in response to nurse-crop stem number. Transmission was determined by applying Beers law to the combined stand, and interception was calculated using the ERIN model.

Discussion

The model has three distinct components: a tree growth model, a model for the response to pruning, and a model for effects of a nurse-crop on the light environment and growth of the blackwood. The tree growth and nurse-crop models are based on existing models. The pruning model is a simple, novel mechanism that captures observed physiological responses. The complete model has yet to be tested using data from a blackwood/nurse-crop plantation, but its individual components give generally plausible responses. The tree growth model reproduces observed growth of a blue gum plantation, the pruning submodel produces a range of plausible responses, as does the submodel for the influence of the nurse-crop.

The growth model

Significant simplifying assumptions were made on how the environment effects tree growth – basically by subsuming these effects into model parameters. However, these can be readily generalised in proven ways, e.g. as follows.

Light use efficiency varies in response to factors such as temperature or water availability. These effects can be modelled using the approach adopted in GROWEST (Fitzpatrick & Nix, 1970) or 3-PG (Landsberg & Waring, 1997), or photosynthetic production can be calculated using a process-based model (e.g. Sands, 1995; Sands, 1996). Beer's law applies to a closed canopy, but it can be generalised for partial canopies (e.g. Jackson & Palmer, 1979), and explicit expressions for light intercepted by individual trees are available (e.g. Charles-Edwards & Thornley, 1973; West & Wells, 1992).

A process-based approach to modelling respiration can be based on dark respiration, tissue maintenance respiration, and construction respiration. Dark respiration is proportional to leaf biomass,

maintenance respiration is proportional to tissue biomass, and construction respiration is a constant fraction of the biomass synthesised. The specific respiration rates depend on factors such as tissue nitrogen concentration and temperature.

West (1993) modelled biomass partitioning in the McMurtrie and Wolf model as the solution to a linear programming problem that maximises leaf production subject to biological and mechanical constraints. However, this approach is too detailed for the simple model applied here. In general, γ_F and γ_R are affected by environmental factors, e.g. water stress, and can be made to vary with long-term conditions. Mortality of suppressed trees can be modelled in response to competition for light (e.g. West, 1987), and density-dependent mortality can be introduced via the self-thinning rule (e.g. Landsberg & Waring, 1997).

The model for canopy development assumes the canopy is closed so there is strong coupling between addition of new foliage and height growth rate. Prior to closure, addition of new foliage will be through branch elongation as well as height growth. Although the model does take enhanced branch growth in young stands into account because η_{BB} declines as stands age, it is still necessary to take into account reduced height growth rate in open stands.

Applications

The basic tree growth model provides a good fit to observed stand development provided the model is initialised with observed data, e.g. at age 2 years, and the predicted long-term trends also appear to be very plausible. However, it was difficult to obtain a good simulation of stem diameter growth when the stand was initialised at an earlier age. (This problem is not unique to this model!) This might be because the model does not properly determine radiation intercepted by an open stand, nor properly simulate canopy development prior to closure.

The growth in canopy LAI and DBH following pruning as predicted by the pruning model was qualitatively in agreement with the observed responses. However, height growth was predicted to be enhanced slightly following pruning, which was not observed by Medhurst et al. (2002). In the model height growth is tied to the production of new foliage and the leaf area density was assumed constant, so the enhanced production of foliage drove increased height growth. In reality, the blackwood canopy was not closed, and new foliage would be accommodated through branch elongation. Over the first year following pruning, leaf area density declined slightly (from 1.35 to 1.26 (± 0.8) m^{-1} , not statistically significant), although the canopy leaf area increased markedly.

The tree growth model can in principle be applied to the nurse crop. Nurse-crop height, however, was calculated using a simple empirical model (Candy 1989), and assumed that nurse-crop canopy leaf area is proportional to canopy height prior to canopy lift. Comparison of observed nurse-crop heights at ages 6 and 8 years with output from the empirical model suggested a site index of about 33 m at age 20.

Beer's law and the ERIN model were applied to predict light interception by the blackwood and nurse-crop in May 2000. Figure 6.6a suggests total stand interception declines more rapidly than might be inferred from Beer's law. Figure 6.6b shows that less than 40% of the incoming radiation is intercepted by the blackwood, and this declined markedly with increased nurse-crop stem number. This is largely because the stand-level LAI of blackwood was less than 1. Data collected in May 2002 can be used to validate application of the ERIN model.

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Chapter 7: General Discussion and Conclusions

Mixed species plantings

In an attempt to mimic conditions found in native forests, the most common approach in Australia to growing blackwood in plantations has been with nurse-crop species such as *Eucalyptus nitens*, *E. globulus* or *Pinus radiata*. In order for a nurse-crop to be effective in improving apical dominance and stem form a number of factors need to be considered, such as the relative growth rates of the species, row spacings, methods of improving blackwood growth, and the optimal light environment for blackwood growth and form. This research has examined these factors in the context of a blackwood/*P. radiata* plantation but has also examined alternative systems that have the potential to better match the environmental conditions associated with the production of good form in blackwood in native forest systems.

In the blackwood/*P. radiata* plantation, the improvement in form achieved by pruning at age five-six years was transient and clearly such a one-off pruning operation will not produce the stem form required for producing solid-wood products. Form pruning needs to commence earlier, perhaps as early as two to three years of age, for an acceptable improvement in form to occur without disrupting growth. More frequent, less severe pruning operations may also be preferable as (a) the vigour of the blackwood as it competes with the nurse-crop for resources is maintained and (b) there is a greater effect on form than a similar intensity of pruning carried out at a later age, as branches can be removed before they become large.

As there was virtually no growth of *A. melanoxylon* crowns over the winter period followed by rapid crown growth during the spring-early summer period, the pattern of stem diameter growth was similar to that of foliage production. Scheduling pruning to precede the rapid rate of crown growth in the spring-early summer period will reduce the time required for crown recovery and minimise any effects on growth.

The early and strong response to heavy thinning of the nurse-crop indicates that it was already suppressing growth of the blackwood. However, silvicultural management of blackwood – nurse-crop systems such as the one used in this experiment needs to concentrate on producing good form as a priority over high growth rates. The clear incompatibility between these two goals, as demonstrated by the change in growth and form of blackwood without a nurse-crop, means that form in the first 6 m of the stem must be established before promoting growth. The vigour of the blackwood can be maintained with a low intensity nurse-crop thinning at an early stage in the rotation.

Species with dense crowns are ideal as nurse-crops because they provide greater sidelight suppression. The species commonly used, i.e. *E. nitens*, *E. globulus*, *P. radiata*, have this characteristic. However, as they tend to have faster growth rates than blackwood, suppression of the blackwood is likely without the low intensity thinning suggested above for *P. radiata*. The eucalypts commonly grow faster than the *P. radiata*!

An alternative that was examined in this study is to use tall shrubs such as *Pomaderris*, *Phebalium* and *Melaleuca* species. Many of these have a maximum height of 6 – 9 m (commonly the desired clearwood log length), and a growth rate comparable to that of the blackwood. If planted at the close spacings used here, (i.e. a 1 m grid) they should be able to promote good stem form up to their maximum height, after which the blackwood crowns can emerge above the nurse-crop and drive blackwood diameter growth. The potential negatives are that (a) seedlings of these species tend to be expensive and a lot are required, and (b) the planting spacing makes access difficult for any management operations. In the artificial shading experiment where shade cloth was used to mimic

nurse crops of 50%, 100% and 150% of blackwood height, height growth of the blackwood was greatest with the 150% treatment. Daily light in this treatment was reduced by 50 – 60% in the lower two thirds of the crown. This suggests that there is an optimal nurse-crop height for inducing favourable stem form.

With careful management nurse-crops can improve stem form and apical dominance, and reduce the need for form pruning. Often management will be a compromise between improving stem form and maximizing blackwood growth. While some of the systems discussed above are unsuitable for large-scale plantations because of the costs involved and operational constraints, they may be an option for smaller-scale plantations.

What can we learn from physiological measurements?

Blackwood has a capacity to recover its crown leaf area from severe levels (50%) of form pruning. This was related to an increase in the light-saturated net CO₂ assimilation (A_{max}). This observed increase in photosynthetic capacity, however, was not fully realised because of the presence of the nurse-crop and this can lead to a significant reduction in diameter growth. This conclusion was supported from measurements that showed that the effect of the 50% pruning treatment on diameter growth was greater in the low compared to the high intensity thinning treatments. Thus crown responses to a given level of pruning will be slower, and the ability of the recovering crown to photosynthesise will be less, than the values measured here if thinning removes less than 66% of the nurse-crop. The rapid recovery from less severe levels (25%) of form pruning was probably associated with the transient increase in photosynthetic capacity that occurred in the first few weeks after pruning. Increasing severity of form pruning is also associated with the removal of a greater proportion of branches in the middle and upper levels of the canopy. These branches contribute a much greater proportion of the carbon gain to the tree than those in the lower level of the crown. Thus, while the increase in photosynthetic capacity at the leaf level was observed only in the upper and middle parts of the crown, levels of canopy photosynthesis at these levels would have been more compromised in the 50% compared to the 25% pruning treatment. In addition, the reduced levels of incident light caused by the presence of the nurse-crop would have meant less than full expression of these enhanced levels of photosynthesis. Taken together, these factors would have contributed to the very large difference (around 8 months in the time for canopy recovery between the two treatments).

The logic for using nurse-crop systems is to minimise the need for intervention, particularly pruning. As elaborated above, the reality is that some pruning is still required in these systems. The faster growth of the nurse-crop compared to the blackwood leads to the intensification of shading of the blackwood with time. The physiological study confirmed that any form pruning should be light to minimise reduction in growth of the blackwood by ensuring that the benefits of compensatory processes are not compromised. Less frequent pruning will be required than is necessary when blackwood is grown in pure stands but must be used as required at least until good form has been established in the first 6 m of the stem. In the blackwood-*P. radiata* system used here, the last form pruning rather than the first form pruning would have occurred at around the beginning of the experiment. Judicious thinning of the nurse-crop can then be undertaken without experiencing the prejudicial effects on form that could not be managed through form pruning at this stage in the stand's development.

Modelling response to pruning and nurse-crop competition

A model was developed that predicts the growth of blackwood in response to pruning and to thinning of the nurse-crop. This was a first attempt at developing a process-based model for a mixed species plantation that considers the effect of silvicultural intervention at two levels.

There are several distinct aspects that must be considered as part of the future development of this model. First, the tree growth model must be made responsive to the environment. In particular, effects of temperature on light-use efficiency, and of soil nutrition and water availability on biomass partitioning to roots must be re-instated. Second, the manner in which canopy development (and hence

height growth) is modelled must be modified to take into account lateral growth prior to canopy closure. Third, the nurse-crop model must be verified, especially the prediction of the light environment of the blackwood. Data on light interception has been collected at the Beulah plantation and can be used for verification.

The model must then be explicitly parameterised for blackwood and tested using data from a realistic blackwood/nurse-crop system. This requires acquisition of suitable data sets covering the long-term growth of blackwood, and preferably including measures of canopy leaf area, height and diameter. The model must be implemented in a standard environment. It is suggested that MS Excel might be a suitable platform as it allows the user to work in a familiar environment and makes all the power of spreadsheets available.