Tree growth-competition relationships in thinned *Eucalyptus* plantations vary with stand structure and site quality

David I. Forrester, Stephen R. Elms, Thomas G. Baker

David I. Forrester

Department of Forest and Ecosystem Science, The University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia; Cooperative Research Centre for Forestry, Private Bag 12, Hobart 7001, Australia; and Institute of Silviculture, Freiburg University, D-79085 Freiburg, Germany. Email: davidif@unimelb.edu.au

Stephen Elms

HVP Plantations, 50 Northways Road, Churchill, VIC 3842, Australia; and Cooperative Research Centre for Forestry, Private Bag 12, Hobart 7001, Australia

Thomas G. Baker

Department of Forest and Ecosystem Science, The University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia; and Cooperative Research Centre for Forestry, Private Bag 12, Hobart 7001, Australia

Abstract

Growth responses to thinning can vary with site quality and age, however the direction of the response varies. An understanding of the mechanisms behind thinning responses could help forest managers optimise production as well as inform modellers and ecologists about the functioning of tree stands. Thinning was used to create a range of stand densities in eleven *Eucalyptus* plantation stands on seven sites in south-eastern Australia. Basal area periodic annual increment (PAI; $\text{cm}^2 \text{year}^{-1}$) of individual dominant and codominant trees was then related to competition, such that $\text{PAI} = a + b \ln(\text{Competition})$. Competition was defined as the sum of the basal area of neighbouring trees within a radius of 6.5 m. The relative (%) and absolute ($\text{cm}^2 \text{year}^{-1}$) responses to competition were quantified using b , which was correlated with site quality and stand structure of unthinned stands. Stand structure was quantified using statistics or parameters that describe the diameter distribution for the given age, species and site, including skewness, the coefficient of variation and parameters of the Weibull probability distribution. Relative and absolute responses both increased with increasing site quality and in stands with more

negatively skewed diameter distributions (higher proportion of larger trees) or lower coefficients of variation. Absolute thinning responses often increased with increasing size class, while relative thinning responses often decreased. Variables describing diameter distributions (size-class structure) were able to describe some of the variation in competition responses that site quality could not. This indicates why stands on similar site qualities but with different stand structures can have correspondingly different thinning responses. Stand structural variables may be more useful predictors of thinning responses in stands that experience large temporal changes in diameter distributions compared with site quality, which is a more static variable. Thus, knowledge about the development of diameter distributions might help to refine thinning regimes.

Keywords: Eucalyptus globulus; Eucalyptus grandis; Eucalyptus nitens; fertilizer; competition symmetry; Weibull distribution; diameter distribution

Introduction

Thinning can be used to increase growth rates of remaining trees, reduce forest water use and drought stress, and improve resistance to pests and diseases (Bréda et al. 1995; Kolb et al. 2007; Forrester et al. 2010; Forrester et al. 2012b). For a given species, relative and absolute thinning responses can vary with resource availability (e.g. site quality or fertilizer application), size class and thinning age (Medhurst et al. 2001; Mäkinen and Isomäki 2004b). Site or fertilizer effects can be related, at least in part, to how they influence the symmetry of competition between trees. Competition for below-ground resources is often considered to be relatively symmetric (Weiner 1985; 1986; Hara 1993). Assuming below-ground resource uptake is proportional to fine-root surface area, a tree that is twice as large as its neighbour will obtain twice as much of the resource. In contrast, competition for light is more asymmetric because taller plants can shade smaller plants more than vice versa so a tree that is half the size of its neighbour may absorb much less than half as much light (Weiner 1985; 1986; Hara 1993; Kikuzawa and Umeki 1996).

In the context of thinning, the larger retained trees often have a greater absolute response on higher quality sites, or where fertilizer is applied, compared with large trees on lower quality sites or where fertilizer is not applied (Stoneman et al. 1996; Ruha and Varmola 1997; Mäkinen and Isomäki 2004a), but their relative thinning response can be smaller (Harrington and Wierman 1990; Messina 1992; Brockley 2005). This relative response could be expected because on higher quality sites, water and nutrients are not as limiting to growth relative to light, and since dominant trees already obtain the most light, removing smaller competing trees has a relatively smaller effect. 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 growth of the larger trees. However, there are cases where relative responses increased with

increasing site quality or with rate of fertiliser application (Stoneman et al. 1996; Mäkinen and Isomäki 2004a; La Sala 2006), due to greater increases in leaf area index and basal area growth per unit leaf area index in fertilised stands than in unfertilised stands (Stoneman et al. 1996), and cases where there were no obvious trends (Messina 1992; Blevins et al. 2005; Omule et al. 2011). Therefore there are clearly factors in addition to site quality that influence these responses.

Application of the same theory about the symmetry of competition also suggests that relative, but not absolute, thinning responses by dominant trees are smaller than intermediate trees, and that this difference increases as stands age and dominance classes become more pronounced. Relative responses declined with increasing size class in *Pseudotsuga menziesii*, *Betula papyrifera* and heavily thinned *Pinus sylvestris* stands (Moore et al. 1994; Pukkala et al. 1998; Mäkinen and Isomäki 2004b; Simard et al. 2004). Conversely, absolute responses to thinning of even-aged stands often increase with increasing size class, with the larger and faster growing trees responding the most to thinning (Ruha and Varmola 1997; Medhurst et al. 2001; Mäkinen and Isomäki 2004b). Similarly, absolute and relative thinning responses will likely be greater when thinning is done close to the peak current annual volume increment, and eventually decline as growth rates decrease as stands age and trees differentiate into more size classes (Ruha and Varmola 1997; Mäkinen and Isomäki 2004b; a).

Thus site quality, size class and age all appear to influence thinning responses. However, the lack of consistent trends, even for a given species, suggests that other stand characteristics might also be indicators of responses to thinning. If symmetry of competition influences these responses, then information about stand structure is likely to be useful. For example, when diameter distributions are positively skewed and there is a high proportion of smaller trees in the stand, larger trees are already relatively free of competition and therefore less responsive to thinning than in stands that are negatively skewed where many large trees are competing with each other. Parameters that describe diameter distributions have proven useful in growth models (Peng 2000; Álvarez González et al. 2002; Lasch et al. 2005; Nord-Larsen and Cao 2006; Wang et al. 2011). These models account for the skewness, kurtosis and variability of the diameter distributions, often by including parameters that describe the shape and scale of the Weibull distribution. These parameters can vary with fertility and age (Nord-Larsen and Cao 2006) and may be able to capture the information required to predict thinning responses.

The aim of this study was to determine whether absolute and relative responses to reductions in competition in *Eucalyptus* plantations are related to (1) stand structure quantified in terms of the

shape of the diameter distribution of unthinned stands as described by skewness, kurtosis, coefficient of variation (CV) and parameters of the Weibull distribution of tree diameters, and (2) if so, whether size-class structure is more closely related to competition responses than are site quality and stand age? A third aim was (3) to determine which size classes have the greatest absolute and relative responses.

Methods

Field experiments comprising combinations of seven sites and three species (*E. globulus*, *E. nitens*, *E. grandis*) were established between 1991 and 2003 in Victoria, Australia (Table 1) to examine plantation growth and yield responses to thinning treatments.

Site characteristics

Across the sites: (i) the means of daily minimum and maximum temperatures vary between 2-5°C and 11-14°C respectively in July, and 10-14°C and 23-30°C respectively in January, (ii) mean annual pan evaporation varies from 1132 to 1500 mm, and (iii) mean annual rainfall varies from 483 to 1178 mm. The Mangalore and Shepparton experiments were irrigated at rates of about 300 and 730 mm year⁻¹ respectively. The previous land use at the Carrajung and Rennick sites was *E. regnans* and *Pinus radiata* plantations, respectively, and at all other sites was pasture. Site quality was quantified as the mean annual volume increment (MAI; m³ ha⁻¹ year⁻¹) of unthinned stands at age 10 years (MAI₁₀; see Table 1). The sites were ranked in potential productivity: Carrajung > Shepparton > Buffalo River = Rennick > Tostaree = Mangalore > Bradvale, varying from 7 to 37 m³ ha⁻¹ year⁻¹.

Establishment and experimental treatments

The experiments were planted at 1000 to 1300 trees ha⁻¹ with container grown seedling stock. Establishment involved: (i) soil deep ripping and bedding (Rennick was not deep-ripped), (ii) weeding using pre-planting (all sites) and post-planting (Shepparton and Tostaree) application of knock-down and pre-emergent herbicides, and (iii) fertiliser application to each seedling within 12 months of planting (equivalent to 0-280 kg ha⁻¹ N, 18-110 kg ha⁻¹ P, 0-67 kg ha⁻¹ K).

All experiments contained an unthinned reference and one, two or three thinning treatments which retained approximately 300, 400 or 500 trees ha⁻¹ (Table 2). All experiments were arranged in

randomized block designs with three replicates. Retained trees were selected on form (i.e. single-stemmed, straight, vertical), size (larger diameters), and spacing (uniformity) criteria, immediately prior to thinning. Thinning was carried out at canopy closure (Buffalo River, Mangalore and Shepparton), up to six months post-canopy closure (Bradvale and Carrajung) or about one (Rennick) and four (Tostaree) years post-canopy closure. Any coppice that grew on the stumps of thinned trees was removed annually. The main treatment plots of 0.12 - 0.15 ha contained internal tree measurement plots of 0.07-0.12 ha. More details about the experimental designs are presented in Stackpole et al. (2004), Forrester and Baker (2012) and Forrester et al. (2012a). Fertilizer application treatments were also included at Carrajung where either nil or 300 kg ha⁻¹ N was applied in a factorial design at the same time as thinning (age 3.2 years). Fertiliser application treatments were also applied at Tostaree but the effects were not significant and the treatments are combined in the present study.

Growth measurements and statistical analyses

Tree diameter over bark at 1.3 m height (cm) was measured for 6673, 3423 and 1507 *E. globulus*, *E. nitens* and *E. grandis* trees, respectively, two to four times and the positions of all trees were mapped. Trees were grouped into three main size-classes based on diameter; largest-diameter 200 trees ha⁻¹ (D_{200}), the next largest 200 ($D_{200-400}$) and then the next largest 200 ($D_{400-600}$).

The growth of individual trees was quantified as basal area periodic annual increment (PAI; cm² year⁻¹). The effects of competition, as affected by thinning, on PAI were examined on an individual tree level. This enabled a wider range, and higher number, of competition intensities to be examined than would be possible at the stand level where there were at most four thinning treatments, including an unthinned reference. A greater number of competition intensities at the tree level results from differences in relative tree sizes and spacing, and because the buffers between treatments can be used to provide intermediate conditions. Individual tree PAI was described as a function of local competition:

$$\text{Basal area PAI} = \text{Constant} + \text{Slope} \ln(\text{Competition}), \quad (1)$$

where competition is a competition index. Many competition indices have been used to quantify individual tree growth (e.g. Biging and Dobbertin, 1992). These often consider the number and size of neighbours, where size might be quantified as tree diameter, basal area, volume, biomass, height

or crown size. Several approaches are also used to determine which trees are competitors, e.g. a fixed radius from the focal tree, or whether neighbouring tree crowns are inside an inverted cone above the focal tree (Biging and Dobbertin, 1992; Pretzsch, 2009, p. 293). Potential asymmetry of competition is sometimes accounted for by considering whether the focal tree is larger or smaller than its competitors. In this study, competition was relatively symmetric, as indicated by linear relationships between individual tree basal areas and their PAIs (Hara 1993) (data not shown). Competition was quantified as the sum of the basal areas (cm^2) of neighbouring trees within a radius, r , of a focal tree. This very simple distance-dependent index was used because it can be calculated quickly and easily by foresters and its simplicity facilitates interpretation. The optimal radius was determined using least squares where the coefficient of determination (R^2) of the relationship between PAI and competition was regressed against r using the method described by Vanclay (2006) and Forrester et al. (2011) in Simile v4.7 (Simulistics, www.simulistics.com). The competition was recalculated along a continuous range of r until the maximum R^2 was found. All trees within a two-tree buffer of the edge of the plots were considered competitors of focal trees but not as focal trees themselves. The optimal r was often about 6.5 m, so this radius was used for all species and sites. This is similar to the 5-m radius that was found to be optimal in another *E. globulus* plantation (Forrester et al. 2011). For the fitting of Equation 1 competition was ln-transformed so that the relationship was linear, to satisfy assumptions of normally distributed residuals and to remove heteroscedasticity. To compare the responses of different size classes, size class was added as a dummy variable to Equation 1 (see Figure 1).

Absolute PAI competition responses were calculated for each experiment and increment period using the fitted Equation 1 (Table 3) and for a reduction in competition from 3000 to 800 cm^2 . The relative response was this value relative to the PAI at competition = 3000 cm^2 , expressed as a percentage. Similarly, the Slope of Equation 1 can be used as a measure of the competition responses. Therefore, the effects of size-class structure and site quality on competition responses were quantified by examining the relationships between the Slope and MAI₁₀, or the parameters used to describe the size-class structure of diameter distributions at the start of the given basal area growth period.

Size-class structure was quantified as the skewness, kurtosis and coefficient of variation of the diameter distribution of unthinned treatments at each age, species and site. The shape (α) and scale (β) parameters of the cumulative distribution function for the Weibull distribution were also used, such that

where y is the cumulative proportional frequency of diameters in each 2-cm class ($0 \leq y \leq 1$) and x is the midpoint of the 2-cm diameter class expressed as a proportion ($0 \leq x \leq 1$) of the maximum size-class. All statistical analyses were performed in Genstat™ (VSN International Ltd, Hemel Hemstead, U.K.).

Results

Basal area PAI declined with increasing competition at all sites (Figure 1; Table 3), although at Tostaree this relationship was often not significant. PAI-competition relationships were influenced by size class for all sites and species, such that for a given level of competition, basal area increment increased with increasing size-class (Figure 1). Absolute responses to reducing competition from 3000 to 800 cm² were similar for each size class or increased with increasing size-class from $D_{400-600}$ to $D_{200-400}$ to D_{200} (Figure 1). Relative competition responses were more variable, usually declining with increasing size-class, except for *E. nitens* at Buffalo River and *E. globulus* at Shepparton where it increased with increasing size-class. This resulted from a very small thinning response by the smaller size-classes at these sites (Figure 1d,e).

The Slope of the relationship between basal area PAI and ln Competition (Equation 1) was used to model competition responses of D_{200} (Figure 2). Absolute responses ranged from about 3 to 63 cm² year⁻¹ and relative responses from 11 to 136% when comparing the basal area increments of trees growing with a competition of 3000 cm² with those experiencing only 800 cm². This analysis was only done for D_{200} trees because these are usually the most economically important in thinned *Eucalyptus* plantations and because the lowest levels of competition did not often exist for smaller size classes, which had been thinned out of more intensively thinned plots.

Competition responses were correlated with site quality and size-class structure. The Slope of Equation 1 was negatively correlated with site quality (MAI₁₀) (Figure 3a; Table 4). Based on this relationship and the trends shown in Figure 2, the absolute and relative thinning responses generally increased with increasing site quality. The Slope was also negatively correlated with the Weibull parameters and positively correlated with the skewness and coefficient of variation of unthinned stands at the start of the given basal area growth period (Figure 3b-e; Table 4). Thus competition

responses were higher in stands that were more negatively skewed (higher proportion of large trees) and less variable. The Slope was not correlated with kurtosis ($P > 0.05$).

Generally as site quality increased, unthinned *E. nitens* stands were more negatively skewed and less variable (Figure 4). The same variables were not correlated for *E. globulus* stands. Size-class structure statistics and parameters (skewness, coefficient of variation, kurtosis or the Weibull parameters) did not change with age (data not shown). However, since site quality and size-class structure were both correlated with competition responses but not necessarily with each other, it appears as though these variables describe different, but useful information for predicting thinning responses. Multiple linear regressions were used to examine whether pairs of variables could be combined to increase the goodness of fit of models used to estimate the Slope of Equation 1, and hence the thinning response. The highest goodness of fit was obtained with Weibull- β and either MAI₁₀, the coefficient of variation, or Weibull- α (Adj $R^2 \geq 0.57$; Table 4). Examples of diameter distributions with a range of MAI₁₀, skewness and coefficients of variation are shown in Figure 5a-c. These are representative of high, medium and low competition (or thinning) responses shown in Figure 2.

Discussion

Absolute and relative competition responses of D_{200} were correlated with site quality and size-class structure. Even though size-class structure was related to site quality for *E. nitens* this was not the case for *E. globulus*, and for both species, site quality and size-class structure complemented each other to more accurately describe the stand conditions that influenced competition responses. Absolute and relative responses by D_{200} both increased with increasing site quality, in more negatively skewed, and more uniform stands.

Competition between trees is influenced by tree size, spacing and resource availability, and this study indicates that information about stand structure in terms of diameter distributions, as well as site quality, may be a useful way to summarise that information in order to predict thinning responses in *Eucalyptus* plantations. The potential of structural information to predict tree growth responses, though not necessarily to thinning, has been demonstrated in growth models that include information about diameter distributions or size cohorts in order to assign trees to specific diameter classes (Kellomäki and Väisänen 1997; Lasch et al. 2005; Wang et al. 2011). Others studies have included information about stand structure by describing tree growth as a function of competition from trees that are larger than the focal tree (Wykoff 1990; Monserud and Sterba 1996; Corral

Rivas et al. 2005; Yang et al. 2009), by combining such competition indices with the relative spacing of trees within the stand (Schröder and Gadow 1999; Schröder et al. 2002), and by determining which trees are most likely to be competing neighbours (Biging and Dobbertin 1992).

In the Carrajung *E. nitens* experiment, more detailed examination of the mechanisms behind the thinning responses showed a combination of physiological and crown structural responses, which sometimes interacted with pruning and fertiliser application treatments. In thinned stands the D_{200} trees had larger leaf areas and crowns, larger branches, longer crowns and a higher proportion of foliage in the lower crowns (Forrester et al. 2012a). This enabled D_{200} trees to absorb 24% more light and transpire 23% more water than D_{200} trees in unthinned stands (Forrester et al. 2012b; in press). In terms of the physiological responses, the lower crowns were better lit in thinned stands, resulting in faster rates photosynthesis, and 13% and 21% increases in light- and water-use efficiencies, respectively, by D_{200} trees in thinned stands compared with those in unthinned stands (Forrester et al. 2012b; in press). Within unthinned stands, the capture and use-efficiency of resources was shown to increase with tree size in this and other stands (Forrester et al. 2012; Campoe et al. in press). This study shows that thinning responses also depend on site quality and size-class structure, probably because they modify the physiological and crown structural responses described above, and these effects likely vary between size classes.

Absolute responses by D_{200}

Absolute competition responses by D_{200} were greater in stands that were more negatively skewed and had lower coefficients of variation. These size-class structures were more typical of faster growing stands and this explains why absolute responses to thinning often increase with site quality or fertilizer treatments (Stoneman et al. 1996; Ruha and Varmola 1997; Mäkinen and Isomäki 2004a). However, there are also cases where absolute responses have not increased with increasing site quality or fertilizer application (Harrington and Wierman 1990). This could occur if size-class structure is strongly affecting competition for responses. For example if D_{200} are located in a more positively skewed stand, then they are competing with more smaller than larger trees. Such trees may be less responsive to thinning than D_{200} in a stand that is more negatively skewed and/or more uniform where D_{200} are not as dominant relative to their neighbours.

Relative responses by D_{200}

Relative competition responses by D_{200} were also higher in stands with more negatively skewed diameter distributions or that were more uniform. Such size-class structures could develop when the larger trees in the stand are growing at a similar rate and are not able to out-compete each other to differentiate into size classes. In the present study the more negatively skewed or less variable stands occurred on higher quality sites. Here thinning had a greater relative effect on growth than in stands where (i) size classes were more positively skewed so that D_{200} were relatively more dominant, and (ii) stands were less uniform with a greater coefficient of variation. Greater relative thinning responses by dominant or codominant trees with increasing site quality or rates of fertilizer application have also been shown in *E. marginata*, *E. obliqua* and *Pinus sylvestris* stands (Stoneman et al. 1996; Mäkinen and Isomäki 2004a; La Sala 2006).

The opposite has also been found. On lower quality sites or in unfertilized stands of species such as *Thuja plicata* and *Pinus contorta*, which are more shade-tolerant than eucalypts, relative responses of the dominant or codominant trees to thinning were greater than on higher quality sites (Harrington and Wierman 1990; Brockley 2005). This may occur when competition is more asymmetric. In the young *Eucalyptus* stands in the present study, competition was relatively symmetric. This was indicated by minimal temporal changes in coefficients of variation of tree diameters (Kikuzawa and Umeki 1996) and linear relationships between individual tree basal areas and their PAIs (Hara 1993). In stands where size-class distribution is more spread out and with a higher coefficient of variation, for example in older stands or when the species is more shade tolerant (Nord-Larsen and Cao 2006), competition for light will become more asymmetric. Relationships between individual tree basal area and PAI may then slope upwards as larger trees grow proportionately more for their size than the smaller trees that they shade (Hara 1993). Thus unlike in the present study, thinning responses will be lower on higher quality sites because small trees cannot compete with larger trees for light, and higher on lower quality sites where soil resources are more limiting, and smaller trees can compete with larger trees for soil resources.

Thinning responses by different size-classes

The relative responses usually increased with decreasing size-class ($D_{400-600} > D_{200-400} > D_{200}$), which has also been observed in many other studies (Moore et al. 1994; Pukkala et al. 1998; Mäkinen and Isomäki 2004b; Simard et al. 2004). This trend is likely because thinning does not only give smaller trees more water and nutrients, which is the case for larger trees, but it also increases light availability, which to some extent is not the case for larger trees. For example at

Carrajang, thinning increased absorbed photosynthetically active radiation by about 50% for trees with diameters of about 10 cm compared to 30% for 30-cm trees during the first year after thinning (see Forrester et al. (in press)). Nevertheless, this is often of little consequence because the smaller trees represent a much lesser proportion of the stand's growth.

In comparison to the D_{200} , the absolute response of $D_{200-400}$ and $D_{400-600}$ was similar or smaller. This is not surprising because PAI was linearly related to tree basal area, so the larger the tree the faster it grew. Decreasing absolute thinning responses with decreasing size class have been found in many other studies (Ruha and Varmola 1997; Medhurst et al. 2001; Mäkinen and Isomäki 2004b). Smaller trees are likely to have smaller leaf areas and fine-root masses, reducing their ability to take up resources, and they may also use those resources less efficiently than larger trees (Campoe et al. in press). However, some studies have shown that the most dominant trees do not have the largest absolute responses (Pukkala et al. 1998). This is likely related to stand age, shade tolerance and whether the stand is even-aged.

Genetic variability may also influence diameter distributions, which is important to consider, although it was not examined in this study. For example, all of the stands used in this study originated from seedlings as opposed to clonal cuttings, and size-class structure can be influenced by the degree of inbreeding within seed-origin stands (Costa e Silva et al. 2010). Inbred individuals will fall behind out-crossed individuals at some stage during stand development, and the proportion of inbred individuals varies between species, stands and sites (Costa e Silva et al. 2010; Grosser et al. 2010).

Management implications

Competition between trees is influenced by site quality as well as stand structure, which incorporates information about tree size and spacing. Diameter distributions appear to capture some of this information and were as good as, or better than, site quality at predicting thinning responses. Furthermore, site quality does not necessarily vary for a given site, while variables used to describe size-class structure can vary. Thus the latter may be more useful in stands that experience large changes in diameter distributions as they develop. This study also indicates that stands on similar site qualities but with different size-class structures can have correspondingly different thinning responses. Thus, knowledge about how diameter distributions develop might help to refine thinning regimes. *Eucalyptus* plantations with negatively skewed diameter distributions, which are fast growing and less variable are likely to show the greatest absolute and relative thinning responses,

and the larger size-classes will have the largest absolute thinning responses. More uniform (e.g. clonal) *Eucalyptus* plantations might therefore also respond particularly well to thinning.

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Table 1. Site, silviculture, and growth descriptors for unthinned stands aged 10 years. Climate data were estimated using ESOCIM. Australian Soil Classification (ASC,) Soil Order (Isbell 2002). Top height is the mean height of the largest-diameter 100 trees ha⁻¹.

		Bradvale	Buffalo River	Carrajung	Mangalore	Rennick	Shepparton	Tostaree
Latitude, longitude		37°49' S, 143°25' E	36°46' S, 146°40' E	38° 23' S, 146° 41' E	36°54' S, 145°11' E	37°54' S, 150°59' E	36°18' S, 145°23' E	37°47' S, 148°11' E
Altitude (m, a.s.l.)		250	290	610	140	60	100	40
Soil description		Cracking clay A horizon, structureless grey clay B horizon	Clay loam A and B horizons	Silty loam to clay loam A horizon, light clay to medium clay B horizon.	Loam A horizon, light to medium clay B horizon	Uniform coarse sand	Loam A horizon, heavy clay B horizon	Loamy sand A horizon, light to medium clay B horizon
ASC Soil Order		Vertosol	Dermosol	Dermosol	Kurosol	Podosol	Sodosol	Kurosol
Mean daily	January	25.6	29	22.3	28.5	23.4	29.8	25
max. temp. (°C)	July	11.3	11.4	10.2	12.1	12.9	12.4	13.8
Mean daily	January	10.6	11.7	11.1	13	11.1	14.2	12.2
min. temp. (°C)	July	3.2	2.1	3.9	3	4.7	2.7	3
Mean annual pan evap. (mm)		1160	1245	1039	1359	1274	1500	1247
Mean annual rainfall (mm)		618	1178	1124	603	760	483	835
Irrigation (mm year ⁻¹)		Nil	Nil	Nil	300 *	Nil	730 †	Nil
		<i>E. globulus</i>	<i>E. globulus</i> / <i>E. nitens</i>	<i>E. nitens</i> unfert / fert	<i>E. globulus</i> / <i>E. grandis</i>	<i>E. globulus</i>	<i>E. globulus</i> / <i>E. grandis</i>	<i>E. globulus</i> / <i>E. nitens</i>
Planted		Aug-97	Oct-92	Jun-03	Oct-92	Aug-97	Sep-93	Sep-91
Planting density (trees ha ⁻¹)		1000 (4 m × 2.5 m)	1111 (3.0 m × 3.0 m)	1000 (4 m × 2.5 m)	1235 (2.7 m × 3.0 m)	1000 (4 m × 2.5 m)	1333 (3.0 m × 2.5 m)	1143 (3.5 m × 2.5 m)
Density (trees ha ⁻¹)		917	799 / 743	826 / 774	696 / 848	895	873 / 938	836 / 702
Top height (m)		13.9	27.1 / 26.7	24.8 / 26.1	20.6 / 19.0	22.1	25.7 / 22.4	23.8 / 22.2
Basal area (m ² ha ⁻¹)		13.9	22.0 / 24.9	33.7 / 35.5	20.1 / 19.4	28	27.4 / 18.7	20.4 / 18.9
Mean diameter (cm)		13.5	18.4 / 20.4	22.0 / 23.1	19.3 / 16.6	19.4	19.7 / 15.7	17.0 / 17.9
Mean annual increment (m ³ ha ⁻¹ year ⁻¹)		7.3	21.6 / 24.7	33.1 / 36.4	15.5 / 13.4	21.9	25.3 / 15.1	16.9 / 14.4

*Groundwater (electrical conductivity 0.6 dS m⁻¹) applied 3-5 times annually from October to May.

† Secondary treated municipal effluent (electrical conductivity 1.4 dS m⁻¹) applied 10-12 times annually from October to May.

Table 2. Thinning intensity described in terms of tree density and basal area retained in thinned treatments. T300, T400 and T500 denote thinning to about 300, 400 and 500 trees ha⁻¹, respectively.

Site	Species	Age thinned (years)	Density prior to thinning (trees ha ⁻¹)	Basal area prior to thinning (m ² ha ⁻¹)	Density after thinning (trees ha ⁻¹)			Basal area retained after thinning (m ² ha ⁻¹)			Basal area retained (%)		
					T300	T400	T500	T300	T400	T500	T300	T400	T500
Bradvale	<i>E. globulus</i>	5	965	6.2	300	410	540	2.4	3.9	4.3	39	64	69
Buffalo River	<i>E. globulus</i>	3.5	999	9.7	231		475	3.1		6.5	32		67
	<i>E. nitens</i>	3.5	995	13.3	235		455	4.5		7.7	34		58
Carrajung	<i>E. nitens</i>	3.2	903	10.4	306			4.1			39		
Mangalore	<i>E. globulus</i>	2.7	984	7.3	331		537	3.6		5.5	49		75
	<i>E. grandis</i>	3.8	939	7.6	334		537	2.4		3.3	32		43
Rennick	<i>E. globulus</i>	5	962	15.7	342	413	482	7.7	9.5	9.6	45	51	58
Shepparton	<i>E. globulus</i>	3.2	1071	11.4	361		574	5.6		7.7	49		68
	<i>E. grandis</i>	4.2	1065	9.6	361		583	4		6	42		63
Tostaree	<i>E. globulus</i>	7.5	999	18.3	246		444	6.3		10.6	34		58
	<i>E. nitens</i>	7.5	1010	16.5	246		442	7.1		10.4	43		63

Table 3. Parameter estimates of Eqn. 1: basal area PAI (cm²) = Constant + Slope ln (competition; cm²) for trees belonging to the largest-diameter 200 trees ha⁻¹ (D_{200}) size class. se is standard error.

Site	Species	Growth period (age, years)	Constant (se)	Slope (se)	Adj. R ²	n	P
Buffalo River	<i>E. globulus</i>	3.5 to 5.5	116 (12)	-13.6 (1.9)	0.42	72	< 0.001
Buffalo River	<i>E. globulus</i>	5.5 to 7.3	216 (28)	-23.3 (4.3)	0.30	67	< 0.001
Buffalo River	<i>E. globulus</i>	7.3 to 9.6	178 (26)	-18.5 (3.6)	0.27	68	< 0.001
Buffalo River	<i>E. nitens</i>	3.5 to 5.5	273 (25)	-33.6 (3.8)	0.58	57	< 0.001
Buffalo River	<i>E. nitens</i>	5.5 to 7.3	397 (76)	-46.4 (11.1)	0.26	47	< 0.001
Buffalo River	<i>E. nitens</i>	7.3 to 9.6	362 (63)	-41.9 (8.6)	0.31	52	< 0.001
Bradvale	<i>E. globulus</i>	8.0 to 10.0	64 (5)	-7.4 (0.8)	0.35	169	< 0.001
Bradvale	<i>E. globulus</i>	10.0 to 12.8	149 (11)	-17.4 (1.6)	0.41	178	< 0.001
Mangalore	<i>E. globulus</i>	6.3 to 10.1	156 (38)	-16.5 (5.1)	0.07	125	0.001
Mangalore	<i>E. grandis</i>	6.3 to 10.1	84 (16)	-8.5 (2.2)	0.11	110	< 0.001
Rennick	<i>E. globulus</i>	4.1 to 7.6	289 (26)	-32.2 (3.7)	0.38	123	< 0.001
Rennick	<i>E. globulus</i>	7.6 to 9.6	430 (36)	-48.6 (4.7)	0.41	153	< 0.001
Rennick	<i>E. globulus</i>	9.6 to 12.7	237 (28)	-24.6 (3.6)	0.24	149	< 0.001
Tostaree	<i>E. globulus</i>	7.5 to 9.2	84 (11)	-7.3 (1.7)	0.04	425	< 0.001
Tostaree	<i>E. globulus</i>	9.2 to 10.4	45 (16)	-1.3 (2.4)	-	403	0.577
Tostaree	<i>E. globulus</i>	10.4 to 15.8	38 (12)	-0.4 (1.7)	-	404	0.813
Tostaree	<i>E. nitens</i>	9.2 to 10.4	72 (14)	-4.1 (2.1)	-	427	0.056
Tostaree	<i>E. nitens</i>	10.4 to 15.8	42 (12)	-0.4 (1.8)	-	412	0.815
Shepparton	<i>E. globulus</i>	5.2 to 7.5	244 (45)	-23.7 (5.9)	0.11	117	< 0.001
Shepparton	<i>E. globulus</i>	7.5 to 9.1	178 (55)	-17.3 (7.0)	0.04	115	0.015
Shepparton	<i>E. grandis</i>	5.2 to 7.5	104 (30)	-8.8 (4.2)	0.04	83	0.041
Shepparton	<i>E. grandis</i>	7.5 to 9.1	113 (30)	-12.1 (4.0)	0.09	83	0.004
Carrajung (unfert)	<i>E. nitens</i>	3.2 to 4.4	252 (26)	-24.0 (3.9)	0.27	99	< 0.001
Carrajung (unfert)	<i>E. nitens</i>	4.4 to 6.3	357 (28)	-36.9 (4.0)	0.40	126	< 0.001
Carrajung (unfert)	<i>E. nitens</i>	6.3 to 8.1	392 (30)	-40.0 (4.0)	0.43	135	< 0.001
Carrajung (fert)	<i>E. nitens</i>	3.2 to 4.4	273 (25)	-25.9 (3.7)	0.30	111	< 0.001
Carrajung (fert)	<i>E. nitens</i>	4.4 to 6.3	318 (27)	-30.6 (3.8)	0.33	128	< 0.001
Carrajung (fert)	<i>E. nitens</i>	6.3 to 8.1	400 (35)	-40.9 (4.7)	0.35	142	< 0.001

Table 4. Equations describing the Slope of Eqn. 1 in Table 3 as a function of one or two of the explanatory variables (all ln-transformed) shown in the second line of the table. Site quality is quantified using MAI₁₀ and size-class structure is quantified using statistics and parameters that describe the diameter distribution such as the coefficient of variation (CV), skewness, and Weibull β or α parameters. N = 27 and $P < 0.001$ for all equations. Standard errors are in parentheses.

Intercept	Coefficients for explanatory variables					Adj. R ²
	MAI ₁₀	CV	Skewness	Weibull- β	Weibull- α	
3.8 (6)	-1.16 (0.26)					0.42
-65.5 (11)		1.58 (0.38)				0.38
-10.4 (3)			26.8 (6.3)			0.39
112.2 (25)				-233 (43.4)		0.51
8.5 (8)					-7.0 (1.9)	0.33
-27.5 (21)	-0.75 (0.36)	0.81 (0.51)				0.45
2.5 (6)	-0.78 (0.28)		16.4 (6.8)			0.51
85.5 (27)	-0.61 (0.28)			-164 (52)		0.57
8.2 (8)	-0.88 (0.4)				-2.4 (2.7)	0.41
-42.1 (14)		1.00 (0.42)	17.2 (7.1)			0.48
53.5 (29)		1.00 (0.32)		-179 (42)		0.63
82.7 (30)			12.1 (7.2)	-173 (55)		0.54
102 (23)				-185 (44)	-4.1 (1.6)	0.59

Figure 1. Examples of the influence of size class on the relationship between basal area PAI and competition. Competition was expressed as the sum of the basal area of neighbouring trees within a radius of 6.5 m (Eqn. 1). For these multiple regressions (size class is included as a dummy variable) the Adj. $R^2 = 0.52, 0.52, 0.28, 0.30, 0.27$ and 0.23 for (a) to (f), respectively. Size classes are indicated as the 200 largest-diameter trees ha^{-1} (D_{200}), the next largest 200 ($D_{200-400}$), and then the next largest ($D_{400-600}$).

Figure 2. Example modelled relationships between basal area PAI of D_{200} and competition, with constants and slopes representing the range of observed relationships (Eqn. 1, Table 3). The indicated absolute ($\text{cm}^2 \text{ year}^{-1}$) and relative (%) competition responses are the difference in increment from a competition of 3000 cm^2 to 800 cm^2 . The higher lines are representative of higher quality sites, where diameter distributions of unthinned stands are more negatively skewed, have lower coefficients of variation and higher Weibull- β values (see Figure 3).

Figure 3. Relationships between the Slope (of the relationships between D_{200} basal area PAI and Competition, Equation 1, Table 3) and site quality (MAI_{10} ; a), the coefficient of variation (b), skewness (c) and the Weibull- β (d) or Weibull- α (e). All relationships are significant ($P < 0.001$; see Table 4).

Figure 4. Plots of site quality (MAI_{10}) and size-class structural parameters such as the coefficient of variation (a), skewness (b) and Weibull- β parameter (c) of unthinned stands, indicating the poor correlation between site quality and size-class structure for *E. globulus*.

Figure 5. Diameter distributions for the unthinned treatments in stands exemplifying large (a), medium (b) and small (c) responses to reductions in competition from 3000 cm² to 800 cm².

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Author/s:

Forrester, DI;Elms, SR;Baker, TG

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