The effect of solid-wood silviculture on growth, form and wood properties in *Eucalyptus* plantations: an Australian perspective
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**Keywords:** Pruning; thinning; fertiliser; leaf area index; site quality; stand structure

**Abstract**

Thinning, pruning and fertiliser application are important silvicultural treatments used to grow solid-wood products from *Eucalyptus* plantations. The growth and physiological responses, as well as changes in wood properties in response to these treatments are reviewed, particularly from an Australian perspective. These treatments are examined in
terms of their production ecology, such that growth responses to each treatment are described as a function of how they affect light and water availabilities, capture and use efficiency, and biomass partitioning. These silvicultural treatments are sometimes carried out simultaneously and can therefore potentially interact. These interactions as well as those with site quality are also examined. While site quality is a useful variable for explaining thinning responses, stand structure, in terms of the skewness and variability of diameter distributions, appears to describe some of the variability that site quality does not, and may also help to understand mechanisms behind thinning responses.

Forrester et al. (2010c) reviewed the growth and physiological responses of eucalypts to thinning, pruning and fertiliser application, with a particular focus on Australian plantations. More recently, Beadle et al. (2011) reviewed the effect of thinning and pruning in eucalypt plantations on wood properties. The current review combines and updates this information. In addition, new sections have been added that discuss how thinning and pruning can interact to influence growth, and how growth responses to thinning and pruning are influenced by site quality and fertiliser application. There is also a new section that discusses the production ecology of thinning, pruning and fertiliser application in order to show some of the main mechanisms responsible for the growth responses. The production ecology considers how resource uptake and resource-use efficiencies change following each treatment and contribution of each of these mechanisms to the growth response.

This review has also considered overseas experience in eucalypt plantations where thinning and pruning are used in commercial plantations. Several more detailed case studies from Argentina, Brazil, Chile and Uruguay about thinning and pruning regimes, as well as mixed-species plantations, are available in Forrester (2008).
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1. Background

Fast-growing commercial plantations of *Eucalyptus* species play an important role worldwide to satisfy both an increasing demand for wood and the provision of environmental services (Ekström, 2005; Arroja et al., 2006). The total area of *Eucalyptus* plantations now exceeds 19 million hectares (Iglesias Trabado and Wilstermann, 2008) of which about 1.2 million hectares have sawlog potential (FAO, 2005). The majority of this global resource is distributed in about one dozen countries and owned by either a few large corporations or numerous smallholders (Cossalter and Pye-Smith, 2003; Montagu et al., 2003; FAO, 2005). The resource mainly consists of extensive mono-specific plantations. Genetically improved material is planted at 800 – 2,000 trees ha$^{-1}$. Most plantations are intensively managed, remain unthinned, and in sub-tropical and tropical environments are harvested in as little as six years. In the tropics average annual growth rates of wood volume can reach 70 m$^3$ ha$^{-1}$ year$^{-1}$ (Cossalter and Pye-Smith, 2003; McRae, 2003; Nutto et al., 2006; Stape et al., 2010).

Approximately 35% of this resource is in the temperate and mediterranean zones of countries such as Argentina, Australia, Chile, Portugal and Spain. *Eucalyptus globulus* (Southern Blue Gum) and *E. nitens* (Shining Gum) are the most common species planted and are considered to have the most potential to produce high quality sawlogs. The other 65% is in sub-tropical and tropical zones of countries such as Australia, Brazil, China, India, South Africa, Uruguay and Vietnam. *Eucalyptus cloeziana* (Gympie Messmate), *E. dunnii* (Dunns White Gum), *E. grandis* (Flooded Gum), *E. pellita* (Large-Fruited Red Mahogany), *E. pilularis* (Blackbutt), *E. saligna* (Sydney Blue Gum), *E. urophylla* (Timor White Gum), *Corymbia* species and their hybrids are the most commonly planted species (Cossalter and Pye-Smith, 2003; Montagu et al., 2003). The majority of this resource is managed for products other than solid wood, mainly pulpwood, poles and firewood. In Australia, the hardwood plantation area is currently 0.98 million hectares, however, only about 11% of the resource is managed for sawlogs (Gavran and Parsons, 2011).

In Australia, particularly in Tasmania, *E. nitens*, has been the most commonly planted
species managed for solid-wood production (Beadle et al., 2008). The other major species planted in Australia is *E. globulus*, particularly as an exotic in the Mediterranean climates found in Western Victoria, south-east South Australia and south-west Western Australia. These species are the major focus of this review. Warm-temperate to subtropical species such as *E. pilularis*, and more recently *E. dunnii* and *Corymbia citriodora* ssp. *variegata* (Spotted Gum), have also been planted and managed for solid-wood production in New South Wales and Queensland (Nichols et al., 2010).

Eucalypt plantations are also managed for solid wood in other countries either because pulpwood production is not technically and/or economically feasible or to replace hardwood sawlogs that cannot be supplied from natural forests (Montagu et al., 2003; Ronggui et al., 2003; Donnelly and Flynn, 2004; INFOR, 2004; Nutto and Touza-Vázquez, 2004; Valencia and Cabrera, 2005; Nutto et al., 2006). Predicted market opportunities for appearance and structural eucalypt plantation-grown timber or engineered-wood products have also motivated some growers to manage their plantations for either pruned sawlogs/veneer logs suitable for high-value solid- and/or engineered-wood products (Ronggui et al., 2003; Donnelly and Flynn, 2004; INFOR, 2004; Flynn, 2005; Nolan et al., 2005; Venn, 2005; Nutto et al., 2006). Examples of commercial market experiences with eucalypt plantation-grown timber are represented by Lyptus® in Brazil; Grandis® and Vida Grandis™ in Argentina; Eucanova® in Uruguay; Ibersilva-Plantation Wood® in Spain and EcoAsh™ in Australia (Flynn, 2005; ENCE, 2006; e-grandis, 2007; FEAPlantations, 2007; Urufor, 2007).

Compared to industrial eucalypt plantations for pulpwood, those managed for solid wood in Australia are in an earlier state of development. This is related to current market maturity and the need to develop wood-processing industries based on this resource that can pay prices for saw and veneer logs that recover the cost of the additional silviculture that is required, relative to pulpwood production. There is a need to refine new applied silvicultural and processing technologies (Flynn, 2005; Baker and Volker, 2006; Cameron and Willersdorf, 2006). These are crucial issues that define economic viability, financial risk and certainty for investment in this sector.
This review focuses on the silvicultural treatments of fertilising, pruning, initial spacing and thinning, their production ecology and how they interact with each other, the site and the age at which they are applied. These treatments can also influence wood properties and stem shape. Basic density and microfibril angle (which together determine wood strength and stiffness), shrinkage and collapse, growth stresses and tension wood, incidence of decay, spiral grain and end splits have been identified as key traits that contribute to the quality of sawn timber and veneer (Raymond, 2002). Some of these variables are also examined in the context of thinning, pruning and fertiliser application.

2. Production ecology

Tree and stand growth is related to the availability of light, water and nutrients, the capture of those resources and the efficiency with which they are used to fix carbon or to produce biomass or wood. The relationship between these variables can be described using the production ecology equation (Monteith, 1977; Binkley et al., 2004; Richards et al., 2010):

\[
\text{Gross primary productivity} = \text{resource supply} \times \text{proportion of resource captured} \times \text{efficiency of resource use}
\]

With regards to plantations the focus is more commonly on above-ground biomass or wood production (tonnes of above-ground biomass or m\(^3\) wood ha\(^{-1}\) y\(^{-1}\)), which can be described as a function of the supply (e.g. litres of water ha\(^{-1}\) y\(^{-1}\)), capture (proportion), and resource-use efficiency (e.g. m\(^3\) wood produced per litre of water), minus carbon allocation to respiration and non-woody tissues, i.e. net primary productivity (Binkley et al., 2004). In the case of nutrients, the supply includes pre-existing site nutrients as well as any added as fertiliser.

The production ecology helps to show the contribution of different mechanisms to differences in growth rates. This information could potentially be used to refine
silvicultural regimes. Measurements of variables of the production ecology equation have been used to examine a wide range of forest types, including *Eucalyptus* plantations, and treatments, including productivity gradients (Stape et al., 2004), fertiliser application (Hubbard et al., 2004), mixed species systems (Binkley et al., 1992; Forrester et al., 2010b; Forrester et al., 2012d), the influence of stand structure (Binkley et al., 2010; Ryan et al., 2010), dominance classes (Binkley et al., 2010; Campoe et al., 2013a) and stand age (Almeida et al., 2007; Forrester et al., 2010a). In a review of these studies Binkley (2009) found that when stem growth increased, light capture also increased (by a median of 40% and mean of 85%). In about 90% of studies, when stem growth rates increased, so did light-use efficiency (by a median of 50% and mean of 70%). There were increases in both light interception and light-use efficiency in about half of the studies, while in the others, either one or the other increased, not both. Water use showed similar trends, such that when stands were more productive in 90% of cases they also used more water (median of 25%) and used it more efficiently (median of 70%). In about half of the studies there were increases in both water use and water-use efficiency, while in the others the stem growth responses resulted from either one or the other, not both. For both water and light, increases in resource use were associated with either no change or increases in resource-use efficiency (not significant decreases). This makes sense when higher resource availabilities mean that less carbon needs to be invested into fine roots or leaves to capture a given amount of that resource. It is important to note that the Binkley review examined stem growth, as opposed to merchantable timber. Both may follow similar trends but this will depend on how carbon partitioning is influenced by resource availabilities and tree sizes. The review by Binkley (2009) also revealed that the application of this production ecology approach to silvicultural treatments such as thinning and pruning has received very little attention.

3. Fertiliser, nutrient uptake, and canopy development

The eucalypt species used in plantations are capable of rapid early growth but this is accompanied by high demand for nutrients and water and thus potential for their depletion. Decisions about appropriate fertilising regimes in plantations should be linked
to knowledge of nutrient dynamics and how this depends on the stage of development. The demand for, and distribution and storage of, nutrients can be divided into two major phases (Grove et al., 1996). The first phase occurs prior to canopy closure when the accumulation of nutrients increases up to a maximum that is reached just prior to or around the time the canopy closes (Cromer et al., 1993a; Misra et al., 1998a). Canopy closure is linked with maximum rates of biomass production (Ryan et al., 1997; Forrester et al., 2010a). The nutrients captured are largely used to build the canopy and there is little redistribution due to leaf senescence as rates of litterfall are still low. Growth may be limited by nutrient and water availability as the roots have not fully explored the soil profile. Therefore it is during this phase that trees are most responsive to fertiliser application and weed control, as well as the cultivation and residue-management practices used prior to planting (Grove et al., 1996).

The development of a plantation is closely linked to the growth and size of its tree crowns, which can be described using the leaf area index (LAI: foliage area per unit land area: Beadle, 1997); the LAI for eucalypt plantations varies between about two and nine (Beadle, 1997). Generally LAI is higher in cooler than warmer climates, where canopy photosynthesis may be optimised at lower LAI and a higher proportion of carbon allocated to the stem (Beadle, 1997). Maximum LAI and thus the initial rapid growth phase ahead of canopy closure may occur within the first year for *E. grandis* (Cromer et al., 1993b) or within about 3-6 years for *E. globulus* and *E. nitens* (Beadle et al., 1995; Forrester et al., 2010a). Significant growth responses to fertiliser application are commonly observed during this period (McKimm and Flinn, 1979; Cromer et al., 1981; Cromer et al., 1993a; Bennett et al., 1996; Duncan and Baker, 2004; Hubbard et al., 2004; Stape et al., 2006; Turnbull et al., 2007b; Smethurst et al., 2003; Smethurst et al., 2004).

Growth responses to improved nitrogen (N) availability usually lead to an increase in LAI (Cromer et al., 1993b; Bennett et al., 1997; Smethurst et al., 2003; Hubbard et al., 2004; Turnbull et al., 2007b; Forrester et al., 2012b). This results from an increase in leaf growth as well as reductions in rates of leaf and branch senescence (Ryan et al., 2004; Wiseman et al., 2006; Forrester et al., 2012b). The larger crowns lead to increases in light
absorption and transpiration (Figure 1) (Hubbard et al., 2004; Forrester et al., 2012c; Campoe et al., 2013a; Forrester et al., 2013). In some cases there are also changes in leaf-level rates of photosynthesis and resource-use efficiencies (Kellomäki et al., 1982; Smolander and Oker-Blom, 1989; Green and Mitchell, 1992; Clearwater and Meinzer, 2001; Binkley et al., 2004; Forrester et al., 2012c; Campoe et al., 2013a; Forrester et al., 2013), but this is not always the case (Sheriff et al., 1986; Pereira et al., 1992; Teskey et al., 1994; Zhang et al., 1997; Tang et al., 1999; Close et al., 2004; Hubbard et al., 2004; Allen et al., 2005; Turnbull et al., 2007b). Responses to fertiliser application are also often associated with changes in biomass partitioning, such that a higher proportion of biomass is allocated above-ground and of that a higher proportion may be allocated to leaves at the expense of wood (Misra et al., 1998b; Giardina et al., 2003; Litton et al., 2007; Forrester et al., 2012b; Poorter et al., 2012).
Figure 1. The production ecology of thinning, pruning and fertiliser application for SCT_{200}. Each treatment was carried out at age 3.2 years. Treatments include: unthinned (T0) and thinned from 900 to 300 trees ha^{-1} (T1), unpruned (P0) and pruning that removed the lower half of the live canopy and 75% of leaf area (P1), nil fertiliser (F0) and 300 kg N ha^{-1} (F1). Light-use efficiency (LUE) is above-ground biomass growth per unit of absorbed PAR and water-use efficiency (WUE) is above-ground biomass growth per unit of transpiration. Error bars are least significant difference. Modified from Forrester et al. (2012c) and Forrester et al. (2013).
The responses to fertiliser application depend on species, site characteristics and silvicultural practices such as cultivation, weeding, thinning and pruning. Growth responses will probably be lower when other resources such as soil moisture or other nutrients are also limiting to growth. For example the growth increment of *E. grandis* and hybrids with *E. urophylla* in Brazil was higher in fertilised plots during wet seasons than dry seasons (Stape *et al.*, 2006).

The second phase of stand development, following canopy closure, the LAI may stabilise for a short period and then decline (Almeida *et al.*, 2008; du Toit, 2008; Forrester *et al.*, 2010a). Current annual increments will also typically decline (Ryan *et al.*, 1997). Nutrient accumulation is largely due to increasing wood mass, which requires fewer nutrients than canopy development, so the rate of nutrient accumulation slows. Fine roots will have explored most of the soil and nutrient cycling processes develop (Attiwill, 1979; Grove *et al.*, 1996). Inter-tree competition will intensify and light and water may become more limiting to growth. Thus in most cases fertiliser responses are not sustained, and are no longer significant by the end of the rotation (Jourdan *et al.*, 2008). This type of response is sometimes referred to as a Type 1 response (Snowdon, 2002). Type 2 responses, where the inherent fertility of the site is improved, are sometimes observed on highly depleted soils (Snowdon, 2002; Gonçalves *et al.*, 2008). If responses to fertiliser after canopy closure occur, they are more likely to happen after the LAI of the stand is reduced via insect defoliation, pruning or thinning (Gonçalves *et al.*, 2004). Nevertheless, fertiliser responses are variable and in a study containing 131 twin plots of *E. grandis* or hybrids with *E. urophylla* in Brazil, (Stape *et al.*, 2006) found that even though growth declined with age, the response to fertiliser was greater as the stands aged, although this may have been confounded by ongoing improvements in silvicultural technology (Stape *et al.*, 2006).

4. Productivity over successive rotations

Several studies have shown that productivity of plantations, including those of *E. globulus*, can decline in subsequent rotations, although declines in productivity are
certainly not always observed (Corbeels et al., 2005; Mendham et al., 2011). When there are productivity declines there are a range of potential causes, and these will depend on factors including the resources that most limit growth on a given site, previous land use, and plantation management.

Site preparation (soil cultivation) and residue management (e.g. removal of organic matter, burning, windrowing) can have negative impacts on soil physical and chemical properties and thus a detrimental impact on nutrient and water availabilities (Gonçalves et al., 2008). An understanding of these effects has resulted in less intensive or ‘minimum cultivation’ of soils in many of the world’s commercial eucalypt plantations, especially on soil types that are more susceptible to poor site preparation (Gonçalves et al., 2008). Similarly, harvesting residues that may have been windrowed or burnt in the past, are often left on site and more evenly distributed relative to windrowing practices (Corbeels et al., 2005; Gonçalves et al., 2008). Even with good site preparation and harvest residue management the timely application of fertiliser can be necessary to prevent declines in productivity with successive rotations (Corbeels et al., 2005; Gonçalves et al., 2008). This may be particularly so when plantations are planted on ex-agricultural land where prior fertiliser inputs were relatively high.

Productivity declines in second rotations due to depletion of soil water have been shown in *E. globulus* plantations in south-western Australia (Mendham et al., 2011). The annual rainfall at the sites examined ranged from 558 to 991 mm. It was found that first-rotation plantations used stored soil water that was not replenished (as quickly as it was used) as the stands developed, and that although some of this water was replenished after harvesting, this was usually not enough to avoid a reduction in water availability for the following rotation and hence a reduction in productivity. Higher stockings used more water and it was suggested that soil water of most soils that are more than 4 m deep probably will not be replenished in the second rotation.
5. Stand density

Eucalypt plantations for solid wood production are often planted at about 1000 trees ha\(^{-1}\). Initial spacing must allow for selection of the required number of final crop trees (Gerrand et al., 1997a), which is important because there is often significant variation in tree form and growth rate within eucalypt plantations. However, there is a trade-off between achieving large individual tree sizes and maximising stand production. Initial spacing will strongly influence tree- and stand-level growth dynamics. At closer spacings stand leaf areas and biomass develop more rapidly and the site is ‘fully occupied’ sooner. Early stand growth rates will be faster at closer spacings and the peak current or mean annual increments can occur sooner (Schäfer and Ponce, 2007; Stape and Binkley, 2010; Chen et al., 2011; Forrester et al., submitted-b). At the tree level, the more intense competition for light, water and nutrients will result in a smaller average tree size, but this competition (e.g. for light) improves stem form and controls crown architecture by restricting branch sizes and accelerating rates of branch shedding, thereby improving wood quality (Neilsen and Gerrand, 1999; Henskens et al., 2001; Pinkard and Neilsen, 2003; Alcorn et al., 2007; Forrester et al., 2012b). Pruning large branches on *E. globulus* and *E. nitens* has been associated with the development of stem defect (Mohammed et al., 2000).

On the other hand, wider spacing results in larger average tree sizes and faster individual tree growth rates (Stape and Binkley, 2010). This classic spacing effect has been reported for many species including *E. cloeziana*, *E. pilularis* (Alcorn et al., 2007), *E. nitens* (Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003), *E. globulus* (Schäfer and Ponce, 2007; Forrester et al., submitted-b.), *E. grandis* (Schönau, 1974; van Laar and Bredenkamp, 1979a; Bredenkamp, 1987; Cameron et al., 1989; Schönau and Coetzee, 1989; Kearney et al., 2007), *E. pellita*, *E. camaldulensis* (River Red Gum) (Thoranisorn et al., 1990; Bernardo et al., 1998), *E. urophylla* (Bernardo et al., 1998; Xue et al., 2011), *E. dunnii* (Stape and Binkley, 2010) and other broadleaf (Niemistö, 1995) and coniferous species (Bramble et al., 1949; Malimbwie et al., 1992; Harms et al., 1994; Deans and Milne, 1999). The steepness of the relationship between mean diameter and initial spacing (i.e. the spacing effect) can increase as stands age as reported for *E. globulus* (Forrester et al., submitted-b) and *E. grandis* (Bredenkamp, 1987; Cameron et al., 1989).
That is, the effect of spacing on mean tree size increases with age.

However, the smaller number of trees take longer to fully occupy the site so stand growth rates will tend to be slower and peak stand growth rates will occur later (Stape and Binkley, 2010). Wider spacings, either due to initial spacing or thinning are characteristic of longer rotations and regimes used to produce sawlogs, while closer spacings are often used to produce biomass or pulp-logs on shorter rotations. Wider spacing (or thinning) may also be used to reduce stand transpiration (and interception losses), at least initially (Bréda et al., 1995; Kallarackal and Somen, 1997; Forrester et al., 2012c), to increase the amount of water stored in the soil (Butcher, 1977; Donner and Running, 1986; Cregg et al., 1990; Bréda et al., 1995) and potentially to reduce the susceptibility of stands to drought (Butcher, 1977; Laurent et al., 2003; White et al., 2009).

Increases in site quality or fertiliser application may accelerate these growth dynamics. However, whether spacing and site quality (or fertiliser application) are additive or interact with each other has received little attention. This is important when considering the applicability of spacing studies to a range of site qualities. No significant interaction between initial spacing and fertiliser application was found for average tree diameter or stand volume in *E. urophylla × grandis* hybrid plantations (Chen et al., 2011). In *E. globulus* plantations in south-western Australia, there was a significant interaction between site and spacing (Forrester et al., submitted-b.). At higher quality sites the effects of spacing on growth were greater and lasted longer, while at lower quality sites spacing resulted in negligible differences in the growth rates of the largest-diameter potential sawlog crop trees by age 10 years.
6. Pruning

6.1. Production ecology of pruning

With regards to the production ecology of pruned trees, the removal of leaves reduces the amount of light intercepted and rates of transpiration (Gyenge et al., 2009; Forrester et al., 2012c; Alcorn et al., submitted-b; Forrester et al., 2013). This reduction in resource use can reduce growth, although *Eucalyptus* growth is often unaffected in vigorous unthinned stands (post canopy closure) as long as no more than about 40-50% of the length of the live crown is removed in a single pruning lift (see Table 1) (Bredenkamp et al., 1980; Pinkard and Beadle, 1998b; Pinkard et al., 2004; Forrester et al., 2010c). In comparison, the growth of *Pinus* species can slow after only about 20-30% of the live-crown length has been removed (Lückhoff, 1949a; Adlard, 1969; Karani, 1978). The relative insensitivity of eucalypts to pruning occurs at least partly because the reduction in resource capture is often countered by an increase in the efficiency of the remaining crown.

For example, pruning removed 75% of a trees’ leaf area in a 3.2-year-old *E. nitens* plantation but during the year after pruning, above-ground biomass growth of the 200 largest-diameter potential sawlog crop trees ha\(^{-1}\) (SCT\(_{200}\)) was reduced by only 12%, because while they absorbed 37% less photosynthetically active radiation (PAR), their light-use efficiency increased by 36%, and light-saturated rates of photosynthesis were about 19% higher in pruned trees (19 weeks after pruning) compared with unpruned SCT\(_{200}\) (Forrester et al., 2010c; Forrester et al., 2012c). In the same stand, 2-3 years after pruning, above-ground biomass growth of the SCT\(_{200}\) was no longer affected by pruning, but transpiration was 12% lower and water-use efficiency was 21% higher compared with unpruned SCT\(_{200}\) (Figure 1)(Forrester et al., 2012c).

There are three mechanisms behind the changes in light-use efficiency following pruning. Firstly, light-use efficiency can increase immediately following pruning because the shaded, least efficient, lower crown is removed (Linder, 1985; Forrester et al., 2013).
Secondly, the retained leaves become more light-use efficient because rates of photosynthesis can increase within days of pruning and may remain higher for several months as the crowns are rebuilt (Pinkard and Beadle, 1998a; Pinkard, 2003; Pinkard et al., 2004; Forrester et al., 2012c). Thirdly, a loss of foliage can lead to shifts in biomass partitioning to above-ground in order to restore the balance between fine roots and leaves (Cannell, 1985; Strauss and Agrawal, 1999; Frost and Hunter, 2008; Eyles et al., 2009).

The duration of reductions in transpiration is likely to depend on the species, the intensity of pruning and the climatic conditions following pruning. For example pruning 50% of the live-crown length (55-57% of leaf area) of four-year-old *E. cloeziana* and *E. pilularis* trees reduced transpiration by 59% for *E. cloeziana* and 39% for *E. pilularis* during the first eight days after pruning (Alcorn et al., submitted-b). By 36 days after pruning there were no longer any pruning effects on transpiration. In contrast, transpiration was still lower for pruned *E. nitens* trees 2-3 years after pruning 50% of the live-crown length (75% of leaf area) (Forrester et al., 2012c).

6.2. *Species differences in branch and crown dynamics and implications for pruning*

Variability between species results from differences in shade tolerance, crown architecture and growth rates. Shade tolerant species can maintain foliage at lower light intensities than shade intolerant species because they have lower light compensation points. Light compensation occurs at the irradiance level where a leaf’s net carbon exchange is zero, and rates of photosynthesis and respiration balance (Lambers et al., 1998). Therefore with a given set of resources, more shade tolerant species develop deeper live crowns that will rise later than those of less shade tolerant species. For example, in four-year-old plantations on the same sites, the live-crown heights of *E. pilularis* and *E. cloeziana* were 3.8 and 1.0 m, respectively (Alcorn et al., 2008b). The light compensation points of both species declined from the upper to the lower canopy, and were lower in the lower canopy of *E. cloeziana* than that of *E. pilularis* (Alcorn et al., 2008a). As pruning of live branches only is recommended (see below), this suggests that
E. cloeziana could be pruned later than E. pilularis for a given set of growing conditions, as long as branch size does not become unacceptably large (Alcorn et al., submitted-a).

Rapid rates of crown rise in species such as E. dunnii and E. grandis restrict the scheduling of pruning to narrower time windows (Lückhoff, 1967; Maree, 1979; Smith et al., 2006). Thus solid wood growers of E. grandis in Argentina (SGS Qualifor, 2005b) and Uruguay (SGS Qualifor, 2005a) follow strict pruning regimes that begin at about age 1.5 years and include 3 to 5 pruning lifts to between 9 and 10.5 m.

It is important to note that crown architecture varies considerably with species, site and age. On a given site more shade tolerant species develop deeper live crowns that will rise later. For example, on the same site live-crown lengths of E. pilularis were 3.8 m while those of E. cloeziana were 1.0 m, at age four years (Alcorn et al., 2008b). Large differences in the vertical distribution of foliage can exist between species or even clones of the same species (Jarvis and Leverenz, 1983; Reis et al., 2004) which influences the amount of light absorbed by tree crowns (Larson, 1965). This distribution changes with age (Pinkard and Beadle, 1998c; Medhurst and Beadle, 2001; Forrester et al., 2012b) and with tree dominance in unthinned stands (Medhurst and Beadle, 2001). Site is also important because as site quality increases, the canopy closes sooner and the live-crown rises more rapidly (Alcorn et al., submitted-a; Alcorn et al., in press). In addition to increasing crown sizes, thinning and fertiliser application can also influence vertical leaf area distributions (Brix, 1981; Medhurst and Beadle, 2001; Ryan et al., 2004; Forrester et al., 2012b). This variability means that pruning to a certain height, stem diameter or proportion of live-crown length will have a different effect on growth depending on the location and size of the most active parts of the crown (Forrester et al., 2010c).

6.3. Timing of pruning

The optimal time to prune depends on the leaf area development of the stand. The LAI generally increases until neighbouring canopies meet and the canopy closes. Soon after, the LAI reaches equilibrium or gradually declines (Jarvis and Leverenz, 1983; Beadle and
Long, 1985; Cromer et al., 1993b). After canopy closure the lower canopy is shaded and eventually its leaves are unable to maintain a positive carbon balance. This results in leaf and branch death. Dead branches can lead to numerous defects, including knots, decay and kino-trace defect (Yang and Waugh, 1996; Washusen et al., 1998; Mohammed et al., 2000; Washusen et al., 2000). Pruning should therefore be timed to occur before the live crown begins to rise i.e. soon after canopy closure, so that no dead branches are pruned. Furthermore, to maximise the benefits of pruning, branches should not only be alive, but small and no greater than 3 cm in diameter (Gadgil and Bawden, 1981; Glass and McKenzie, 1989; Gerrand et al., 1997b; Wardlaw and Neilsen, 1999; Mohammed et al., 2000). Small branches are not only easier to prune but occlude more rapidly; occlusion must occur before clear wood can be produced. Rapid occlusion also reduces the risk of decay fungi entering through pruned branch stubs (Marks et al., 1986; Glass and McKenzie, 1989; Wardlaw and Neilsen, 1999; Mohammed et al., 2000).

The age at which canopy closure occurs and the rise of the live crown begins will depend on the species, site resources and stand density. At lower stand densities, more light reaches the lower canopy and the live crown rises more slowly (Marks et al., 1986; Jack and Long, 1996; Kearney, 1999; Neilsen and Gerrand, 1999). Furthermore, with decreasing density, crown length and width generally increase (van Laar and Bredenkamp, 1979b; Pinkard and Neilsen, 2003). This leads to the development of larger branches (Neilsen and Gerrand, 1999). Branch longevity and size for a given tree diameter can also increase as site quality increases or more fertiliser is applied (Wiseman et al., 2006). Simple decision matrices’ can be developed that show when to prune for different site qualities to achieve specific objectives relating to branch sizes, maximum knotty-core diameters, maximum amount of live crown removed and other variables (e.g. Alcorn et al., submitted-a).
6.4. Resource availability and crown development

Canopy development is also influenced by water and nutrient availability (Cromer et al., 1993a; Beadle, 1997). When nutrients are limiting, trees may re-translocate them from old, shaded foliage to well-lit younger and more efficient foliage (Field and Mooney, 1983; Dell et al., 2001). This may accelerate the lift of the live crown and reduce the live-crown length and LAI. Therefore tree growth may be more sensitive to pruning on low quality sites where they have fewer resources to maintain lower canopy foliage or to rebuild the canopy after pruning. In an *E. nitens* plantation, Pinkard and Beadle (1998b) found that reductions in rates of diameter and height increments following the removal of 70% of the live-crown length were less pronounced on a higher (mean height 9.5 m at age three years) than on a lower (mean height 7.5 m at age three years) quality site. Maintenance of growth rates after pruning on lower quality sites may be achieved by combining pruning with fertiliser application or irrigation, which can increase crown size or branch growth rates (Messina, 1992; Wiseman et al., 2006; Forrester et al., 2012b).

Nevertheless, it is important to note that the increase in LAI from fertilising *E. nitens* (Smethurst et al., 2003) is driven by reduced branch senescence and faster branch growth in the lower crown (Wiseman et al., 2006), and not the upper crown which was found with other tree species (Brix, 1981); branching density of *E. nitens* is not affected by fertiliser application (Wiseman et al., 2006). However, these larger branches in the lower crown may make occlusion following pruning slower.

6.5. Pruning intensity and leaf area index

The amount of foliage that can be removed before growth is reduced depends on species attributes, resource availability, and timing in relation to canopy closure. Pinkard and Beadle (2000) used a physiological approach to predict when growth will be influenced by pruning. This was based on the strong link between biomass production and light interception (Landsberg and Waring, 1997), which is influenced by leaf area and its distribution within the canopy (Beadle and Long, 1985; Linder, 1985). This can be
described using the LAI. The LAI that results in about 95% of the incident radiation being absorbed at a site determines the maximum production potential for that species (Jarvis and Leverenz, 1983). This optimal LAI varies with species. An optimal LAI of 6.0 was reported for *E. globulus* by Beadle et al. (1995) and 4.0 for *E. nitens* by Pinkard et al. (1999). The optimal LAI is not always the maximum attained for a given species. However, if actual LAI is greater than this optimum, parts of the canopy are potentially operating below the compensation point and contributing little to biomass production (Nobel and Long, 1985). Conversely, if LAI is less than this optimum, radiation will filter through to the ground and production will not be at its potential. Therefore appropriate pruning intensity can be estimated from knowledge of the optimal LAI, actual LAI at the site and how LAI varies with height in the canopy. For example, Pinkard and Beadle (2000) noted that in a three-year-old *E. nitens* plantation the relationship between cumulative LAI and percentage crown length was linear. From this relationship they showed that removing 40% of the live-crown length would reduce LAI from about 7 to 4 without reducing light interception below 95%. In a vigorously growing plantation, around 40-50% of the live-crown length of eucalypts and acacias can be pruned before growth is affected (Table 1). Less can be removed from conifers (25-40%) before reducing growth rates (Table 1), and when resource availability restricts potential growth rates.

Pruning is more likely to reduce growth if done before the canopy closes. After canopy closure the lower foliage that might be pruned is shaded and contributes less to carbon fixation than well lit, lower canopy foliage in stands before canopy closure. Pinkard and Beadle (2000) showed that the LAI of an *E. nitens* plantation increased up to 7.8 at age 3.5 years and then declined to 4.0 at age 4.6 years. When crowns were verging on canopy closure at age 3.0 years the photosynthesis from the lower 50% of crown length produced about 30% of biomass, but this declined rapidly after canopy closure so that by age 3.5 years the lower crown was contributing very little to biomass production (Pinkard et al., 1999). Therefore pruning on this site at age 3.5 years would leave larger crowns and should have less impact on growth. Similarly, prior to canopy closure in an *E. nitens* plantation, removing only 20% of the leaf area reduced volume growth (Pinkard, 2002),
whereas after canopy closure, even the removal of 55% of the leaf area or 50% of the live-crown length in a fast-growing plantation did not reduce volume growth (Pinkard and Beadle, 1998b).

6.6. Physiological responses to pruning

Trees are able to maintain growth rates following pruning through changes in leaf physiology, leaf morphology, canopy architecture and by modifying biomass allocation to facilitate leaf area development (Pinkard and Beadle, 1998b, 1998c; Pinkard, 2003; Pinkard et al., 2004; Forrester et al., 2012b). For example, *E. nitens* can increase rates of photosynthesis by as much as 175% after pruning 50% of the live-crown length and maintain growth rates achieved by unpruned stems (Pinkard and Beadle, 1998d). Changes in light-saturated rates of photosynthesis following pruning can occur throughout the canopy within a few days to weeks after pruning and can persist for over a year (Pinkard and Beadle, 1998d, 2000). These processes have been observed in *E. nitens* (Pinkard and Beadle, 1998b; Forrester et al., 2012c) and *E. globulus* (Pinkard, 2003; Pinkard et al., 2004). Leaf morphology also changes with pruning such that larger leaves are produced, which increases the area for light capture and photosynthesis (Pinkard and Beadle, 1998c). In addition, rates of crown development of *E. nitens* and other species can increase after pruning (Pinkard and Beadle, 1998a; Zeng, 2003). This has been shown through higher rates of branch growth and leaf expansion, leaf development in the upper canopy, greater leaf area or mass to branch basal area or wood ratios and reduced leaf senescence (Pinkard and Beadle, 1998c; Zeng, 2003; Forrester et al., 2012b). Knowledge about such physiological changes can be used to refine pruning regimes. That is, it might be possible to prune below the optimum LAI if the resulting physiological changes will be strong enough to compensate for this loss of leaf area (Pinkard et al., 1999).

Physiological responses to pruning may also be influenced by changes in canopy architecture due to changes in branch angle. Branch angle (from vertical) plays a large role in determining the crown projected area and overall shape of a tree crown. In
general, branch angle decreases with increasing crown height. Branch angle in the upper crowns increased after pruning of a three-year-old *E. nitens* stand which may have been a response to allow greater light penetration and crown activity to recover from the pruning event (Pinkard and Beadle, 1998d).

Silvicultural practice to produce logs of specified pruned length (e.g. 6.0 m) and restrict knotty-core defect diameter (e.g. to <15 cm) requires pruning in several lifts to minimize impacts on growth (Neilsen, 1991). The effect of the second-lift pruning on growth will likely depend on how well the tree has rebuilt its crown since the first lift and regained the carbohydrate reserves that were used to recover from the first-lift pruning, in addition to the species and site factors discussed above. For example, growth may be reduced more by later pruning lifts which remove the same proportion of crown length as in the first lift when there is insufficient time for canopy recovery (studies 12-14 in Table 1).

Second-lift pruning was examined in an *E. nitens* plantation where a first lift at age 3.2 years retained the upper 50% of the live-crown length (25% of leaf area) and a second lift at age 4.7 years also retained the upper 50% of the live-crown length (28% of leaf area). By age 8.1 years, diameters of trees that received only the first lift were 5% smaller than unpruned trees and those that received two lifts were 13% smaller. Trees that received two lifts were also 5% shorter than unpruned trees and these differences in height were increasing. Similarly, increasing reductions in growth with repeated artificial defoliations were found for *E. globulus* (Pinkard et al., 2007). Scheduling of these later lifts could be aided by knowledge of how LAI responded after the first lift. For example, 13 months after removing 50% of live-crown length of three-year-old *E. nitens* trees the LAI had increased from 3.5 immediately after pruning to 5.5. Thus a second pruning to about an LAI of 4 should not reduce growth (Pinkard and Beadle, 2000). However, if the trees were pruned again six months after pruning by removing another 50% of current live-crown length, LAI would have been reduced from 4.6 to about 3.3, a reduction that probably would have reduced the growth rate of the trees (Pinkard and Beadle, 2000).
7. Thinning

7.1. Production ecology of thinning

The production ecology of thinning can involve increased availabilities of light, water and nutrients, increased uptake of those resources by individual trees and an increase in resource-use efficiencies (Stogsdill et al., 1992; Bréda et al., 1995; Wang et al., 1995; West and Osler, 1995; Tang et al., 2003; Medhurst and Beadle, 2005; Forrester et al., 2012c; Forrester et al., 2013; Gspaltl et al., 2013). For example, in a 3.2-year-old *E. nitens* plantation thinning from about 900 to 300 trees ha\(^{-1}\) increased the above-ground biomass growth of the SCT\(_{200}\) by 34%, the absorption of PAR by 24% and the light-use efficiency by 13%, during the first year after thinning (Figure 1)(Forrester et al., 2013). In the same stands, but 2-3 years after thinning, growth of the SCT\(_{200}\) was 49% greater, transpiration was 23% greater and water-use efficiency was 21% greater than that of SCT\(_{200}\) in unthinned stands (Figure 1)(Forrester et al., 2012c).

Increases in resource-use efficiencies suggest that there were increases in photosynthesis and/or partitioning of carbon above-ground (Ryan et al., 2010). In the same *E. nitens* plantations, thinning increased light availability in the lower halves of the crowns (Figure 2), which resulted in greater rates of photosynthesis (Forrester et al., 2012c) and similar responses have been reported in other stands (Wang et al., 1995; Tang et al., 2003; Medhurst and Beadle, 2005; Sala et al., 2005; Gauthier and Jacobs, 2010). Less is known about the effects of thinning (or initial spacing) on carbon partitioning between above- and below-ground tissues. There may be minimal change when thinning or declining stand density increase partitioning to fine roots and leaf area by about the same rate, as found for *Pinus taeda* (Loblolly Pine) and *Pinus elliottii* (Slash Pine) (Burkes et al., 2003). However, increases or decreases in the ratios of fine-root biomass to leaf biomass as stocking increased have been found for *Pinus sylvestris* (Scots Pine), *Populus deltoides* (Eastern Cottonwood), and *Eucalyptus* spp. (Nilsson and Albrektson, 1993; Puri et al., 1993; Bernardo et al., 1998).
Resource-use efficiencies can also increase with increasing size class within a stand (Binkley et al., 2010; Campoe et al., 2013a,b). That is, larger and more dominant trees grow faster than smaller trees not only due to higher resource capture but because they can use those resources more efficiently. Therefore, if the smaller, inefficient trees are removed the resource-use efficiency of the stand may increase. This increase would be in addition to any improvement in resource efficiencies of the SCTs themselves.

Figure 2. Vertical light profiles in a Eucalyptus nitens stand near Carrajung, Victoria, Australia, thinned (from 930 to 300 trees ha\(^{-1}\)) and pruned (half of the green crown length) at age 3.3 years. Light transmission is the percentage of photosynthetically active radiation above the canopy. Error bars are standard errors of difference (Forrester et al., 2012c).
The effects of pruning, thinning or fertiliser application on light-saturated rates of photosynthesis are often transitory with differences declining as the crowns expand and the canopy closes (Pinkard, 2003; Pinkard et al., 2004; Forrester et al., 2012c; Forrester et al., 2013). Thus while initial growth responses can be both structural and physiological, as the crowns of the retained trees expand, or pruned crowns rebuild, the relative contribution of physiological differences such as photosynthesis or resource-use efficiencies decline (Albaugh et al., 1998; Forrester et al., 2013).

7.2. Thinning regimes

Eucalypt plantations grown for solid-wood production are often established at around 1000 trees ha\(^{-1}\). This ensures that sufficient final crop trees meet criteria for pruning and thinning based on form, size and spacing, and that the development of large branches is inhibited. Thinning is required to reduce competition between the unpruned and pruned trees, to accelerate growth of the pruned trees and to shorten rotation lengths, which is a financial requirement (Nolan et al., 2005; Smith and Brennan, 2006). Thinning has also been linked to higher recoveries of solid wood (Nutto and Touza-Vázquez, 2004), less tension wood formation, less end-splitting and less drying degrade (Washusen, 2002; Smith and Brennan, 2006).

The timing of first thinnings in *Eucalyptus* plantations is variable (Table 2). Thinning influences the future size distributions of a stand and the products it will deliver, so regimes will also depend on market demands (Smith et al., 2006). The first thinning operations of *E. nitens* plantations in Tasmania, Australia are often at age 8-10 years, when the canopies have been closed for about four years (Neilsen, 1991; Wood et al., 2009). The objective of this relatively late thinning is to ensure some commercial income, to control early weed competition and to improve tree form (Gerrand et al., 1993; Candy and Gerrand, 1997; Nolan et al., 2005). The disadvantage of thinning so long after canopy closure is that competition becomes more intense and growth rates of SCTs are reduced (Medhurst et al., 2001; Wood et al., 2011). Relative and absolute responses to later age thinning also tend to be smaller than when thinning is done earlier (Figure 3).
(Schönau, 1982, 1984a; Ruha and Varmola, 1997; Mäkinen and Isomäki, 2004a, 2004b) although significant later-age (at ages 7.5-13.2 years) absolute thinning responses by SCT$_{200}$ or SCT$_{250}$ (e.g. 4 m$^2$ ha$^{-1}$ five years after thinning) have been reported for E. nitens and E. globulus growing on high quality sites (studies 4, 7 & 10 in Table 2) (Medhurst et al., 2001; Forrester and Baker, 2012; Forrester et al. submitted-a), as well as for the sub-tropical species E. dunnii or Corymbia citriodora ssp. variegata (e.g. 1-2 m$^2$ ha$^{-1}$ year$^{-1}$) (study 23, Table 2) (Glencross et al., 2011). In one of those studies there was no significant effect of thinning age on absolute SCT$_{200}$ thinning responses (Figure 3).

The rate at which thinning responses decline as thinning age increases are likely to be related to the rate at which the periodic annual increment declines after it peaks when the canopy closes.

The absence of a thinning-age effect on absolute responses suggests that there is some flexibility in the thinning age in E. nitens plantations. However, it is important to note that while the absolute thinning response may be slow to decline, the size of the SCTs will be smaller after later-age thinning due to the extended period of competition they experience prior to thinning. To maximise the size of the SCTs it is often recommended to thin early at or just prior to the peak growth rates (Smith et al., 2006). To avoid losses in potential thinning responses, stands are thinned earlier, at about the time of canopy closure in E. nitens or E. grandis plantations in Argentina, Chile and Uruguay, where grass competition may then be controlled by grazing (SGS Qualifor, 2005a, 2005b; Valencia, 2008). Recent work with E. nitens in Tasmania indicated that a final stocking of 150-200 trees ha$^{-1}$ would maximise the yield of high-quality pruned sawlogs, and that this is achieved sooner when thinning is done earlier (Wood et al., 2011).
Figure 3. The influence of thinning age on the absolute (a; m$^2$ ha$^{-1}$) and relative (b; %) thinning responses of SCT$_{200}$ in stands thinned when they were Young (age 3.2 years) or Old (age 13.2 years). Both stands were adjacent to each other and were thinned in the spring of 2006. Modified from Forrester et al. (submitted-a).
It is important to note that the relationship between log size and value is not linear. Log prices usually go up as various thresholds of log prices are reached (Nolan et al., 2005). As a result, even when heavily thinned stands have lower total stand volumes, or lower sawlog volumes, than less heavily thinned or unthinned stands, their internal rate of return (IRR) and net present value (NPV) can still be higher because there are more trees in the highest and most valuable sawlog size classes (Candy and Gerrand, 1997; Seling et al., 2001; LaSala et al., 2004; Wood et al., 2009; Cassidy et al., 2012). For example the highest NPV and IRR after thinning *E. pilularis* were in stands thinned to 87, 125 or 250 trees ha⁻¹, compared with those thinned to 450, 700 or unthinned stands (Cassidy et al., 2012). The highest IRR was from the 125 trees ha⁻¹ treatment. However, the optimal IRR for the best three treatments occurred at age 26 years where it then reached a plateau, thereby giving some flexibility to the clearfelling age. In light of these results it is worth asking why such a small proportion of Australia’s plantations are managed for solid wood. This was answered by Cassidy et al. (2012) who noted that:

“Hardwood logs have not usually been traded in competitive markets in Australia. The public sector has historically controlled the majority of the sawlog being provided to the market place at a price that allows processors to make a return. The timber prices received by the public sector represent a discount to the real cost (Nolan et al., 2005) of producing the logs in managed plantations. For a sustainable plantation hardwood products industry to develop, the price paid for logs grown specifically for high value products must reflect the growing costs and the products that may be produced from the log.”

There is a continuum of thinning regimes used in *Eucalyptus* plantations due to the variability in species, economics and objectives (Smith and Brennan, 2006). Some of these are shown in Table 2. These range from light, frequent thinning, to heavy early thinning. For example in Chile many growers of *E. nitens* thin lightly every one to two years, just prior to canopy closure with the aim to maintain an open canopy (Study 5; Table 2). In Uruguay and Argentina there are examples of intensive early thinning of *E. grandis* to about 400-500 trees ha⁻¹ at age 1.5 years, with two further thinning operations to a final stocking of about 130 to 250 trees ha⁻¹ (studies 18 and 19 in Table 2). The more shade intolerant nature of species such as *E. grandis* compared to *E. nitens*, means that
there is a smaller time window to complete operations before canopies close and competition leads to rapid crown rise; more frequent interventions such as those in *E. nitens* in Chile may be less feasible for species such as *E. grandis*. These South American regimes described for *E. grandis* are intense enough to allow enough light through the canopy to sustain pasture and hence livestock and an additional source of income. Similar regimes are used for *E. saligna, E. nitens* and *E. globulus* in farm forestry in Australia (Hingston, 2007; Moore, 2008).

Such regimes aim to maintain an open canopy for the majority of the rotation to maximise growth rates. These regimes therefore benefit from the larger thinning responses at around canopy closure (and the maximum periodic annual increments) but maintain higher total stand growth by thinning relatively lightly. Regimes that allow the canopy to close can lead to compromises in final crop tree growth rates and potential problems with tension wood and end-splitting (Washusen, 2002; Waugh, 2004).

7.3. *Growth responses to thinning*

Many studies have shown that the growth of SCTs in eucalypt plantations and native eucalypt forests increases over those in unthinned stands (Table 2; Figure 4). Generally the dominants and co-dominants produce the greatest basal area or volume responses (Medhurst et al., 2001; Forrester and Baker, 2012). Height growth responses are more variable. For example, no responses (studies 1, 3, 4 and 14 in Table 2), lower height growth in thinned stands (studies 8, 12 and 17) or increased in height growth in thinned stands (study 11) have all been observed. Generally the intermediate trees are more likely to show increased height growth while the dominants show no changes or reductions in rates of height growth.
Figure 4. Basal area of the largest diameter 200 trees ha\(^{-1}\) in two Eucalyptus globulus stands in Victoria, Australia, thinned from about 1300 to 300 or 500 trees ha\(^{-1}\). At one site (top) the thinning response was greater when stands were thinned to 300 trees ha\(^{-1}\) compared to 500 trees ha\(^{-1}\). However, at the other site (bottom) the magnitude of the response was similar for each thinning treatment, despite a similar site quality, thinning intensity and age of thinning at both sites. Bars are standard errors of difference (Forrester and Baker, 2012).

Depending on the thinning intensity, the reduction in stand basal area or volume may be accompanied by a reduction in the cumulative total stand basal area or volume increment following thinning. Total stand basal area increment was not reduced seven years after thinning *E. nitens* from 1000 trees ha\(^{-1}\) down to 400 trees ha\(^{-1}\), while thinning to 100, 200 or 300 trees ha\(^{-1}\) resulted in significant reductions in basal area increment (Medhurst et al., 2001: study 1 in Table 2). However, maximising the size/value of the potential sawlog crop trees is often more important than maximising total stand volume production (Shield, 2008).
Growth responses of SCTs generally increase as thinning intensity increases, although there will be an intensity beyond which further thinning will not lead to further increases in growth of the final crop trees. This intensity appears to be variable, will be a function of stand development and is difficult to predict (Figure 4). It may depend on which resources are most limiting to growth, even if the net effect or all resources results in similar site qualities. Additionally, differences in stand structure may influence the thinning response (see section 9.4).

Most, if not all, *Eucalyptus* species that are capable of producing lignotubers also have the ability to coppice (Jacobs, 1955), including *E. globulus*. While coppice occupies a similar position in a stand to seedlings it is often capable of faster growth rates over the first five or more years (Smith 1962; Blake 1980; Crombie 1997; Sims et al. 1999). This coppice can potentially compete with retained trees after thinning. Several studies in native eucalypt forests have shown that thinning responses can be reduced if coppice is not controlled (Henry, 1960; Abbott and Loneragan, 1983; Kellas et al., 1998; Connell et al., 2004). A similar study in an *E. globulus* plantation showed that thinning at age 10 years from about 850 to 400 trees ha\(^{-1}\) increased the basal area of the SCT\(_{200}\) by about 11% five years after thinning when coppice was removed but by < 1% when coppice was retained (Forrester et al., 2012a). Therefore the coppicing stumps appeared to be as competitive as the original trees that were removed. This was probably the result of competition for water.

7.4. Physiological responses to thinning

Physiological responses to thinning have been examined in several *E. nitens* plantations (studies 3 and 7 in Table 2). In study 3 thinning from 1254 to 250 trees ha\(^{-1}\) was done at age 8 years and in study 7, thinning from 900 to 300 trees ha\(^{-1}\) was done at age 3.2 years. Thinning changed the light distribution within the stand so that relative light availability was higher in the middle and lower crown positions of the thinned compared to unthinned plots (Medhurst and Beadle, 2005; Forrester et al., 2012c). This resulted in the retention
and continued growth of live branches in the lower crown (Medhurst and Beadle, 2001; Forrester et al., 2012b). The changed light environment also altered the nitrogen distribution within the canopy and positive relationships were found between foliar nitrogen and the fraction of incident light or light-saturated rates of photosynthesis. Similarly, thinning led to increased light intensity, canopy nutrition or rates of photosynthesis in *Pinus ponderosa* (Ponderosa Pine) (Skov et al., 2003), *Pinus taeda* (Ginn et al., 1991; Peterson et al., 1997; Tang et al., 1999; Tang et al., 2003) and *Betula papyrifera* (Paper Birch) (Wang et al., 1995).

The changes in the lower crown structure were the main drivers behind the observed growth responses to thinning of *E. nitens* (Medhurst and Beadle, 2005; Forrester et al., 2012b). However, the increase in leaf area occurred on the north-east aspect (Medhurst and Beadle, 2001) where 48% of the crown dry mass (foliage and branches) occurred significantly increasing crown asymmetry (Medhurst et al., 2007; Medhurst et al., 2011). Despite these increases in canopy asymmetry a later study found no obvious thinning treatment differences in the magnitude or direction of stem eccentricity (Medhurst et al., 2007; Medhurst et al., 2011). Similarly, thinning did not influence pith displacement in *E. grandis* (de Lima et al., 2007). Thinning had little direct effect on other basic elements of crown structure such as branching density, angle and orientation (Medhurst and Beadle, 2001).

**7.5. Epicormic branches**

It is important to note that by opening up a stand through thinning, the increased light availability can stimulate the growth of epicormic branches (Schönau and Coetzee, 1989; Gerrand et al., 1997b; Montagu et al., 2003) and weeds. For example, retaining stand densities of 670 trees ha\(^{-1}\) until age 11 years in study 13 of Table 2 resulted in trees with shorter and narrower live crowns than those in plots thinned to 220 trees ha\(^{-1}\). The increased light availability after a later thinning from 670 to 220 trees ha\(^{-1}\) resulted in epicormic branches as well as the expansion of existing canopies. While this did not have a significant impact on the volume growth trajectory, the pruned sections of the
boles could no longer produce clear wood without pruning the epicormics. The production of epicormic branches appears to be much less likely in stands thinned earlier and before the crown rises significantly.

7.6. Stand stability

Windthrow is another problem that has been observed after eucalypt plantations have been thinned (Williamson, 1979; Gerrand et al., 1997b; Forrester and Baker, 2007; Wood et al., 2008; Wood et al., 2009). While initial spacing is of little consequence for stability given the adaptive response of trees to wind over time (Quine et al., 1995), sudden changes in stand density associated with thinning, open the canopy to wind penetration (Cremer et al., 1982), and can dramatically increase the vulnerability of a stand to windthrow (Mayhead et al., 1975; Savill, 1976; Cremer et al., 1977; Incoll, 1977; Savill, 1983). This is especially true of older stands with tall, slender stems (Ruel, 1995), or stands containing species with high crown drag coefficients (Quine et al., 1995). This increase in risk is especially pronounced in the initial few years after thinning (Savill 1983), and may be exacerbated following post-thinning fertiliser application where an initial crown response can result in an increase in the crown or ‘sail’ area upon which the wind forces act (Valinger and Lundqvist, 1992).

Consequently, for *E. globulus* and *E. nitens* plantations in Tasmania, it is recommended that thinning occurs before the mean dominant height (tallest 50 trees ha$^{-1}$) exceeds 20 m or the height to diameter ratio exceeds 1.0 (Wood et al., 2005). On sites where trees have developed small crowns it may be wise to apply multiple light thinnings to reduce the likelihood of epicormic branching (Kerruish, 1978; Schönau, 1984b; Schönau and Coetzee, 1989) as well as windthrow.

Windthrow can also result when silvicultural inputs such as irrigation or fertilizer have adverse consequences on root growth. In a study of *E. nitens* and *E. globulus*, Moroni et al. (2003) demonstrated that root length density and root frequency were greater on drought-simulated soils compared to those under irrigation. Changes in biomass
allocation to favour above-ground growth at the expense of below-ground growth has been observed following fertilizer application and irrigation (Giardina et al., 2003; Ryan et al., 2008; Stape et al., 2008). While this increases volume production, it may also increase drought susceptibility and reduce stand stability.

7.7. Combining pruning and thinning

The removal of leaf area inevitably means that the remaining foliage needs to work harder, otherwise growth rates will decline. Pruning needs to be intense enough to confine the branch-related defect to a small knotty core but not so intense as to reduce growth. Such a reduction could extend the rotation length, slow down the branch occlusion process, increase the chance of infection, and make it difficult for the pruned tree to compete with its unpruned neighbours. Pruned trees will generally be selected based on stem form, branch size and angle, tree size and spacing, and generally in that order (Gerrand et al., 1997a). Thus some dominant but poorly formed trees may not be pruned and could compete with selected crop trees. A temporary decline in dominance of pruned trees has been observed in plantations of *E. nitens*, *E. cloeziana* and *E. pilularis* (studies 10 and 16 in Table 1; Gerrand et al., 1997b). However, long term losses of dominance appear not to have been reported. In contrast, longer term reductions in dominance have been observed in *Pinus* species (studies 20 and 26 in Table 1). As a result thinning in *Pinus* is often carried out at a similar time to pruning to remove the inter-tree competition imposed on pruned trees by unpruned trees. The resulting faster growth rates of retained trees can also accelerate rates of branch occlusion and maximise the quantity of clear wood produced.

7.8. Growth and yield models of thinned or pruned stands

Growth and yield models are useful for predicting the effects of different treatments on stand development and subsequently what will be produced at the end of a rotation. Candy (1997) produced models for *E. nitens* using data from (mainly unthinned) plantations in Tasmania and New Zealand. These models were recently re-parameterised
for *E. globulus* and *E. nitens* using additional data sets from southern Australia, and predict mean dominant height or basal area increments, the influence of timing and intensity of thinning on basal area increments, stand mortality and volume, and the diameter below which diameter increment ceases (Musk, 2011). The effects of thinning on individual *E. globulus*, *E. nitens* and *E. grandis* trees of varying sizes have also been modelled (Wang et al., 2011). Other growth models have been developed for unthinned *E. globulus* plantation growth (Wang and Baker, 2007a) and to predict site index or mean dominant height (Wang et al., 2007). These and other growth and yield models, as well as stem taper functions have been incorporated into the Farm Forestry Toolbox that can be used to predict stand growth and potential wood products. The Farm Forestry Toolbox is available at [www.privateforests.tas.gov.au](http://www.privateforests.tas.gov.au). Possible interactions between pruning, thinning, fertiliser application or site quality have so far not been taken into account in these models.

8. Thinning and wood properties important for solid-wood

8.1. Stem shape

The stem shape of plantation eucalypts can be altered by silvicultural decisions made throughout the rotation. An understanding of the effect of silvicultural operations on stem shape is crucial as this plays a major role in determining the recovery of select grade solid-wood products from eucalypt plantations (Shi and Walker, 2006).

Indices of stem form such as the ratio of tree height to tree diameter at breast height, stem form or taper, and cross-sectional eccentricity of growth rings reflect the requirements of a tree for mechanical stability in response to its growing conditions. There is a general consensus that stem taper is a function of growth response to bending stresses applied to the stem as a result of wind action in the canopy (Jacobs, 1954; Larson, 1965; Osawa, 1992; Valinger, 1992). Reduced wind exposure and decreased stem sway were suggested as a possible reason for wood stiffness (MoE) of six-year-old *E. cloeziana*, *E. pilularis* and *E. dunnii* increasing by 11% from stockings of 714 to 1250 trees ha\(^{-1}\); MoE was also
significantly correlated with stem slenderness (Warren et al., 2009). Slender *E. nitens* trees, i.e. those with greater height:diameter ratio, were more elliptical in cross-section than stocky trees regardless of thinning treatment (Medhurst et al., 2011); in addition this study showed that pith eccentricity was linked to the dynamic loading imposed on the stem by the prevailing wind (Figure 5). Thus decisions regarding initial stocking and thinning intensity have important log-quality implications for forest owners in these respects.

Figure 5. Relationship between out-of-roundness (non-circularity) at 3.0 m stem height and DBH/height² used as a stem shape index (Moore and Maguire, 2004) at age 22 years in an *E. nitens* thinning trial. Open and closed symbols are trees from thinned (200 trees ha⁻¹ at age 6 years) and unthinned treatments, respectively. Regression line generated using pooled data (r² = 0.75) (Medhurst et al., 2011).
Low initial stocking and thinning promote the growth of tree diameter in eucalypts but generally do not alter height growth (Neilsen and Gerrand, 1999). Changes to height:diameter ratios can affect wood quality. In a study of 10-year-old *E. globulus* plantations, Washusen et al. (2008) found that slender trees in unthinned plots had lower outerwood microfibril angle than stocky trees in thinned plots. A study of a 22-year-old *E. nitens* thinning trial showed that while stem taper tended to increase with thinning, significantly greater taper of the bottom six-metre log was only apparent in heavily thinned stands of 100 trees ha\(^{-1}\) (Wang and Baker, 2007b).

Pruning of the green crown to produce knot-free clearwood can potentially alter stem shape or taper by concentrating stem growth above the pruned height. However, pruning at intensities of 50% or less of green crown removal has not altered stem form in a range of eucalypt plantation species (Pinkard and Beadle, 1998d; Alcorn et al., 2008b).

### 8.2. Basic density

Wood density is a measure of cell wall material per unit volume. While relatively straightforward to measure, basic density is an expression of complex relationships between cell wall thickness, cell diameter, earlywood-to-latewood ratio, and chemical content. Nevertheless, there is a view that of all the traits that define wood, basic density is one to which all end-users can relate (Walker, 1993). This is justified because basic density often correlates well with other wood properties, such as strength and stiffness (Alexiou, 1994), dimensional stability (Chafe, 1990) and permeability (Kollman and Côté, 1968).

The basic density of wood within a eucalypt tree is not uniform. In a study of *E. globulus* and *E. nitens*, basic density initially declined from the base and then increased up the tree in a linear fashion: minimum density was recorded at 50% height level (Raymond and Muneri, 2001). Basic density also increases from pith to bark (Harwood et al., 2005; Medhurst et al., 2012). In concert with these changes, as with most species, mean basic density of eucalypts increases with age (Hein and Brancheriau, 2011).
Our understanding of the environmental variables that influence the wood density in eucalypts has improved with detailed studies that link wood production to climate (Drew and Downes, 2009; Drew et al., 2009a, 2009b; Drew et al., 2011). The wood density of plantation-grown *E. globulus* appears to be particularly sensitive to soil water availability; reduced water availability leads to an increase in wood density (Downes et al., 2006; Drew et al., 2009b); these authors also found that the average wood density formed each month was strongly correlated with the average air temperature of that month. Taken together, soil water availability and air temperature explained 65% of the variation in wood density of *E. globulus* (Drew et al., 2009b). In *E. nitens* the seasonal variation in wood density is reduced if the variation in water stress is also low. There are marked decreases in wood density coincident with rainfall/irrigation to relieve drought stress (Drew et al., 2009a). Large changes in basic density from pith to bark and within the annual growth cycle are generally undesirable for solid-wood processing. Silvicultural treatments such as thinning and fertilising that aim to maintain relatively continuous individual tree growth throughout the rotation will produce wood that is of significantly more homogenous density compared with stands of more fluctuating periods of growth (Drew et al., 2011). While wood density is a heritable trait in eucalypts (Stackpole et al., 2010), the importance of soil water availability and air temperature in driving wood density suggest site-specific tailored silvicultural regimes are needed to control wood density variation.

8.3. **Tension wood**

Tension wood in eucalypts is formed by the production of cells with distinct anatomical and chemical properties that allow a tree to react to changes in its environment that have caused a non-optimal orientation of stem or branches. A distinctive characteristic of tension wood is a thick, gelatinous inner layer of the cell wall. This non-lignified layer is loosely attached to the other layers of the cell wall and the orientation of the microfibrils is nearly parallel to the fibre axis (Du and Yamamoto, 2007). During maturation, the tension wood fibres contract strongly in the longitudinal direction, thereby creating a very strong tensile stress to “pull” the leaning stem upright (Du and Yamamoto, 2007). In
E. globulus, tension wood is detected by the presence of these gelatinous fibres using microscopy and by high longitudinal and tangential shrinkage during drying (Washusen and Ilic, 2001). Although this shrinkage appears similar to collapse in normal wood, there is no recovery following steam reconditioning as occurs with collapse (Washusen et al., 2002). This is thought to be related to the absence of lignin in the S2 layer of the cell wall as lignin is a necessary part of the recovery process (R. Washusen, pers. comm.).

Tension wood is a major factor limiting the recovery of wood processed from eucalypt plantations, and when located at the periphery is associated with very high growth stresses that result in board distortion (Washusen, 2005) and poor accuracy during sawing and sizing. When it is located anywhere within the log or board, tension wood results in high transverse and longitudinal shrinkage during drying, resulting in drying degrade and loss of marketable product volume (Washusen, 2000). The role of silviculture in mitigating the prevalence of tension wood deserves careful attention. A Chilean study of peripheral growth strain in E. nitens between ages three and 14 years suggested that stem slenderness is correlated with growth stress at a young age, while other factors such as crown symmetry are more influential in older stands (Biechele et al., 2009). However, stocking density did not influence levels of peripheral longitudinal growth strain for 22-year-old E. nitens grown at a range of stocking densities in a thinning trial in north-east Tasmania (Valencia et al., 2011). Tension wood formation in E. globulus was correlated with form factor and stem taper (Washusen, 2002). These results suggest that manipulation of stand density by thinning early in the rotation can reduce the formation of tension wood in some, but not all circumstances. On the other hand, later-age thinning, or a poor growth response to thinning may contribute to tension wood formation in eucalypt plantations (Washusen et al., 2005; Washusen et al., 2008). The combination of increased exposure to wind and slower stem diameter growth to improve stability may contribute to tension wood formation in such situations. Studies of silvicultural effects on tension wood in E. globulus suggest that fertiliser application at time of thinning may be a useful strategy in minimising tension wood formation (Washusen et al., 2005; Washusen et al., 2008).
8.4. Microfibril angle

Cellulose occurs as long crystalline microfibrils in the cell wall that have great stiffness in the direction of the microfibril axis. Microfibril angle (MFA) is the winding angle of these cellulose microfibrils in the dominating S$_2$ layer of the secondary cell wall. Wood stiffness is a function of cellulose content and its distribution in the cell wall. Microfibril angle is an important characteristic for sawn timber because the stiffness of the cell increases approximately linearly as MFA decreases (Cave, 1968): at the same time, longitudinal shrinkage decreases, though in a highly non-linear manner, and tangential shrinkage increases (Walker and Butterfield, 1995). Microfibril angle alone accounted for 87% of the variation in wood stiffness, expressed as Young’s modulus of elasticity (MoE), in plantation-grown E. globulus, E. nitens and E. delegatensis (Alpine Ash) (Yang and Evans, 2003).

The MFA of eucalypts tends to start at about 20° at the pith (Evans et al., 2000). The MFA declines rapidly throughout the earlywood and tends to reach a relatively stable value by the fifth growth ring; the MFA of the outer wood of eucalypts typically ranges between 10 and 15° (Donaldson, 2008; Medhurst et al., 2012). The MFA of eucalypts also declines with tree height to a height of approximately 10 m or 60% of merchantable height beyond which it then increases (Evans et al., 2000; Kibblewhite et al., 2004).

Both growth rate and seasonal growth pattern influence MFA of eucalypts (Wimmer et al., 2002; Drew et al., 2009b). From this we can expect that site selection and silvicultural practices that alter the growing conditions and the growth patterns of plantation eucalypts also have the potential to influence MFA. While the bulk of research to date has focused on softwood species, indications are that the age-related radial pattern of MFA and MoE of eucalypts can also be manipulated through judicious silviculture. A number of studies have shown a positive relationship between tree growth rate and MFA (Donaldson, 2008). Thus MFA was higher in E. nitens at a fast- than slow-growing site (Figure 6; Medhurst et al. unpublished). Thinning from 1000 trees ha$^{-1}$ to 200 trees ha$^{-1}$ in plantation-grown E. globulus at age eight years significantly increased mean MFA and
lowered the mean density of wood produced during the following four years (Washusen et al., 2005). Applying fertiliser had the same effect on MFA and density as thinning (Washusen et al., 2005). Higher MFA values were also found in 10-year-old *E. globulus* thinned from 1200 trees ha$^{-1}$ to 300 trees ha$^{-1}$ and/or fertilised with nitrogen at age two years (Washusen et al., 2008). The unfertilised trees had lower MFA than those receiving 250 kg ha$^{-1}$ of N-fertiliser (Washusen et al., 2008). No silvicultural effect on wood density was found in this study. However, outer wood density increased with decreasing soil water availability across the three Western Australian sites used in the study (Washusen et al., 2008). The effect of pruning on wood properties such as MFA and modulus of elasticity has not been extensively examined for softwoods or hardwoods.

![Figure 6. Radial pattern of mean microfibril angle (MFA) at stem height of 1.3 m for *E. nitens* trees from a fast-growing (open symbols; n = 12) and slow-growing plantation (closed symbols; n = 12) (Medhurst et al., unpublished data).](image)

High MFA is associated with increased drying distortion in sawn timber (Briggs and Smith, 1986; Zhang, 1997). Does the silviculturally-induced increase in MFA of outer wood pose significant solid-wood processing problems for plantation-grown eucalypts?
Almost certainly not, as the modest, transient increase in MFA observed following thinning in *E. nitens* Medhurst et al., 2012) resulted in levels well below those associated with excessive shrinkage and low wood stiffness (Apiolaza et al., 2009). For *E. globulus*, increasing MFA in the outerwood from the low values, around 10°, associated with tension wood through thinning is also desirable (Washusen et al., 2008).

9. Interactions between thinning, pruning, fertiliser application and site quality

Pruning, thinning and fertiliser application are often carried out simultaneously and can potentially interact with each other to influence growth. An understanding of these interactions can assist with optimising financial investment and returns. As explained above, pruning, thinning and fertiliser application can each influence above-ground biomass or wood growth via different mechanisms, so interactions between treatments are possible. For example, N fertiliser application can increase growth by increasing leaf area, branch size and branch longevity (Wiseman et al., 2006), and by reducing the proportion of biomass partitioned below ground (Litton et al., 2007). Responses to thinning can be similar (Medhurst and Beadle, 2001; Forrester et al., 2012b), however thinning also gives trees more space to expand their root and crown zones, thereby increasing their supplies of light and water as well as nutrients. In addition to larger crowns, thinning may shift the vertical distribution of foliage towards the lower crown where relative increases in light availability are greatest (Brix, 1981; Medhurst and Beadle, 2001; Forrester et al., 2012b). In contrast, pruning reduces tree leaf area, but usually only from the lower crowns. It also often increases leaf-level rates of photosynthesis in the remaining foliage of the upper canopy (Table 1), which contrasts with thinning where increases in photosynthesis are more likely to occur in the mid or lower crown, where changes in light availability following thinning are greatest (Wang et al., 1995; Tang et al., 2003; Medhurst and Beadle, 2005; Sala et al., 2005; Gauthier and Jacobs, 2010; Forrester et al., 2012c).
9.1. Pruning × thinning

Eucalypts are relatively shade intolerant, with short lived branches and fast-developing canopies, at least when young (Beadle et al., 1995). In unthinned stands pruning effects on growth may be relatively small because lower crown branches are shaded, inefficient and rapidly shed, whether they are pruned or not. Whereas in thinned stands the lower crowns are well lit, the leaves are more efficient and retained for longer, and thus their removal by pruning is likely to have a greater effect on growth. For example, during the first year after pruning the lower half of the live-crown length of 3.2-year-old E. nitens, pruned trees absorbed 29% less PAR than unpruned trees in unthinned stands compared with 49% less in thinned stands (Forrester et al., 2013). By age six years, and in unthinned stands, the leaf area of unpruned trees was only 6% greater than pruned trees and above-ground biomass of pruned SCT$_{200}$ was only 5% lower. However, in thinned stands, leaf areas of unpruned trees were 27% greater than pruned trees and above-ground biomass of pruned SCT$_{200}$ was 11% lower. In the thinned stands the lower crowns (of unpruned trees) were larger, better lit (Figure 2), and had higher light-saturated rates of photosynthesis than trees in unthinned stands, and therefore contributed more to a trees growth (Forrester et al., 2012b; Forrester et al., 2012c; Forrester et al., 2013). It is important to note that whether SCT$_{200}$ trees were pruned or not, they were larger in thinned stands than unpruned trees in unthinned stands.

This thinning × pruning interaction was also found after pruning E. globulus in multiple lifts to 6.5 m. Pruning reduced volume of SCT$_{200}$ at age 10 years by only 8% in unthinned stands but by 24% in stands that were thinned from 1000 to 300 trees ha$^{-1}$ at age 2.7 years (Figure 7) (Forrester and Baker, 2012). Similarly, greater pruning effects on E. nitens were observed before canopy closure, when removal of only 20% of leaf area reduced volume growth (Pinkard, 2002), compared with pruning after canopy closure when removal of 55% of the leaf area or 50% of the live-crown length did not significantly reduce volume growth (Pinkard and Beadle, 1998d). Pruning studies in eucalypt plantations are often done in unthinned stands, but these thinning × pruning interactions suggest that pruning effects might be greater in thinned stands or agroforestry systems (e.g. Fontan et al., 2011).
Figure 7. The interaction between pruning and thinning (at age 2.7 years) on the volume of SCT\textsubscript{200} of E. globulus. Heavy, moderate, and light pruning indicates pruning up the stem to diameters of 7, 12, and 17 cm, respectively, aiming to achieve a maximum knotty core of 10, 15, and 20 cm diameter, respectively. Bars are standard errors of difference. Modified from Forrester and Baker (2012).

It is interesting to note that the opposite interaction occurred in Pinus patula (Mexican Weeping Pine) plantations, where pruning effects were relatively greater in unthinned stands compared with thinned stands (Karani, 1978). These thinning × pruning interactions, whether for Pinus or Eucalyptus are each consistent with the Limiting Resource Model (LRM; Wise and Abrahamson, 2007). This model suggests that growth responses to defoliation depend on the resources that are currently limiting growth and how their capture is changed by a loss of leaf area. The different directions of the interactions for Pinus and Eucalyptus may be due to differences in shade tolerance. Shade tolerant and intolerant species probably both benefit from the retention of their lower crowns in thinned stands. In unthinned stands, the relatively inefficient lower crowns of shade intolerant species (Eucalyptus) probably contribute relatively less to a trees’ growth and to its ability to compete with neighbours, compared with the same foliage of a more
shade tolerant species (*Pinus*). In unthinned stands, the competitive disadvantage for pruned shade tolerant trees will be greater than that for pruned shade intolerant trees and indeed in unthinned stands growth of shade tolerant *Pinus* species is often reduced at lower pruning intensities compared to shade intolerant *Eucalyptus* species (Forrester et al., 2010c).

9.2. **Pruning × fertiliser application or site quality**

Interactions between pruning (or defoliation) and fertiliser application or site quality are variable. There are cases of greater pruning/defoliation effects under higher resource supply (e.g. see review by Wise and Abrahamson (2007)), lower resource supply (Pinkard and Beadle, 1998d; Anttonen et al., 2002; Pinkard, 2002) and no interaction (Pinkard et al., 2006; Wiseman et al., 2009).

Wise and Abrahamson (2007) carried out a meta-analysis where defoliation reduced growth relatively more in fertilised treatments than in controls in 17 out of 24 experiments. Following the LRM, Wise and Abrahamson (2007) showed that this interaction could result when defoliation directly influences light capture or carbon fixation. In fertilised treatments light and carbon are the major growth limiting resources, whereas in control treatments N is more limiting and defoliation has less influence on N use or its acquisition. Additionally, fertiliser application can shift carbon partitioning more above-ground (Giardina et al., 2003) and if trees use their below-ground stores of non-structural carbohydrates to help rebuild their canopies after defoliation (Strauss and Agrawal, 1999; Eyles et al., 2009), trees in fertilised stands may be more disadvantaged by pruning.

With regards to eucalypt plantations, the same interaction occurred at age six years, 2.8 years after pruning an *E. nitens* plantation. Leaf areas of pruned trees were 28% lower than unpruned trees in fertilised stands, but only 12% lower in unfertilised stands, at age six years (Forrester et al., 2012b). In unfertilised stands the unpruned trees shed their lower foliage and resembled pruned trees, while in fertilised stands the lower foliage of
unpruned trees was retained for longer. Differences in biomass partitioning countered these effects so that this interaction was not significant for above-ground biomass of SCT$_{200}$ and therefore pruning may not have had a significant influence on the use or acquisition of the major limiting resources in fertilised stands. There were also no interactions in 5.7-year-old *E. nitens* and *E. globulus* stands that were pruned and N fertilised (Wiseman et al., 2009), or for three-year-old *E. globulus* trees that had been defoliated (up to 50% of leaf area) by an insect, *Gonipterus scutellatus*, and fertilised with N or nitrogen + potassium (Pinkard et al., 2006), or defoliated *Quercus rubra* (Red Oak) grown at different levels of light, water and nutrients (McGraw et al., 1990).

The opposite interaction has also been observed, where pruning effects are relatively greater in unfertilised stands or on lower quality sites. Reductions in growth of pruned trees were less pronounced on higher quality sites than lower quality sites in *E. nitens* plantations (Pinkard and Beadle, 1998d; Pinkard, 2002), and in *E. globulus* plantations, pruning reduced growth on a lower quality site but not on higher quality sites (Forrester and Baker, 2012). In another *E. globulus* experiment, pruning that retained 80% of leaf area reduced growth on a lower quality site, but on a higher quality site pruning did not reduce growth until 40% or less of the leaf area was retained (Pinkard, 2003). Artificial defoliation (loss of 25% of leaf area) reduced growth of three-year-old *Betula pendula* (Silver Birch) trees in unfertilised plots but not fertilised plots (Anttonen et al., 2002) and artificial defoliation of nine-month-old *E. globulus* appeared to reduce diameter growth relatively more without N fertiliser application than with fertiliser application (Pinkard et al., 2007). According to the LRM of Wise and Abrahamson (2007) this interaction suggests that pruning largely influenced the uptake or use of the fertiliser nutrients, (or another resource defining site quality), and therefore had a greater influence where those resources were limiting (the lower quality sites).

9.3. *Thinning × site quality or fertiliser application*

For a given species, relative and absolute thinning responses can vary with resource availability, size class and thinning age (Medhurst et al., 2001; Mäkinen and Isomäki,
2004b). The effects of resource availability (e.g. fertiliser application or site quality), may be related to its influence on the symmetry of competition between trees. Size-asymmetric competition can result when tall trees can shade shorter trees, but not vice versa, so that a tree that is twice as large as another intercepts much more than twice as much light (Weiner, 1985, 1986; Hara, 1993; Kikuzawa and Umeki, 1996). Competition may be more size-symmetric when soil resources are major growth limiting factors and assuming that roots of smaller trees take up similar amounts of water and nutrient resources per unit root area (Weiner, 1985, 1986; Hara, 1993), so a tree that is twice as large as another obtains about twice as much of the resource.

SCTs often have a greater absolute thinning (or initial spacing) response on higher quality sites, or in fertilizer stands, compared with SCTs on lower quality sites or where fertiliser was not applied (Figure 8) (Stoneman et al., 1996; Ruha and Varmola, 1997; Mäkinen and Isomäki, 2004a; Forrester et al., in press, submitted-b). In contrast, relative thinning responses can be smaller (Harrington and Wierman, 1990; Messina, 1992; Brockley 2005). With regards to the symmetry of competition, a lower relative response on higher quality sites could occur because water and nutrients are not as limiting relative to light, dominant trees already obtain the most light, and removing the smaller trees will have relatively little influence on competition for light or the thinning response of the large retained trees. In contrast, on lower quality sites soil resources are relatively more limiting than light, and since smaller trees can compete with larger trees for these resources, their removal could have a relatively larger effect on the growth of the larger trees. There are also, however, examples where relative responses increased with increasing site quality or with the rate of fertiliser application (Stoneman et al., 1996; Mäkinen and Isomäki, 2004a; La Sala, 2006; Forrester et al. in press), as well as examples where there were no obvious trends (Messina, 1992; Mäkinen and Isomäki, 2004a; Blevins et al., 2005; Omule et al., 2011). The lack of consistency in relative thinning responses, even for a given species, suggests that thinning responses may also be related to other stand characteristics.
Figure 8. Example modelled relationships between the periodic basal area increment (PAI) of $SCT_{200}$ trees and competition. Competition is the sum of the basal area of neighbouring trees within 6.5 m of the given crop tree. The different lines represent different combinations of coefficient of variation (CV; %) or skewness (Skew) of diameter distributions of unthinned stands, and site quality (SQ) which is quantified as the mean annual volume increment of unthinned stands at age 10 years in $m^3$ ha$^{-1}$ year$^{-1}$. The indicated absolute ($cm^2$ year$^{-1}$) and relative (%) competition responses are the difference in increment from a competition of 3000 $cm^2$ to 800 $cm^2$. Modified from Forrester et al., (in press).
9.4. Stand structure and thinning responses

Stand structure, in terms of how pronounced the dominance classes have become and whether or not diameter distributions are positively or negatively skewed, accounted for up to 50% of the variability in relative and absolute thinning responses in *E. globulus, E. grandis* and *E. nitens* plantations (Forrester et al., in press). Thinning responses were also related to site quality but stand structure was as good as, or better, than site quality at predicting thinning responses (Forrester et al., in press). The relative and absolute thinning responses of SCT<sub>200</sub> increased in stands with more negatively skewed diameter distributions (higher proportion of large trees) and lower coefficients of variation in diameters (Figures 8 and 9). Such stand structures could develop when growing conditions are relatively homogeneous and genetic variability is not high, so larger trees in the stand grow at similar rates and are not able to out-compete each other to differentiate into size classes. This stand structure was more characteristic of faster growing stands (Forrester et al., in press), and helps to explain why relative (and absolute) thinning responses increase with site quality or fertiliser application in some studies (Stoneman et al., 1996; Mäkinen and Isomäki, 2004a; La Sala, 2006; Forrester et al., in press). The implications for eucalypt plantations are that stands with negatively skewed diameter distributions, that are fast growing and less variable (perhaps clonal stands in particular?) may have the greatest absolute and relative thinning responses (Forrester et al., in press).

In contrast, lower relative thinning responses with increasing site quality or fertiliser application were reported for the shade-tolerant species (relative to eucalypts) *Thuja plicata* (Western Red Cedar) and *Pinus contorta* (Lodgepole Pine) (Harrington and Wierman, 1990; Brockley 2005). This may occur in stands of species that have more asymmetric competition. In the young *Eucalyptus* stands competition was relatively symmetric (Forrester et al., in press).
Figure 9. Diameter distributions for the unthinned treatments in stands exemplifying large (a), medium (b) and small (c) responses to reductions in competition from 3000 cm$^2$ to 800 cm$^2$. Modified from Forrester et al. (in press).
9.5. Thinning responses by different size-classes

Relative and absolute responses can also vary between different dominance classes within a stand. Absolute thinning responses in even-aged stands often increase (or at least don’t decrease) with increasing size class, such that the larger and faster growing trees respond the most to thinning (Ruha and Varmola, 1997; Medhurst et al., 2001; Mäkinen and Isomäki, 2004b). However, dominant trees do not always have the largest absolute responses (Pukkala et al., 1998), which probably relates to stand age, shade tolerance and whether the stand is even-aged.

Relative thinning responses by dominant trees are often smaller than responses of intermediate trees, and this effect can become greater as stands age and dominance classes become more pronounced. For example, relative responses declined with increasing size class in Eucalyptus, Pseudotsuga menziesii (Douglas fir), Betula papyrifera and Pinus sylvestris stands (Moore et al., 1994; Pukkala et al., 1998; Mäkinen and Isomäki, 2004b; Simard et al., 2004; Forrester et al., in press). This pattern is to be expected when smaller trees benefit from thinning, not only because soil resource availability is improved, but because light availability is improved, whereas for more dominant trees increases in light availability may be smaller. For example thinning of E. nitens stands increased the absorption of photosynthetically active radiation by 50% for 10-cm-diameter trees compared to 30% for 30-cm-diameter trees (see Forrester et al. (2013)).

10. Mixed-species plantations

Mono-specific plantations of eucalypts have been managed successfully and sustainably in many countries and few silvicultural alternatives to intensively managed monocultures have been examined. However, several studies have shown that mixed-species stands containing a Eucalyptus sp. with a nitrogen-fixing tree, shrub or cowpea can increase total stand productivity, as well as the growth of the largest diameter 200 crop trees ha⁻¹ (Figure 10) (Forrester et al., 2006b). The success of these stands depends on how site and
species characteristics influence the balance between facilitative and competitive interactions within the stand (Forrester et al., 2006c). Mixtures will not always be more productive than monocultures of the more productive species in the mixture. In addition to increases in biomass or wood production, mixtures can improve soil fertility or nutrient availability (Parrotta, 1999; Kaye et al., 2000; Handa et al., 2005), enhance carbon sequestration (Kaye et al., 2000; Forrester et al., 2006a), facilitate risk management and protection from pests and diseases (Ewel, 1986; FAO, 1995; Montagnini, 2000) and increase water-use efficiency (Figure 4; Forrester et al., 2010b). Innovative silviculturalists could design mixed systems where either the nitrogen-fixing species is thinned, retained to fix more nitrogen, or both species are thinned (Forrester et al., 2004). The nitrogen fixer might also shade the eucalypt stems, accelerate the rise of the live crown, and reduce the size of branches and of the knotty core. Alternatively, N₂-fixing species may be a pasture component or used as a bioenergy crop, and grow underneath widely spaced eucalypts that are managed for solid-wood. Eucalypt solid-wood producers in Argentina and Uruguay (e.g. Cofusa, Pomera, Weyerhaeser etc) are paid by graziers for the (non-N-fixing) pasture under their widely spaced eucalypts (study 18 and 19 in Table 2). In some cases clonal cuttings are planted at initial spacings as low as 500-600 trees ha⁻¹.
Mixed species plantation containing several eucalypt species might also be an option, but so far this has received very little attention. In one experiment *E. pilularis* and *E. grandis* mixtures were compared with their monocultures for 19 years (Forrester and Smith, 2012). For both species inter-specific competition was less intense than intra-specific competition and so their relative volume or basal area yields indicated advantageous mixing effects of about 10-30%. This was associated with changes in stand structure where the diameter distributions of both species became less positively skewed (lower proportions of small trees). Mixing effects were relatively consistent as the stands
developed suggesting that if this competitive reduction effect is used in plantations there is considerable silvicultural flexibility, such that these mixed plantations could be used on both shorter rotations for biomass or pulp-logs as well as longer rotations for solid wood products. Most, if not all eucalypts occur in mixture with another eucalypt, at least in part of their distribution, and *E. pilularis* and *E. grandis* are one of those naturally occurring mixtures. This study also indicates that interactions between co-occurring *Eucalyptus* species in natural forests might actually facilitate stand growth, in addition to simply enabling co-existence.

![Figure 11. Above-ground biomass increment and water-use efficiency (WUE) between ages 14 and 15 years in Eucalyptus globulus and Acacia mearnsii mixtures (757 trees ha\(^{-1}\) *E. globulus* + 757 trees ha\(^{-1}\) *A. mearnsii*; 50E:50A) or monocultures (1515 trees ha\(^{-1}\) *E. globulus*; 100E, or *A. mearnsii*; 100A) near Cann River, Victoria, Australia. Annual transpiration was 358, 419 and 217 mm in 100E, 50E:50A and 100A, respectively. Means sharing the same letter are not significantly different (\(P > 0.05\), ANOVA) for a given variable (Forrester et al., 2010b).](image-url)
11. Synthesis

*Eucalyptus* plantations now cover over 19 million hectares worldwide. These fast-growing species inevitably place a high demand on site resources, a fact that has raised questions about the sustainability of eucalypt plantation silviculture in many countries and contexts. The knowledge base in the area of nutrient dynamics is now quite detailed. In particular, technologies are available for making sure nutrient demand and nutrient supply remain in balance during canopy development, at least for the two major nutrients nitrogen and phosphorus. Similarly, how to apply nitrogen, phosphorus and potassium fertilisers to produce the desired effect is also well understood. What is less detailed is the knowledge base that links nutrient supply to other factors like levels of available water and inter-tree competition that become more limiting to growth and economic yield after canopy closure. Essentially growers have been forced to recognise that the major factor limiting growth at a site will determine the sustainability of yield. Some form of weed control, if only within the tree row, is normally considered an essential part of managing the supply of both water and nutrients to the tree crop.

Stocking or stand density is also a crucial factor in the management of plantations for solid-wood products. While this is also linked to the sustainability of yield, stand density links back to stem form, branch size and the attendant issues that impinge on pruning and thinning strategies. Within stand variability in growth rates and tree form has dictated the need to establish plantations managed for solid wood at stockings normally associated with pulpwood plantations, a policy that is unlikely to change until trees can be selected that combine good form and acceptable branch size when established at low stockings (<1000 trees ha\(^{-1}\)), such as clonal *E. grandis* stands in Uruguay planted at 500-800 trees ha\(^{-1}\).

The last fifteen years have seen some considerable research energy put into pruning strategies for eucalypts. This is simply because so many factors impinge not only on the silvicultural operation itself but also on how this is dictated by the condition of the tree before branches are excised, and the need to minimise potential negative effects on wood
quality associated with responses to decay entry because of pruning or retention of dead branches. To some extent pruning strategy is dictated by the species grown. A higher shade tolerance means the longer retention of live branches which increases the window of opportunity for pruning. Dead branches and rapid crown lift are associated with shade intolerant species, and can also be accelerated with intense inter-tree competition. Our understanding of species behaviour and physiological responses to pruning have certainly provided a platform for predicting when to intervene but does not yet provide us with information about differences between the responses to sequential pruning lifts.

Thinning is often the most powerful tool available to forest managers for influencing the growth rate of final crop trees and their size at harvest. Evidence is also emerging that for eucalypts, thinning can also be used to mitigate at least some of the undesirable development of tension wood and internal growth stresses in the stem. As with pruning, thinning interventions should occur while the trees have a high growth rate and vigour; conversely allowing tree growth and crown size to decline ahead of thinning will inevitably weaken the thinning response. Thus site quality has much to do with how thinning responses can be captured though to some extent it may be possible to retain higher growth rates on lower quality sites through the careful use of fertiliser inputs. The tendency to service markets for commercial products by delaying thinning on sites other than those that support high growth rates may therefore tend to compromise the value of the final sawlog crop because of slower growth rates and longer rotations.

Pruning and thinning operations that respectively change the distribution of crown mass and reduce the mutual shelter offered by unthinned stands will inevitably make the stand more susceptible to windthrow. There are some basic rules though that can minimise windthrow risk. In general these demand particular attention to tree height and site quality: the lower the site quality, the longer it will take for the stand to restabilise and too much encouragement with fertiliser on such sites is likely to slow the process.

More recently the production ecology of thinning, pruning and fertiliser application has been assessed to examine the contribution of the different mechanisms to growth
responses. It is clear that different mechanisms influence the growth responses to each treatment, and since thinning, pruning and fertiliser application are sometimes carried out at similar times in the same plantation, they can interact to influence growth. With regards to thinning and pruning in *Eucalyptus* plantations, pruning effects can be smaller in unthinned stands compared with thinned stands. In unthinned stands, lower crowns of fast growing eucalypt trees are shed rapidly whether they are pruned or not, where as in thinned stands, the lower foliage is well lit and more efficient, and its loss by pruning has a greater effect on tree growth. Pruning interactions with fertiliser application or site quality are variable, with greater pruning effects at higher or lower resource availabilities, as well as no interaction. The Limiting Resource Model (Wise and Abrahamson, 2007) suggests that the interaction will depend on the resources that are currently limiting growth and how their capture is changed by a loss of leaf area.

Thinning responses also vary with site quality. Absolute thinning responses by SCTs often increase with increasing site quality or with fertiliser application, however relative responses are more variable, with increases, decreases and no interaction each reported. This variability may occur because thinning responses are also related to stand structure. Decreases in relative thinning responses may be more likely when competition between trees is relatively asymmetric, and stand structures are such that diameter distributions (of unthinned stands) become more positively skewed (higher proportions of small trees) and have high coefficients of variation. In these stands large tree are already freer of competition. On the other hand, relative and absolute thinning responses of SCTs may increase when diameter distributions (of unthinned stands) become more negatively skewed (higher proportions of large trees) and with lower coefficients of variation. With these stand structures the large trees are competing with lots of other large trees and therefore respond well to thinning. Few studies have examined the influence of stand structure on thinning responses but since stand structure has been shown to explain thinning responses as well as, or better, than site quality, this deserves more attention.

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Table 1. Responses to foliage removal, including pruning

<table>
<thead>
<tr>
<th>Study number</th>
<th>Species</th>
<th>Amount of canopy removed before growth was slowed</th>
<th>Treatments</th>
<th>Response</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Acacia mangium</em> (Black Wattle)</td>
<td>40</td>
<td>Pruned at either 1.5, 3 or 4 years by removing between 4 and 46% of live-crown length, when trees were 9-14 m tall. Plantations were unthinned and planted at 1110 trees ha⁻¹.</td>
<td>Diameter growth was significantly reduced 1 year after pruning when 40% or more of the crown was removed.</td>
<td>(Majid and Paudyal, 1992)</td>
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<tr>
<td>2</td>
<td><em>Acacia melanoxylon</em> (Blackwood)</td>
<td>25</td>
<td>Pruned 0, 25 or 50% of foliage area at age 5 years when trees were 5.6 m tall. Rows of <em>A. melanoxylon</em> planted between every second row of a <em>Pinus radiata</em> nurse crop. <em>A. melanoxylon</em> planted at 500 trees ha⁻¹, and <em>P. radiata</em> planted at 800 trees ha⁻¹ and thinned to about 260 trees ha⁻¹.</td>
<td>Light saturated rates of photosynthesis increased from 2 weeks and this was maintained for about 1.5 to 12 months in the 25 and 50% treatments respectively. This response was higher in the 50% treatment and was confined to the upper two-thirds of the crowns. Growth rates were reduced in the 50% but not the 25% treatment. Foliage area returned to unpruned levels within 2 months in 25% treatment but took about 10 months in the 50% treatment.</td>
<td>(Medhurst et al., 2003, 2006)</td>
</tr>
<tr>
<td>3</td>
<td><em>Alnus glutinosa</em> (Black Alder)</td>
<td>56</td>
<td>Light, moderate and heavy pruning (that removed 28-31, 56-60 and 80-82% of foliage respectively) was done at age 3 years (in a pot trial). There was also an unpruned control.</td>
<td>During the first 30 days after pruning transpiration decreased, water-use efficiency increased and net rates of photosynthesis increased in pruned plants. After 90 days leaf area was highest in light and moderately pruned plants and lowest in heavily or unpruned plants. Biomass production was highest in moderately pruned plants and lowest in the heavily pruned plants.</td>
<td>(Singh and Thompson, 1995)</td>
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<td>4</td>
<td><em>Betula pubescens</em> ssp. <em>Torulosa</em> (Downy Birch)</td>
<td>50</td>
<td>50 or 100% of foliage was removed when trees were 3 to 5 m tall and about 35 years old.</td>
<td>Maximum rates of photosynthesis increased by 35% in 50% defoliated trees. For three years after defoliation, diameter increment was reduced by removing 100% but not 50% of foliage.</td>
<td>(Hoogesteger and Karlsson, 1992)</td>
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<td>5</td>
<td><em>Cryptomeria japonica</em> (Japanese Cedar)</td>
<td>30-35</td>
<td>40-50</td>
<td>Pruned 40, 60 and 76% of live crown at age 5 years when trees were 4.5 m tall. Planted at 2000 stems ha⁻¹ but declined to 1850 trees ha⁻¹ by age 5 years, unthinned.</td>
<td>After 4 years pruning reduced diameter and height growth. Growth losses were less than 10% if no more than 40% was removed.</td>
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<td>6</td>
<td><em>Eucalyptus globulus</em></td>
<td>50</td>
<td>83</td>
<td>Pruned 0, 30, 50 or 70% of live-crown length at age 3 years. Plantation was unthinned and planted at 1100 trees ha⁻¹.</td>
<td>Height increment was significantly reduced in the 50 and 70% after 2 years. Diameter and stem volume increment was significantly reduced in the 70% after 2 years.</td>
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<tr>
<td>7</td>
<td><em>Eucalyptus globulus</em></td>
<td>20 or 60 depending on site quality</td>
<td>Pruned 0, 20, 40, 60 and 80% of tree leaf area by selective (large) branch pruning (SBP) in the lower 2.5 m or lift pruning (LP) of the lower 40% of leaf area. This was done at age 2 years, prior to canopy closure in unthinned plantations that were planted at 1100 trees ha⁻¹. Replicated at a high and low quality site with average heights of 4.3 and 4.4 m.</td>
<td>At the low quality site, about 15 months after pruning, diameter, height and volume increment were reduced when 20% of leaf area was removed. On the higher quality site diameter, height and volume increment were reduced when 80%, 60% and 60% of leaf area was removed respectively. Maximum rates of photosynthesis increased with pruning intensity during the 3 months after pruning at both sites. LP of 40% leaf area had a greater effect on photosynthesis than SBP of 40%.</td>
<td>(Pinkard, 2003)</td>
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<tr>
<td>No.</td>
<td>Species</td>
<td>Treatment Details</td>
<td>Results and Notes</td>
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<td>8</td>
<td><em>Eucalyptus globulus</em></td>
<td>Pruned 0, 50 or 70% of live-crown length at age 1 year, when average height was 1.8 m. Planted at 1200 trees ha⁻¹.</td>
<td>Pruning increased maximum rates of photosynthesis after 1 week however there was little difference after 5 weeks. The response was a function of maximum rates of carboxylation and RuBP regeneration rather than stomatal conductance. Nitrogen content increased but this was accumulated in a non-photosynthetic form. (Turnbull et al., 2007a)</td>
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<td>9</td>
<td><em>Eucalyptus cloeziana</em>, <em>E. pilularis</em>, <em>E. dunnii</em> and <em>E. grandis</em></td>
<td>Pruned 0 and 30% of live-crown length at about age 3.5 years. Planted at 1000 trees ha⁻¹ and unthinned.</td>
<td>After 4 years pruning did not affect diameter or height growth. However, growth of <em>E. dunnii</em> was reduced during the first year after pruning. (Smith et al., 2006)</td>
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<td>10</td>
<td><em>Eucalyptus cloeziana</em> and <em>E. pilularis</em></td>
<td>Pruned 0, 20, 50 or 70% of the length of the live crown at age 3.5 years. Planted at 1136 to 1250 trees ha⁻¹.</td>
<td>Stem increment at 1.3 m was reduced for 8 and 12 months in the 50% and 70% treatments, respectively. Height growth was not affected but in the 70% treatment the height of pruned trees relative to unpruned trees was reduced for 12 months after pruning. Stem form and taper were unaffected. There was no up regulation of photosynthesis or changes in leaf physiology between 6 and 13 months. Transpiration was reduced during the first 8 after pruning but by 36 days there were no longer any differences. (Alcorn et al., 2008b; Alcorn et al., 2008a; Alcorn et al., in press; Alcorn et al., submitted-b)</td>
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<td>11</td>
<td><em>Eucalyptus grandis</em></td>
<td>Pruned at various rates up to 50% of the tree height in single or multiple lifts between ages 1.5 and 3 years. Unthinned.</td>
<td>By age 7 years there were no significant effects on diameter or height growth. Although there were significant reductions in height growth early when 50% of the live crown was removed. (Bredenkamp et al., 1980)</td>
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<td>12</td>
<td><em>Eucalyptus grandis</em></td>
<td>Five pruning treatments: (1) unpruned, (2) pruned to 2.6 m then 6 m (age 1 and 2 years, respectively), (3) pruned to 4.3 m at age 1 year, (4) pruned to 3.4 then 8 m and (5) pruned to 2.6 and then 7.3 m. Trees were 6 m and 11.3 m tall at ages 1 and 2 years, respectively. Thinning treatments were (1) unthinned (1000 trees ha⁻¹), (2) to 670 and (3) to 500 trees ha⁻¹ at age 1 year.</td>
<td>By age 2 and 3 years diameter increment and average diameter decreased with pruning intensity and increased with thinning intensity. Height growth was not affected at 2 or 3 years after pruning or thinning. (Terzaghi and Altsuler, 2004)</td>
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<tr>
<td>13</td>
<td><em>Eucalyptus grandis</em></td>
<td>Pruned 0, 33, 40 and 50% of tree height in 3 lifts. Started pruning at age 1.5 years when trees were 5 m tall and completed it at about age 3 years.</td>
<td>By age 4 years the removal of 40% or more of the live-crown length led to temporary but significant loss of diameter increment, mean stand diameter, and height growth. (Lückhoff, 1967)</td>
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</tr>
<tr>
<td>14</td>
<td><em>Eucalyptus grandis</em></td>
<td>30 or 50% of the live-crown length was removed in each of 3 lifts at ages 2, 3 and 6 years. When pruning started trees were 5.7 m tall. Repeated at 4 planting spacemments of 1196, 1329, 1495 and 1707 trees ha⁻¹.</td>
<td>After 7.5 years pruning in both treatments had reduced diameter and height growth. Stand volume was 18.1% lower in the 30% treatment and 25.5% lower in the 50% treatment. Interaction between stocking and pruning responses not examined. Site quality was low. (Schönau, 1970, 1974)</td>
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<tr>
<td>15</td>
<td><em>Eucalyptus nitens</em></td>
<td>Pruned 0, 50 or 70% of live-crown length at age 3.5 years. Trial was replicated on two sites with mean heights of 7.5 or 9.5 m. Stands were unthinned and planted at 1000 or 1430 trees ha⁻¹.</td>
<td>By age 5.5 years, both pruning treatments resulted in reductions in diameter and height growth but this was only significant in the 70% treatment. (Pinkard and Beadle, 1998b)</td>
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<tr>
<td></td>
<td>Species</td>
<td>Trees ha⁻¹</td>
<td>Thinning</td>
<td></td>
<td>Average height</td>
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</tr>
<tr>
<td>16</td>
<td><em>Eucalyptus nitens</em></td>
<td>40</td>
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<tr>
<td></td>
<td>Replicated on 3 sites, plantations were planted at 1100 trees ha⁻¹ and unthinned. Average heights were 2.0, 3.7 and 6.1 m. Estimated time until canopy closure was &gt;15, 9 and 3 months. Treatments included SBP of 0, 20, 40, 60 and 80% of leaf area or LP of the lower 40% of the leaf area.</td>
<td></td>
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<td></td>
<td>15 months after pruning, pruning effects on diameter, height and volume increment were inconsistent. In general, reductions increased with pruning severity and were generally lower on the higher quality site that was closer to canopy closure and higher on the lowest quality site. A loss in dominance was only suggested on the medium quality site.</td>
</tr>
<tr>
<td>17</td>
<td><em>Eucalyptus nitens</em></td>
<td>1429</td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Planted at 1429 trees ha⁻¹. Pruned and thinned at age 6 years when average live-crown height was 8.1 m. Pruned to 0, 3.5 and 7 m. Thinned to 400, 800 or unthinned (1100 by age 6 years) trees ha⁻¹.</td>
<td></td>
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<td></td>
<td>Average live crown height (8.1 m) was above the most intense pruning treatment height (7 m) thus mainly dead branches would have been pruned, and there was no significant pruning effect on tree size or size of various aboveground biomass components.</td>
</tr>
<tr>
<td>18</td>
<td><em>Eucalyptus nitens</em></td>
<td>50</td>
<td>75</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Planted at 1000 trees ha⁻¹. Pruned 50% of live-crown length (75% of leaf area) at age 3.2 years, when trees were about 9 m tall. Then a second lift of 50% of live-crown length (72% of leaf area) at 4.7 years. A thinning treatment was also included where stands were thinned at 3.2 years to 300 trees ha⁻¹.</td>
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<td></td>
<td>Pruning reduced growth of SCTs, especially in thinned stands. Pruned trees intercepted less light and had lower levels of transpiration but were more light- and water use efficient, and also had higher light-saturated rates of photosynthesis than unpruned trees.</td>
</tr>
<tr>
<td>19</td>
<td><em>Eucalyptus nitens</em>, <em>Eucalyptus globulus</em> and <em>Eucalyptus grandis</em></td>
<td>30%</td>
<td></td>
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<tr>
<td></td>
<td>Planted at 1100-1300 trees ha⁻¹ and thinned between ages 2.5 to 4.2 years to either 300 or 500 trees ha⁻¹. Pruned in multiple lifts to confine the knotty core to 10, 15 or 20 cm diameter.</td>
<td></td>
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<td></td>
<td>Pruning only influenced SCT volume at the lowest quality site and there its influence increased as thinning intensity increased.</td>
</tr>
<tr>
<td>20</td>
<td><em>Pinus patula</em> (Mexican Weeping Pine)</td>
<td>25</td>
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</tr>
<tr>
<td></td>
<td>Pruned 25, 50 or 75% of live-crown length at age 4-5 years. Plots were also thinned from 1680 down to 150, 250, 750 or 1500 trees ha⁻¹.</td>
<td></td>
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<td></td>
<td>By age 14 years in the unthinned plots pruning 25% of live-crown length reduced growth. At other densities, significant reductions in height and diameter growth occurred where more than 40% of the live-crown length had been pruned. In all treatments there was a reduction in the dominance class of pruned trees relative to unpruned trees.</td>
</tr>
<tr>
<td>21</td>
<td><em>Pinus patula</em></td>
<td>25</td>
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<tr>
<td></td>
<td>On four sites trees were pruned to 25, 50 or 75% of tree height and thinned to 620 or 740 ha⁻¹ between the ages of 4 and 9 years.</td>
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<td></td>
<td>All treatments reduced diameter growth and the reduction increased with pruning intensity. By age 12 years diameter increment was only significantly lower in the 75% treatment and mean diameter was significantly lower in the 50% and 75% treatments. Height was reduced only in 50 and 75% treatments. By age 12 years average height was only significantly different in the 75% treatment.</td>
</tr>
<tr>
<td>22</td>
<td><em>Pinus caribaea</em> (Caribbean Pine)</td>
<td>25</td>
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<tr>
<td></td>
<td>On three sites trees were pruned to 25, 50 or 75% of tree height and thinned to between 740 and 1090 ha⁻¹ between the ages of 4.5 and 7.5 years.</td>
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<tr>
<td>23</td>
<td><em>Pinus taedea</em> (Loblolly Pine)</td>
<td>25</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Pruned to 25, 50 or 75% of tree height and thinned to between 740 and 1124 trees ha⁻¹ and ages ranged from 4 to 6 years.</td>
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<tr>
<td>24</td>
<td><em>Pinus taedea</em></td>
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<tr>
<td></td>
<td>Trees were either unpruned or pruned to 5 m at age 15 years in stands planted at 308, 568 or 932 trees ha⁻¹.</td>
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<td></td>
<td>By age 19 years diameter, height and biomass partitioning were not affected by pruning.</td>
</tr>
<tr>
<td></td>
<td><strong>Pinus patula</strong></td>
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<tr>
<td>25</td>
<td>Pruned 28, 49 or 72% live-crown length at age 8 years. Thinned to about 250 trees ha$^{-1}$.</td>
<td>Diameter increment was suppressed for 3 years in the most intense treatment but recovered by age 11 years. By 11 years diameter in the 72% treatment was still lower than that of other treatments. Height increment appeared to be affected for 1 year after pruning but by 11 years mean height was similar in all treatments.</td>
<td>(Adlard, 1969)</td>
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<thead>
<tr>
<th></th>
<th><strong>Pinus radiata</strong> (Monterey Pine)</th>
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<tbody>
<tr>
<td>26</td>
<td>Pruned between 20 and 80% of live-crown length in 1 to 4 lifts in unthinned stands planted at 2300 trees ha$^{-1}$.</td>
<td>Removing over 40% resulted in significant loss in dominance, height and basal area growth.</td>
<td>(Sutton and Crowe, 1975)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th><strong>Pinus radiata</strong></th>
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</thead>
<tbody>
<tr>
<td>27</td>
<td>Pruned up to about 2 m at age 4 years when trees were between 4.4 and 6.8 m tall. Trees were either grown with an understorey of lucerne (<em>Medicago sativa</em>) or with no understorey. Stand was thinned from 1000 to 800 to 600 to 400 trees ha$^{-1}$ at ages 2, 3 and 4 years respectively.</td>
<td>At age 5 years pruning had reduced biomass increment by 27% with no understorey and 16% with an understorey. Pruning did not affect the partitioning of aboveground biomass to foliage, branches or stem wood. Foliage production of unpruned trees was affected more by water deficit than pruned trees.</td>
<td>(Bandara et al., 1999)</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th></th>
<th><strong>Pinus resinosa</strong> (Red Pine)</th>
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</thead>
<tbody>
<tr>
<td>28</td>
<td>At ages 2, 4 or 11 years, pruning removed 0, 25, 33, 50, 66 or 75% of foliage mass.</td>
<td>Conductance and net rates of photosynthesis increased after defoliation especially in 25-50% treatments until foliage mass was restored. Growth was reduced in treatments with a severity of 50% or more.</td>
<td>(Reich et al., 1993)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th><strong>Pinus sylvestris</strong> (Scots Pine)</th>
<th></th>
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</thead>
<tbody>
<tr>
<td>29</td>
<td>Pruned 0, 1-20, 20-40, 40-60 or 60-100% of live-crown length.</td>
<td>3 years after pruning diameter and volume growth was lower in pruned plots than in unpruned plots. Height growth was not significantly influenced by pruning.</td>
<td>(Långström and Hellqvist, 1991)</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th></th>
<th><strong>Pinus sylvestris</strong></th>
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</tr>
</thead>
<tbody>
<tr>
<td>30</td>
<td>Pruned 0, 1-20, 20-40, 40-60 or 60-100% of live-crown length. Pruned between ages 15 and 50 years when trees were 5.6 to 7.8 m tall. Planted at 2000 trees ha$^{-1}$.</td>
<td>After 5 years diameter growth was significantly lower when 40% or more of the canopy had been removed. Significant reductions in height growth occurred when pruning intensity was 60% or more.</td>
<td>(Uotila and Mustonen, 1994)</td>
</tr>
</tbody>
</table>
Table 2. Thinning responses in *Eucalyptus* plantations

<table>
<thead>
<tr>
<th>Study Number</th>
<th>Location</th>
<th>Species</th>
<th>Thinning treatments (including age thinned)</th>
<th>Response or regime description</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Goulds Country, St Helens, Tasmania, Australia</td>
<td><em>E. nitens</em></td>
<td>Thinned at age 6 years from 890 to 100, 200, 300 or 400 trees ha⁻¹</td>
<td>By age 12 years cumulative basal area increments of the best 100, 200, 300 and 400 trees ha⁻¹ were greater than equivalent numbers of trees in unthinned controls. There was no difference in increments of the best 100 trees ha⁻¹ in the 100 and 200 treatments. The best 200 in the 200 treatment were greater than those in the 300 and 400 treatments. Height increments were not affected but live-crown depths were increased by thinning. By age 21 years the individual tree size of SCTs increased with increasing thinning intensity. There was no significant effect on mean dominant height. Total stand volume was lower in the 100 treatment.</td>
<td>(Medhurst et al., 2001; Wood et al., 2011)</td>
</tr>
<tr>
<td>2</td>
<td>Hastings, Geestown, Tasmania, Australia</td>
<td><em>E. nitens</em></td>
<td>Thinned at age 3 years from 1250 to 100, 200, 300 or 400 trees ha⁻¹</td>
<td>By age 6 years volume growth of best 300 and 400 trees ha⁻¹ was increased by thinning but the best 100 or 200 trees ha⁻¹ did not show a significant response (although there was a trend that growth was slowing in the control plots).</td>
<td>(Gerrand et al., 1997b)</td>
</tr>
<tr>
<td>3</td>
<td>Creekton, Dover, Tasmania, Australia</td>
<td><em>E. nitens</em></td>
<td>Thinned at age 8 years from 1254 to 100, 250 or 600 trees ha⁻¹</td>
<td>There was no significant response in basal area growth of the top 100, 250 or 600 trees ha⁻¹ compared to equivalent trees in the control. Height increments were not affected but live-crown depths were increased by thinning.</td>
<td>(Medhurst et al., 2001)</td>
</tr>
<tr>
<td>4</td>
<td>Lisle, Scottsdale, Tasmania, Australia</td>
<td><em>E. nitens</em></td>
<td>Thinned at age 9 years from 1038 to 100, 250 or 600 trees ha⁻¹</td>
<td>By age 11 years cumulative basal area increments of the best 100 trees ha⁻¹ in the 100, 250 and 600 treatments were greater than those in the control. That of the best 250 trees ha⁻¹ in the 250 treatment was greater than those in the 600 and unthinned treatment. That of the best 600 trees ha⁻¹ in the 600 treatment were greater than the unthinned. Height increments were not affected but live-crown depths were increased by thinning.</td>
<td>(Medhurst et al., 2001)</td>
</tr>
<tr>
<td>5</td>
<td>Region X, Chile</td>
<td><em>E. nitens</em></td>
<td>Initial stocking of 1333 to 1600 trees ha⁻¹. Thin in 3 to 7 steps to 200-400 trees ha⁻¹ starting at age 5 with the latest thin at between age 9 and 13 years. Prune in 2 to 4 lifts starting at 2 to 3 years old and going up to between 7 and 12 m by age 5.5 years (no dead branches pruned).</td>
<td></td>
<td>Valencia, 2008</td>
</tr>
<tr>
<td>6</td>
<td>Los Alamos, Arauco, Chile</td>
<td><em>E. nitens</em></td>
<td>Planted at 1429 trees ha⁻¹. Pruned and thinned at age 6 years when average live-crown height was 8.1 m. Thinned to 400, 800 or unthinned (1100 by age 6 years) trees ha⁻¹. Pruned to 0, 3.5 and 7 m.</td>
<td>By age 15 years, growth and the size of each biomass component increased with thinning intensity. However, such comparisons are difficult to interpret because dominance classes were not differentiated so the treatments effects may have been influenced by the additional smaller trees retained in the unthinned treatments.</td>
<td>(Muñoz et al., 2008)</td>
</tr>
<tr>
<td>7</td>
<td>Carrajung, Australia</td>
<td><em>E. nitens</em></td>
<td>Planted at 1000 trees ha⁻¹, but 900 trees ha⁻¹ when thinning was done at age 3.2 years down to 300 trees ha⁻¹. Also included unpruned or pruning 50% of the live-crown length, and not fertilised or application of 300 kg ha⁻¹ of N fertiliser.</td>
<td>Thinning significantly increased the SCT growth by increasing crown sizes, especially lower crowns, which then increased light interception and transpiration of individual trees. SCTs in thinned stands also had higher light availabilities in their lower crowns, higher rates of photosynthesis and were more light- and water-use efficient.</td>
<td>(Forrester et al., 2012b; Forrester et al., 2012c; Forrester et al., 2013)</td>
</tr>
<tr>
<td>8</td>
<td>Shepparton, Buffalo River and Mangalore, Australia</td>
<td><em>E. nitens</em>, <em>E. globulus</em> and <em>E. grandis</em></td>
<td>Planted at 1100-1300 trees ha⁻¹ and thinned between ages 2.5 to 4.2 years to either 300 or 500 trees ha⁻¹. Pruned in multiple lifts to confine the knotty core to 10, 15 or 20 cm diameter.</td>
<td>Thinning increased the growth of SCTs in each experiment, usually to a greater degree as thinning intensity increased. Thinning responses increased with increasing site quality.</td>
<td>(Forrester and Baker, 2012; Forrester et al., in press)</td>
</tr>
<tr>
<td>Location</td>
<td>Species</td>
<td>Description</td>
<td>Thinning Effects</td>
<td>Reference</td>
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<tr>
<td>Bradvale and Rennick,</td>
<td><em>E. globulus</em></td>
<td>Planted at 1000 trees ha⁻¹. Thinned at age 5 years to about 300, 400 or 500 trees ha⁻¹.</td>
<td>Thinning increased the growth of SCTs in each experiment, usually to a greater degree as thinning intensity increased. Thinning responses increased with increasing site quality.</td>
<td>(Forrester et al., in press)</td>
<td></td>
</tr>
<tr>
<td>Tostaree, Australia</td>
<td><em>E. globulus</em> and <em>E. nitens</em></td>
<td>Planted at 1000 trees ha⁻¹. Thinned at age 7.5 years to about 300 or 500 trees ha⁻¹.</td>
<td>Thinning increased the growth of SCTs in each experiment, usually to a greater degree as thinning intensity increased. The larger size-classes had the largest thinning responses.</td>
<td>(Forrester and Baker, 2012; Forrester et al., in press)</td>
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</tr>
<tr>
<td>Yallourn North and Dargile, Australia</td>
<td><em>E. globulus</em> and <em>E. tricarpa</em> (Red Ironbark)</td>
<td><em>E. globulus</em> planted at 1000 trees ha⁻¹ and thinned at age 10 years to about 400 trees ha⁻¹. <em>E. tricarpa</em> planted at 1700 trees ha⁻¹ and thinned at age 62 years down to about 130 trees ha⁻¹.</td>
<td>Thinning increased the basal areas of SCTs but only in plots where coppice competition was controlled. When coppice was allowed to grow on the cut stumps there was no thinning response in the <em>E. globulus</em> plantation and the thinning response in the <em>E. tricarpa</em> plantation was reduced.</td>
<td>(Forrester et al., 2012a)</td>
<td></td>
</tr>
<tr>
<td>Tasmania, Australia</td>
<td><em>E. globulus</em> and <em>E. nitens</em></td>
<td>Plant at about 1111 trees ha⁻¹ and thin commercially to about 300 trees ha⁻¹ at ages 8 to 12 years. Alternatively, non-commercially thin to 300 trees ha⁻¹ at ages 5 to 6 years on sites prone to windthrow, drought or other problems influenced by stocking. Prune in 3 lifts to 2.4, 4.5 and 6.4 m at ages 3-4, 4-5 and 5-6 years, respectively. Clearfell at 20 to 25 years.</td>
<td>Growth of crop trees (best 200 trees ha⁻¹) in thinned plots was similar but was significantly greater than that of equivalent trees in the unthinned stand. Growth of crop trees and stand basal areas and volumes were similar in thinned plots even though they had been growing at different densities from age 4 to 11 years. Dominant height (largest 100 trees ha⁻¹) was significantly lower in plots thinned at age 4 years to 220 trees ha⁻¹.</td>
<td>(Neilsen, 1990)</td>
<td></td>
</tr>
<tr>
<td>Werribee, Melbourne,</td>
<td><em>E. globulus</em></td>
<td>Early thinning at age 4 years from 1330 to 220 or 670 trees ha⁻¹. The latter treatment was thinned to 220 trees ha⁻¹ at age 11 years. An unthinned control treatment had 2500 trees ha⁻¹.</td>
<td>Growth of crop trees (best 200 trees ha⁻¹) in thinned plots was similar but was significantly greater than that of equivalent trees in the unthinned stand. Growth of crop trees and stand basal areas and volumes were similar in thinned plots even though they had been growing at different densities from age 4 to 11 years. Dominant height (largest 100 trees ha⁻¹) was significantly lower in plots thinned at age 4 years to 220 trees ha⁻¹.</td>
<td>(Forrester and Baker, 2007)</td>
<td></td>
</tr>
<tr>
<td>Fumin, Yunnan, China</td>
<td><em>E. maidenii</em> (Maiden’s Gum)</td>
<td>Thinned at age 7.5 years from 1666 to 996 or 600 trees ha⁻¹.</td>
<td>Thinning significantly reduced stand basal area and volume. Total volume increment to age 10.5 years was similar in thinned and unthinned plots, but the increment of the largest 200 trees ha⁻¹ was greater in the 600 treatment than in other treatments. Thinning did not influence height increment.</td>
<td>(Zhang et al., 2003)</td>
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</tr>
<tr>
<td>Australia</td>
<td><em>E. saligna</em>, <em>E. nitens</em>, <em>E. globulus</em></td>
<td>Plant at about 1000 trees ha⁻¹ and thin to less than 150 trees ha⁻¹ by age 6 years. Prune to at least 6.5 m. Clearfell by about 20 years. Often co-cropped with pasture.</td>
<td>Mean diameters and heights increased with higher thinning intensities, earlier commencement and higher frequency of thinning. Effects on diameter were greater than those on height, but both increased with increasing intensity, frequency and earlier commencement dates of thinning. The MAI was only reduced by the more intense and frequent treatments.</td>
<td>(Hingston, 2007; Moore, 2008)</td>
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<tr>
<td>Cramond, Natal, South</td>
<td><em>E. grandis</em></td>
<td>Factorial design with 4 factors: intensity, commencement, frequency and final stocking. Initial stocking was 1329 trees ha⁻¹ and thinning commenced at age 4, 5 or 6 years.</td>
<td>Mean diameters and heights increased with higher thinning intensities, earlier commencement and higher frequency of thinning. Effects on diameter were greater than those on height, but both increased with increasing intensity, frequency and earlier commencement dates of thinning. The MAI was only reduced by the more intense and frequent treatments.</td>
<td>(Schöna, 1982, 1984a)</td>
<td></td>
</tr>
<tr>
<td>No.</td>
<td>Location/Region</td>
<td>Species</td>
<td>Planting Details</td>
<td>Thinning Details</td>
<td>Growth and Development Notes</td>
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<tr>
<td>17</td>
<td>Waipua, New Zealand</td>
<td><em>E. saligna</em></td>
<td>Planted at 2315 trees ha(^{-1}), and thinned to 760 trees ha(^{-1}) at age 5 years. Thinned to 100, 200 or 400 trees ha(^{-1}) at age 7 years. At age 10 years the 400 treatment was thinned to 200 trees ha(^{-1}).</td>
<td>Height growth was slower in the more intense and frequent thinning treatments. Diameter growth was higher in the more intense treatments. More intense thinning also led to larger branches and deeper live crowns.</td>
<td>(Williamson, 1979)</td>
</tr>
<tr>
<td>18</td>
<td>Rivera region, Uruguay</td>
<td><em>E. grandis</em></td>
<td>Plant at about 1000 trees ha(^{-1}). Thin in 3 steps to 400-450, 200 and 130 trees ha(^{-1}) at ages 1.5-2, 9 and 12 years, respectively. Prune in 5 lifts to 2.3, 4.5, 6.5, 8.5 and 10.5 m at ages 1.5-2, 2-2.5, 2.5-3, 3-4, 4.5-5 years, respectively to achieve a diameter over stubs of 12, 12, 13, 15 and 16 cm, respectively. The number of trees ha(^{-1}) pruned in was 400-450 until last lift when 200 were given the final lift.</td>
<td>Rotation length is about 18 years.</td>
<td>SGS Qualifor., 2005a</td>
</tr>
<tr>
<td>19</td>
<td>Virasoro and Ciriaco area, Argentina</td>
<td><em>E. grandis</em></td>
<td>Plant at about 625 trees ha(^{-1}). Prune in 3 lifts to 3, 6 and 9 m at ages 1.5, 2.5 and 3 years, respectively. Prune 500, 350 and 250 trees ha(^{-1}). Thin in 3 steps to 500, 350 and 250 trees ha(^{-1}) at ages 1.5, 4.5-5 and 7-8 years, respectively.</td>
<td></td>
<td>SGS Qualifor, 2005b</td>
</tr>
<tr>
<td>20</td>
<td>Koolau Forest Reserve, Hawaii</td>
<td><em>E. saligna</em></td>
<td>Thinned at age 6 years from a basal area of about 23 m(^2) ha(^{-1}) (1111 trees ha(^{-1})) to 19.5 or 16 m(^2) ha(^{-1}).</td>
<td>Diameter growth of crop trees (largest 100 trees ha(^{-1}) at age 9.5 years) increased more in the 350 than the 150 treatment. Height growth of crop trees was reduced by thinning. However, average height of all trees increased with thinning intensity. Proportion of total height that was live crown (Live-crown ratio) was increased by thinning for crop trees. Stand volume and volume increment of crop trees was highest in the 350 treatment.</td>
<td>By age 12 years there were no effects of thinning on growth rates. Although these thinning intensities were all relatively light, with even the most intense thinning leaving about 600 trees ha(^{-1}).</td>
</tr>
<tr>
<td>21</td>
<td>Kaingaroa Forest, near Murupara, New Zealand</td>
<td><em>E. regnans</em> (Mountain Ash)</td>
<td>Initial stockings of 2500, 1111, 625 trees ha(^{-1}). Thinned between ages 5 and 11.8 years with final stockings of 2500 0911 after mortality by 19 years), 400, 300, 100 and 50 trees ha(^{-1}).</td>
<td>At age 19 years diameter (but not height) of dominant trees was greater in treatments thinned to lower stockings, the greatest response coming from thinning to low stockings at early ages. By 19 years the growth rates of dominants was not significantly different between treatments.</td>
<td></td>
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<tr>
<td>22</td>
<td>Near Lake Waipapa, New Zealand</td>
<td><em>E. regnans</em></td>
<td>Thinned from about 1167 (had self thinned from 1667) to 150 or 350 trees ha(^{-1}) at age 7 years.</td>
<td>Diameter growth of crop trees (largest 100 trees ha(^{-1}) at age 9.5 years) increased more in the 350 than the 150 treatment. Height growth of crop trees was reduced by thinning. However, average height of all trees increased with thinning intensity. Proportion of total height that was live crown (Live-crown ratio) was increased by thinning for crop trees. Stand volume and volume increment of crop trees was highest in the 350 treatment.</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>North-eastern NSW (1 site) and south-eastern QLD (2 sites), Australia</td>
<td><em>E. dunnii</em> and <em>Corymbia citriodora</em> ssp. variegata</td>
<td>Planted at 1000-1300 trees ha(^{-1}). Thinned at about age 7 years to 500 or 300 trees ha(^{-1}).</td>
<td>Two years after thinning the basal area increments of the largest 250 trees ha(^{-1}) were largest in thinned stands, especially in the 300 treatment. Absolute basal area responses were higher at the higher quality sites but relative responses were similar at both site qualities.</td>
<td></td>
</tr>
</tbody>
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