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ORIGINAL ARTICLE

Quantifying effects on tree growth rates of symmetric and asymmetric inter-tree competition in even-aged, monoculture *Eucalyptus pilularis* forests

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Abstract

Key message **In even-aged, monoculture eucalypt forest, symmetric inter-tree competition was far more important in determining tree growth rates than asymmetric competition. Tree size principally determined competitive ability at any time.**

Abstract In even-aged, monoculture forests, individual tree growth rates are much affected by the amount of the resources required for growth (particularly light, water and nutrients) that are available to them from the site on which they are growing. In turn, those amounts are much affected by competition for them between neighbouring trees. Competition may be 'symmetric', when tree growth rates are directly proportional to tree sizes, or 'asymmetric' when growth rates vary disproportionately with tree sizes. Using a large data set from blackbutt (*Eucalyptus pilularis* Smith) forests of sub-tropical eastern Australia, methods were devised to quantify the effects of symmetric and asymmetric competition; they were determined as the change each causes in individual tree growth rates over growth periods of a few years. It was found that symmetric competition was by far the principal determinant of tree growth rates. Asymmetric competition had much lesser effects, but was sufficient to alter substantially the development with age of the frequency distribution of tree sizes. It is concluded that the size of a tree at any time is the principal determinant of both its metabolic capabilities for growth and its competitive status and, hence, its growth rate.

Keywords Competition · Symmetric · Asymmetric · Basal area growth · Size distribution

Introduction

For a tree in a forest on a particular site at a particular time, three principal factors control its growth. The first is the environmental circumstances of the site; these include the temperature regime, availability of sunlight, amount of rainfall and soil fertility. These, together with the physiological capabilities of the species concerned, will determine the size the tree might reach by any particular age. That size is then the second factor that determines how fast it may grow subsequently (Pretzsch 2021a); this reflects the amount of living tissue it contains to undertake growth processes (Weiskittel et al. 2011, Chap 12). The third factor is the availability to the tree of the resources it requires for growth, light, carbon dioxide, water and nutrients. If other trees are growing nearby to a particular tree, they may compete with it for whatever light, water and nutrient resources are available (Burkhart and Tomé 2012, Chap. 9) and so limit its possible growth. This inter-tree competition is termed 'size-symmetric' if it causes trees to grow at rates directly proportional to their sizes, 'size-asymmetric' if larger individuals grow at rates disproportionately large with respect to their sizes or 'inverse size-asymmetric' if smaller individuals grow at rates disproportionately large with respect to their sizes (Fernández-Tschieder and Binkley 2018).

Over the life of a forest stand, the influences of both symmetric and asymmetric competitive processes will vary. Initially, as seedlings grow and start to compete with each other, competition is believed to be largely symmetric, below ground for water and nutrients. This is the first phase of a suggested model system of stand growth (Binkley 2004;

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Binkley et al. 2006). Differences in growth behaviour of individuals then lead to differences in tree heights, when a second phase of development starts; that involves asymmetric competition for sunlight, when taller trees tend to shade smaller, in addition to the competition for water and nutrients that is already occurring. Finally, often at ages of some decades, an inverse asymmetric growth phase may start when smaller trees gain a growth rate advantage as a consequence of physiological circumstances allowing them to use the limited light available to them more efficiently than taller trees.

Over many years and for many forest types around the globe, models have been developed to predict individual tree growth in relation to the three controlling factors mentioned above. Major texts offer substantial reviews of such modelling work (e.g., Vanclay 1994; Weiskittel et al. 2011; Burkhart and Tomé 2012). Much of this work has investigated the use of different 'competition indices' in describing growth. More often than not, this has led to an impression that asymmetric competitive processes are the more influential in determining individual tree growth (e.g., Lorimer 1983; Biging and Dobbertin 1992, 1995; Forrester et al. 2011; van Breugel et al. 2012). However, a few works have identified symmetric processes as being the more influential (Canham et al. 2004; Stadt et al. 2007; Coates et al. 2009). It has been suggested that, in even-aged monoculture, asymmetric competition is most influential, whilst in complex uneven-aged forest symmetric competition is most influential (Lundqvist 1994).

In a formal discussion of the effects of competitive interactions between organisms on their individual or population growth rates, Welden and Slauson (1986) defined competition 'intensity' in plants as the decrease it causes in growth rates from those they would have under optimal circumstances and 'importance' as the relative decrease. Those definitions were adopted here. They informed the basis of the principal objective of the present work. This was to develop methods to quantify, at both the individual tree and stand levels, the intensity and importance of each of symmetric and asymmetric competition, when either or both are operating within a forest stand. None of the works mentioned above has achieved such a distinction between competitive effects in forests.

Given that the methods developed here are novel, it is difficult to advance any particular hypotheses as to which form of competition is likely to have the greater intensity or importance in forests. However, given the Binkley et al. model of forest growth behaviour, it seemed reasonable to hypothesise that symmetric processes are likely to be more influential at younger ages and that asymmetric processes will become increasingly influential at later ages. To inform the development of these methods, a large data set with tree growth rates was available from even-aged, monoculture blackbutt (*E. pilularis* Smith) regrowth and plantation forests growing in sub-tropical eastern Australia. Further work will be necessary to adapt these methods to other forest types elsewhere in the world.

Materials and methods

Data

Native regrowth and plantation blackbutt forests extend along a coastal strip of eastern Australia, over a latitudinal range of 25−37°S and inland to the Great Dividing Range. Most eucalypts are relatively shade intolerant and many grow in tall-open, even-aged, essentially monoculture forests; blackbutt is of this type (Florence 1996, pp. 87−88).

Data were available from 94, 0.04 to 0.2 ha, permanent sample plots established by the New South Wales and Queensland government forest services in both regrowth and plantation forests across the region of natural occurrence of blackbutt; these data were collated by Mattay and West (1994). Plots were in forest that had regenerated or been planted at some time during 1923–1972. They wers measured during 1931–1984, most commonly four times, but at most 29 times, and usually at intervals that varied in the range 1–4 years. Many of the plots had been thinned from time to time during their lifetimes.

Data were available also from 27, 0.05 ha, plots in an unthinned, experimental blackbutt plantation planted in 2000 and located near Coffs Harbour (30°18′S, 153°08′E). The experiment involved several different spatial arrangements of trees at planting. It had been measured five times over 3−6 years of age. Experimental details are available in West and Smith (2019).

At each measurement, the diameters at breast height (1.3 m) over bark of live trees in a plot were measured. Individual tree growth rates were determined as the annual growth rate in basal area of trees that survived a growth period between any two plot measurements. Often, a sample of trees was measured for height. The site index functions of West and Mattay (1993) were then used to determine plot site productive capacities as site index, being the average height of the 50 largest diameter trees per hectare at an index age of 20 years. The final data set contained a total of 34,903 individual tree growth rates from 1115 growth periods of 121 plots. All or parts of this data set have been used in other works (West and Smith 2019; West 2021; West and Ratkowsky 2022b). A summary of plot and stand circumstances is given in (Table 1).

Table 1 Summary of plot numbers and minimum-mean-maximum stand characteristics at the start of measurement periods of the data set used here

Forest type	Number of plots	Age (year)	Stocking density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Site index (m)
Regrowth	61	6-27-61	74-341-2,012	0.1-22-70	17-27-35
Plantation	33	4-21-47	55-439-1,000	0.3-14-33	13-25-39
Experimental plantation	27	3-4-6	510-985-1,511	4.2-14-29	41-46-50

Models relating tree growth rates to tree size

Tree size and growth can be represented by various characteristics which vary considerably in their ease of measurement. Tree biomass is probably the most definitive characteristic and may even include biomasses of the living tissues that undertake growth processes. However, as discussed in forest measurement texts (e.g., West 2015, Chap. 7), trees can be large and their biomasses very difficult to measure. Stem cross-sectional area at breast height (stem basal area) often correlates well with tree biomass and is easy to measure; that was used here to define tree size.

The methods developed here to quantify the intensity and importance of competitive processes between individual trees in a stand require that various models have been formulated to describe individual tree growth behaviour in a stand. The models found suitable for blackbutt forests growing in sub-tropical eastern Australia are used as examples here. Those models are likely to have application for many other forest types.

Suppose a blackbutt tree is growing in the most ideal environmental circumstances for growth that exist in the region where that species occurs, sub-tropical eastern Australia. That is, it is growing on a site with an optimum temperature regime for the species and which provides more than sufficient resources of light, water and nutrients. Suppose also, its growth is not constrained by competitive interactions with its neighbours for those resources; in essence that means it is open grown. Suppose B_i (m^2) is the basal area at the start of a growth period of the ith tree in a forest area and which is growing under such circumstances. That tree should then be displaying the maximum possible basal area growth rate that a tree of that size may have, ΔB_{Mi} (m^2 yr^{-1}). Based on the entire blackbutt data set available here, West (2021) found that this maximum could be related to tree size as

$$\Delta B_{Mi} = aB_i^m - bB_i \quad (1)$$

where a, m and b are parameters; for blackbutt values of $a=0.025$, $m=0.113$ and $b=0.0344$ were determined. Others have developed similar relationships to predict maximum possible growth rates for individual trees of various species in various parts of the world (e.g., Shifley 1987; Bragg 2001; Thürig et al. 2005; Canham et al. 2006; Coomes and Allen 2007; Bošela et al. 2013; Pommerening et al. 2022).

Suppose now a blackbutt tree is growing on a site that offers less than these ideal environmental circumstances for growth. Site index (or some other measure of site productive capacity, as discussed by West 2015, Chapter 8) may then be used as a measure of the productive capacity for forest growth on that site. For the 121 blackbutt plots in the present data set, site indices varied over the range 13−50 m (Table 1). The entire 34,903 individual tree growth measurements were divided into site index and tree basal area classes. To attempt to quantify maximum possible growth rates in the absence of competitive interactions from neighbouring trees, quantile regression was then used in the same way as done by West (2021), to relate growth rate maxima to tree size in each of eight site index classes. As might be expected, those maxima increased with increasing stand site index; others have similarly found maxima increasing with site index (Pretzsch and Biber 2010; Oboite and Comeau 2021). This led to development of a model to predict the maximum possible basal area growth rate, ΔB_{Ei} (m^2 yr^{-1}), for the ith tree growing free of competitive interactions on a site in sub-tropical eastern Australia with a site index of S (m), as

$$\Delta B_{Ei} = a' B_i^{m'} - b' B_i \quad (2)$$

where $a' = a_1 + a_2 S$, $m' = m_1 + m_2 S$, $b' = b_1 + b_2 S$ and a_1, a_2, m_1, m_2, b_1 and b_2 are parameters.

The 538 individual tree growth rate observations selected by this process for quantile regression from the eight site index classes were pooled. The nonlinear regression model (2) was then fitted to these data using the NLIN procedure of the SAS® statistical package.[1] The fit of the model was close, explaining 92% of the variation in ΔB_{Ei}. The parameter values determined were $a_1 = -0.000750$, $a_2 = 0.000886$, $m_1 = 0.06130$, $m_2 = 0.00498$, $b_1 = 0.000179$ and $b_2 = 0.001260$. The form this model takes for various values of site index is shown in (Fig. 1), together with the maximum growth determined for the whole blackbutt

[1] Documentation for the SAS statistical package is available at https://support.sas.com/en/documentation.html (accessed July 2022).

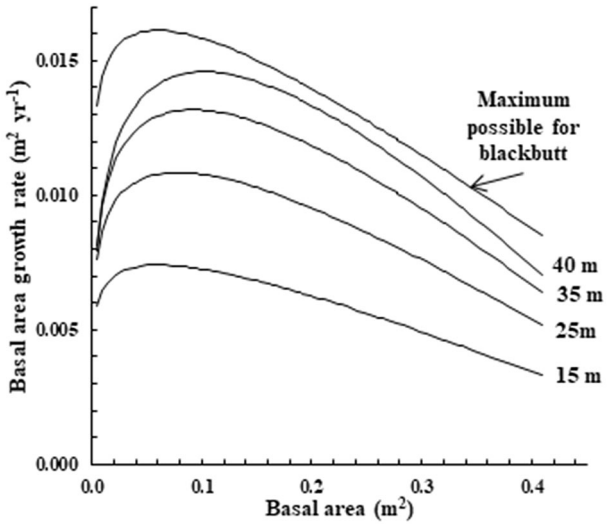


Fig. 1 Maximum possible basal area growth rates (ΔB_{Ei}) in relation to tree basal areas, in the absence of competition for growth resources from neighbouring trees, as predicted for various stand site indices, as indicated, using Model (2). Also shown are the maximum possible growth rates (ΔB_{Mi}) for blackbutt growing in sub-tropical eastern Australia, as predicted using Model (1)

population using Model (1). It was then assumed that Model (2) predicted the maximum growth rate possible for a tree of any particular size, when growing on a site of a particular productive capacity and when its growth rate is not affected by competition for growth resources from neighbouring trees. This model may reasonably be interpreted as defining the first of the three factors, tree size, that control tree growth, as discussed in the Introduction.

The next step in the methods being developed here was to model growth behaviour of trees in individual stands. An example of how this was done is shown for the data from a single growth period of one plot (Plot 1009) selected arbitrarily from the 121 plots available here. Figure 2a shows a scatter plot of basal area growth rates against tree basal areas for that growth period of that plot. Those data suggest there was a group of smaller trees in the plot that were showing little or no growth. Some trees are even shown as having negative growth rates; that is often observed in forest growth data and usually arises through measurement errors with small trees and/or stem shrinkage and swelling in response to differences in soil water availability at different times of measurement (Sheil 1995; Baker et al. 2002; Chitra-Tarak et al. 2015). There are examples of growth suppression of smaller trees developing with age in various forest types in various parts of the world (e.g., West and Borough 1983; Perry 1985; Wichmann 2001; Glencross et al. 2016; West and Smith 2019); the phenomenon may be attributed to any or all of shading of smaller trees by taller as tree crowns expand with age, differences between individuals in their genetic capabilities for growth or small-scale heterogeneity of growth resource availability across the site (Resende et al. 2016, 2018).

West and Ratkowsky (2022b) examined functions that are appropriate to fit such growth data. They considered what they termed the 'bent stick' model (Deleuze et al. 2004),

$$\Delta B_i = (p_1/2)\left\{B_i - p_2 p_3 + \left[(p_2 p_3 + B_i)^2 - 4 p_2 B_i\right]^{1/2}\right\} \quad (3)$$

where ΔB_i (m^2 yr^{-1}) is the observed growth rate of the ith tree in a stand that contains N trees in total and p_1, p_2 and p_3 are parameters. This model is such that in the limit (as $B_i \rightarrow \infty$) it describes the growth of the larger, non-suppressed group of trees as a straight line. It then shows a gradual, curvilinear transition from that line to the trend apparent in the data for the suppressed group. It then passes through the origin, that is, predicting $\Delta B_i = 0$ when $B_i = 0$. The fit to the data of Fig. 2a of that model is shown as the dashed line that is marked ΔB_i; It was fitted using methods described by West and Ratkowsky (2022b) and its parameter value estimates were $p_1 = 0.080$, $p_2 = 0.031$and $p_3 = 1.116$.

In younger or recently thinned stands, there may have been insufficient time for any marked suppression of smaller trees to have occurred. Then, with little evidence of a suppressed group of trees developing, tree growth rate may be related to tree size simply as a straight line

$$\Delta B_i = r_1 + r_2 B_i \quad (4)$$

where r_1 and r_2 are parameters. An example of such a case is shown in (Fig. 2b). The plot shown there (Plot 8) had been thinned shortly before the growth period. Its parameter estimates were $r_1 = -0.000399$ and $r_2 = 0.086841$. In some plots, it was found that the estimate of the intercept of this model (r_1) did not differ significantly from zero, so the model

$$\Delta B_i = c B_i \quad (5)$$

where c is a parameter, was adequate. The example in (Fig. 2c) was such a case; the estimate there of c was 0.107. That plot (Plot 46) too had been thinned shortly before the growth period concerned. West and Ratkowsky (2022b) considered growth behaviour in all 1115 growth periods of all 121 plots available here. They found one or other of Models (3–5) to be appropriate to describe growth behaviour in each case.

Following the definitions of Fernández-Tschieder and Binkley (2018), if only symmetric competition between trees is occurring in a stand, tree relative growth rates [$(1/B_i)\mathrm{d}B_i/\mathrm{d}t$, where t is time] will be unrelated to tree size. Hence, their growth rates will be directly proportional to their sizes as Model (5) assumes. If either Model (3) or (4) is found to

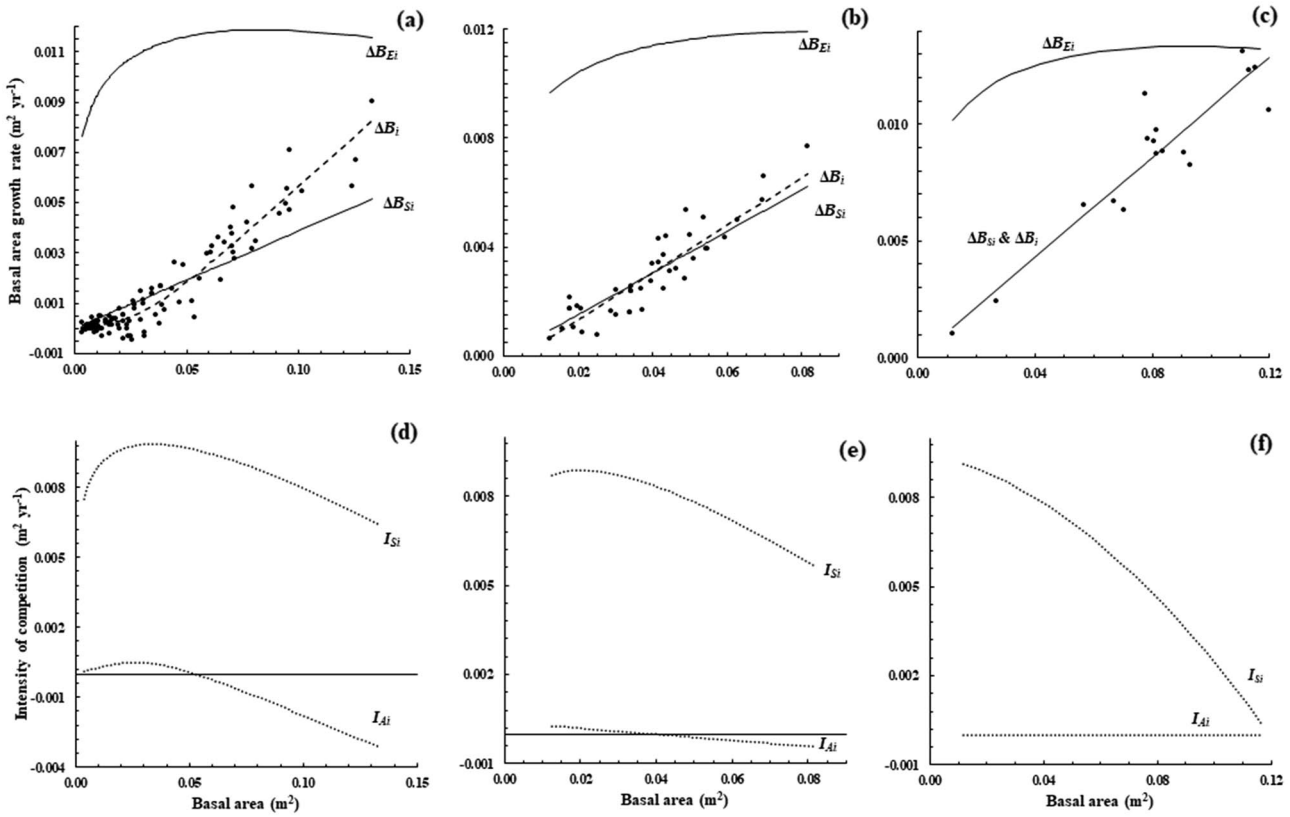


Fig. 2 Results from one growth period of each of three blackbutt plots, chosen as examples from the entire data set available here. The plots, their growth periods and site indices were **a**, **d** Plot 1009, (24−26 years of age, site index 29 m), **b**, **e** Plot 8, (19−21 yr, 29 m), **c**, **f** Plot 46 (15−18 yr, 36 m). A scatter plot (•) of observed basal area growth rates against tree basal areas is shown together with the fit to those data (marked ΔB_i) of **a** Model (3), **b** Model (4) and **c** Model (5). Predicted values of Models (2) (ΔB_{Ei}) and (6) (ΔB_{Si}, as determined using Eqs. 7, 8) for each case are shown also. The trends with tree size in intensity of symmetric (I_{Si}, Eq. 9) and asymmetric (I_{Ai}, Eq. 10) competition in each case are shown also (**d**, **e**, **f**)

be more appropriate, it may be assumed that at least some degree of asymmetric competition is occurring in the stand, competition that may well be in conjunction with symmetric competitive processes also.

Identifying types of competition

The basis of the methods developed here to quantify competitive processes was to presume that it would be possible to consider tree growth behaviour if symmetric competition only was occurring in a stand. This involved three assumptions. Firstly, it was assumed that if the growth rate of the *i*th tree of the *N* trees in a stand under those circumstances was ΔB_{Si} (m^2 yr^{-1}), this would be related to tree size as

$$\Delta B_{Si} = c' B_i \tag{6}$$

where *c'* is the constant of proportionality; of course, this is consistent with Model (5) and with the definition of symmetric competition. The second assumption was that the total growth of all trees in the stand would still be the same as that actually observed, no matter what type of competition was actually occurring. This seemed reasonable, since that total growth is determined principally by the environmental circumstances of a site, the amounts of the resources required for growth that the site provides and the physiological characteristics of the species concerned (e.g., Ryan et al. 2010); there do not seem at present to be research findings that would suggest the form of inter-tree competition occurring would affect that stand total growth. It would then follow that

$$\sum_{i=1\ldots N} \Delta B_{Si} = \sum_{i=1\ldots N} \Delta B_i = c' \sum_{i=1\ldots N} B_i \tag{7}$$

Hence, the value of c' might be estimated as

$$c' = \left(\sum_{i=1\ldots N} \Delta B_i\right) \Big/ \left(\sum_{i=1\ldots N} B_i\right) \tag{8}$$

The solid line marked ΔB_{Si} in each of (Fig. 2a–c) then shows the fit of this assumed Model (6) in each of the example cases there. The estimates there of c' were 0.0387 (Plot 1009), 0.0765 (Plot 8) and 0.1073 (Plot 46). The third

assumption was that if the form of the observed model of growth behaviour in the stand deviated from Model (6), it might be assumed that those deviations were a consequence of asymmetric competitive processes. A test as to whether or not this assumption was reasonable is considered later, through studies described in an Appendix.

Thus, for the example of Plot 1009 (Fig. 2a), there is quite substantial deviation between the two fitted models (marked as ΔB_i for Model 3 and ΔB_{Si} for Model 6). In the case of Plot 8 (Fig. 2b), there is only slight deviation between the two models (Model 4 for ΔB_i in that case). In the case of Plot 46 (Fig. 2c), Model (5) was found to not differ from Model (6). Thus, it might be assumed that asymmetric competition was occurring at least to some extent in Plot 1009, only slightly in Plot 8 and not at all in Plot 46.

Quantifying competition

Given that Model (6) has been fitted for a stand, the reduction in growth rate from the maximum possible for the *i*th tree in that stand as a consequence of symmetric competition, that is, the intensity of symmetric competition that tree is facing (I_{Si},m^2 yr^{-1}), might then be quantified as

$$I_{Si} = \Delta B_{Ei} - \Delta B_{Si} \tag{9}$$

That maximum possible tree growth rate in the absence of competition may be determined using Model (2); its values are indicated for each example plot in the lines marked ΔB_{Ei} in (Fig. 2a–c).

Suppose now that one of Models (3–5) has been found most appropriate for the observed growth behaviour of a stand. The additional effects of asymmetric competitive processes, if any, might then be quantified as follows. Consider the example of Plot 1009 in Fig. 2(a), where Model (3) best described the observed growth behaviour; hence it may be assumed that asymmetric competitive processes were operating in addition to any symmetric processes. It is clear from the fit of Model (3) (the dashed line marked on the figure as ΔB_i) that the growth rates of smaller trees tended to be less than the growth rates they would have had if symmetric competitive processes alone were operating (as indicated by the solid line marked ΔB_{Si} on the figure). These reduced growth rates were assumed to reflect the additional effects of asymmetric competitive suppression. By contrast, larger trees in the stand tended to have growth rates greater than those predicted they would have if symmetric competitive processes only were applying. This suggested that the asymmetric competition was probably for light, where crowns of larger (taller) trees were able to absorb amounts of light disproportionately large with respect to their sizes by shading crowns of smaller trees; that additional light that would allow them those larger trees to increase their growth rates.

Thus, the intensity of asymmetric competition for the *i*th tree in the stand, I_{Ai} (m^2 yr^{-1}), might be quantified in this case as the difference between the growth rates predicted by Model (6) and Model (3), that is,

$$I_{Ai} = \Delta B_{Si} - \Delta \hat{B}_i \tag{10}$$

where $\Delta B_i^{\wedge}$ (m^2 yr^{-1}) is the predicted value of growth for that tree from the fitted Model (3). The value of I_{Ai} will be positive for the group of suppressed trees, but negative for the larger trees. Later here, it was found useful to discriminate between those positive and negative values, terming them I_{Ai+} and I_{Ai-} (m^2 yr^{-1}), respectively.

Similar methods can be used to estimate the intensity of asymmetric competition when Model (4) was found best suited to describe observed growth. It is clear from (Fig. 2b) that those effects for Plot 8 were much smaller than was the case for Plot 1009, so small that it had been found unnecessary to use Model (3) to fit the data in that case. In the case of Plot 46 (Fig. 2c), Models (5) and (6) did not differ, suggesting there was no asymmetric competition operating in that case.

These methods offer measures of growth losses due to competitive processes, hence as competition 'intensities' for individual trees in a stand. Consideration was now given to estimation of competition 'importances' for individuals. In their original definition of importance, Welden and Slauson (1986) did not envisage that competitive processes might increase rather than decrease plant growth rates, as observed here where larger trees received a growth advantage by suppressing smaller trees. To allow for this, the importance of a competitive affect was defined here as the relative degree to which symmetric or asymmetric competition contributed to the combined intensities of both processes. Thus, the importance of symmetric competition, $\tilde{I}_{Si}$ (dimensionless), was defined as

$$\tilde{I}_{Si} = I_{Si} / \left(I_{Si} + |I_{Ai}| \right) \tag{11}$$

whilst that of asymmetric competition, $\tilde{I}_{Ai}$ (dimensionless), then followed simply as

$$\tilde{I}_{Ai} = 1 - \tilde{I}_{Si} \tag{12}$$

It was felt reasonable also to pool both the intensities and importances over all the trees in a stand to give summary values for the whole stand. Thus, pooled symmetric intensity, K_S (m^2 yr^{-1} ha^{-1}), was determined as

$$K_S = \left(\sum\nolimits_{i=1\ldots N} I_{Si} \right) / A \tag{13}$$

where A (ha) was the area of the plot, whilst the pooled asymmetric intensity, K_{Ai} (m^2 yr^{-1} ha^{-1}), was

$$K_A = \left(\sum_{i=1\ldots N} I_{Ai}\right)\Big/A \quad (14)$$

Pooled asymmetric intensity could be split into positive and negative effects, K_{A+} and K_{A-} (dimensionless) respectively, as

$$K_{A+} = \left(\sum_{i=1\ldots N} I_{Ai}\right)\Big/A, I_{Ai} \geq 0 \quad (15)$$

and

$$K_{A-} = \left(\sum_{i=1\ldots N} I_{Ai}\right)\Big/A, I_{Ai} < 0 \quad (16)$$

The pooled symmetric importance, $\tilde{K}_S$ (dimensionless), was then defined as

$$\tilde{K}_S = \left[\sum_{i=1\ldots N} I_{Si}\right]\Big/\left[\sum_{i=1\ldots N} \left(I_{Si} + |I_{Ai}|\right)\right] \quad (17)$$

whilst the pooled asymmetric importance, $\tilde{K}_A$ (dimensionless), was

$$\tilde{K}_A = 1 - \tilde{K}_S \quad (18)$$

Results

Intensity and importance of competitive effects

Figure 2d, e, f show how both symmetric and asymmetric competition intensities, estimated using Eqs. (9, 10), respectively, varied with tree size for the three example plots. For those cases, it appears that symmetric competition caused a far greater reduction in tree growth rates than asymmetric competition, the difference tending to decline as tree size increased. When asymmetric competition applied (Fig. 2d, e), it caused a reduction in growth rate for smaller trees and an increase for larger trees, in both cases with absolute effects far less than those of symmetric competition.

Growth behaviour of trees in each of the 1,115 growth periods of the 121 plots in the entire data set available here were now determined in the same fashion as was done for the three example plots in (Fig. 2). In each case, the intensity and importance of both symmetric and asymmetric competition, when pooled across the whole plot, were determined using Eqs. (13, 15, 16, 17, 18). The minimum, most common (modal) and maximum values found across the data set are shown in (Table 2). It is clear that both the intensity and importance of symmetric competition were consistently much greater than those of asymmetric competition, just as was evident for the three example growth periods in (Fig. 2). Further, the most common (modal) values of the intensities of both positive and negative asymmetric competition (K_{A+} and K_{A-}, see Eqs. 15, 16 were both zero. It was clear from earlier discussion and the examples of (Fig. 2) that asymmetric competition tended to give a growth advantage to larger trees, whilst smaller trees suffered a corresponding growth disadvantage. Thus, there was little or no net advantage or disadvantage over all trees in a plot, leading to the modal values of zero for K_{A+} and K_{A-} in (Table 2).

Table 2 For the entire data set available here, the minimum-mode-maximum of competition intensities (K_S, K_{A+} and K_{A-}) and importances ($\tilde{K}_S$ and $\tilde{K}_A$) when pooled over individual growth periods for each plot in the data set

Variable	Units	Minimum-mode-maximum
K_S	$m^2\ yr^{-1}\ ha^{-1}$	0.15−1.31−17.77
K_{A+}	$m^2\ yr^{-1}\ ha^{-1}$	0−0.00−0.04
K_{A-}	$m^2\ yr^{-1}\ ha^{-1}$	−0.54−0.00−0
$\tilde{K}_S$	%	62−84−100
$\tilde{K}_A$	%	0.01−16−38

As discussed in the Introduction, asymmetric competitive processes have often been identified as being the more influential in forest stands than symmetric processes. Thus, the present findings of the apparent much greater intensity and importance of symmetric over asymmetric competition was rather surprising. In an attempt to confirm that these findings were reasonable, a simulation study was devised to explore how uptake of below-ground growth resources might occur. The study is described in the Appendix; it uses Plot 1009 (Fig. 2a) as an example. It predicts that the number of trees involved in inter-tree competition in Plot 1009 is consistent with the findings of many studies that have explored that issue in many forest types. It concludes that the present findings that the intensity of symmetric competitive processes were far greater than those of asymmetric processes are consistent with the processes of uptake of below-ground resources.

This conclusion from the simulation study was examined further with the results shown in (Fig. 3). This shows a scatter plot of the intensity of symmetric competition when pooled over all the trees of a plot (that is K_S as determined using Eq. 13) against the stocking density of the plot at the start of the growth period concerned. To avoid showing a confusingly large number of results there, the data were reduced to 121 observations by selecting one result at random from each plot from the total of the 1115 growth period results that were available. The results show a tendency for the intensity of symmetric competition to increase as stocking density increased. There is appreciable variation in the results for any particular stocking density; that is not surprising, given the wide variation in ages and thinning histories of the plots. The three example plots shown in Fig. 2 are identified specifically on Fig. 3; those three plots had been chosen deliberately to have a wide range of stocking densities to illustrate these results.

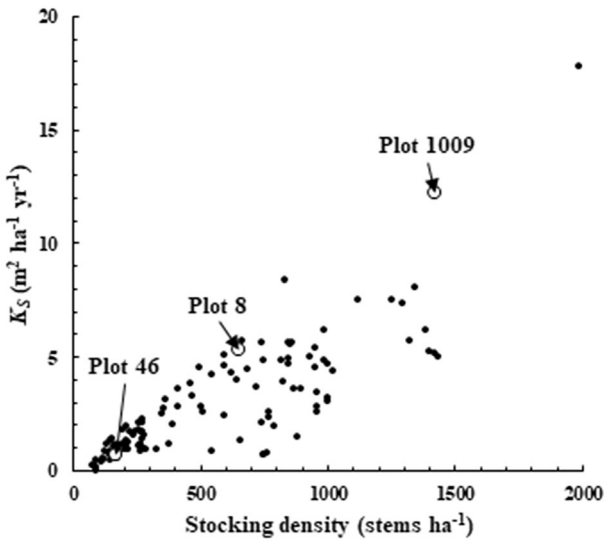


Fig. 3 Scatter plot of pooled symmetric competition intensity (K_S) against stocking density of the plot, at the start of the growth period concerned, determined for the data set available here. To avoid confusion in the figure, just one result was selected at random from each of the 121 plots in the data set. Results for the three example plots shown in Fig. 2 are identified

This steady increase in symmetric competition intensity with increasing stocking density is what might be expected. The more trees present at a site, the less of the below-ground growth resources will each be able to access as others compete with it. The decline in growth rate of any one tree, from what it could be if there was no competition, will then likely be greater as its share of the growth resources declines. As discussed in the Appendix, since root uptake of growth resources can be expected to be generally proportional to root system (hence tree) size, competition below ground may be assumed to be principally symmetric. Thus, the overall intensity of symmetric competition may be expected to increase as stocking density increases.

Tree size development

The results above have shown asymmetric competitive effects to be appreciably less intense and important than symmetric competition effects, at least in the even-aged, monoculture forests used here. However, that is not to say that asymmetric competitive effects did not have a substantial influence on how tree sizes develop with age.

If symmetric competitive effects only were applying in a stand, tree growth rates would be directly proportional to tree sizes, as illustrated for Plot 46 in (Fig. 2c). Under those circumstances, the spread of tree sizes would increase progressively with age, since larger trees would always be growing faster than smaller. However, the shape of the frequency distribution of tree sizes would remain unaltered, meaning that its skewness and kurtosis would remain constant with time. By contrast, if asymmetric competitive processes were operating, alone or in addition to symmetric processes, tree growth rates would increase disproportionately with respect to tree size as illustrated for Plot 1009 in (Fig. 2a). Whilst tree size spread would still increase progressively with time, the frequency distribution of tree sizes would become progressively skewed to the right and would become flattened. That is, both the skewness and kurtosis of the distribution would increase with time.

To illustrate if and how asymmetric competitive processes affected the frequency distribution of tree basal areas, results from Plot 8 will be used as an example. This plot was established in regrowth forest and measured 18 times, at 1−3 year intervals, between 17 and 49 years of age. Shortly before its first measurement it had been thinned from below, from a stocking density of about 1500 to 651 stems ha^{-1}. It was not thinned again, but at some time after 29 years of age, two smaller trees died so its stocking density was finally reduced to 635 stems ha^{-1}. Because of its initial thinning, tree growth proceeded over some years with little evidence of a suppressed group of trees developing; Fig. 2b shows its early growth behaviour over 19–21 years of age. However, by 28 years of age a suppressed group was clearly evident and the use of Model (4) to describe growth behaviour changed to use of Model (3) thereafter; (Figs. 1a, 4) of West and Ratkowsky (2022b) show scatter plots for this plot of growth rate against age for several growth periods over 29–49 years of age, together with the fit to those data of Model (3).

Figure 4 shows how competitive processes developed over the 32 years for which this plot was measured. Figure 4a shows that the intensity of symmetric competition pooled over the plot (K_S) tended to increase with age, although reaching a more or less constant value sometime after 35 years of age. Figure 4b shows how the positive intensity of asymmetric competition (K_{A+}) increased with age, leading to increased reduction in growth rates of smaller trees. Figure 4c (K_{A-}) shows how the growth advantage then gained by larger trees through asymmetric competition increased with age as smaller trees were suppressed.

Figure 4d shows the change with age of the 'growth dominance statistic'. This statistic may be used to help determine what competitive processes are applying in a stand (Binkley 2004; Binkley et al. 2006). It quantifies the extent to which either larger or smaller trees are growing at rates that are disproportionate with respect to their sizes. It takes values in the range −1 to +1. If symmetric competition only is occurring, its value is zero. If its value is positive, size-asymmetric competition is occurring, and, if negative, inverse size-asymmetric competition applies. However, it does not determine if both symmetric and asymmetric competition are occurring at the same time. Its method of computation is described in detail by West (2014, 2018). Figure 4d shows

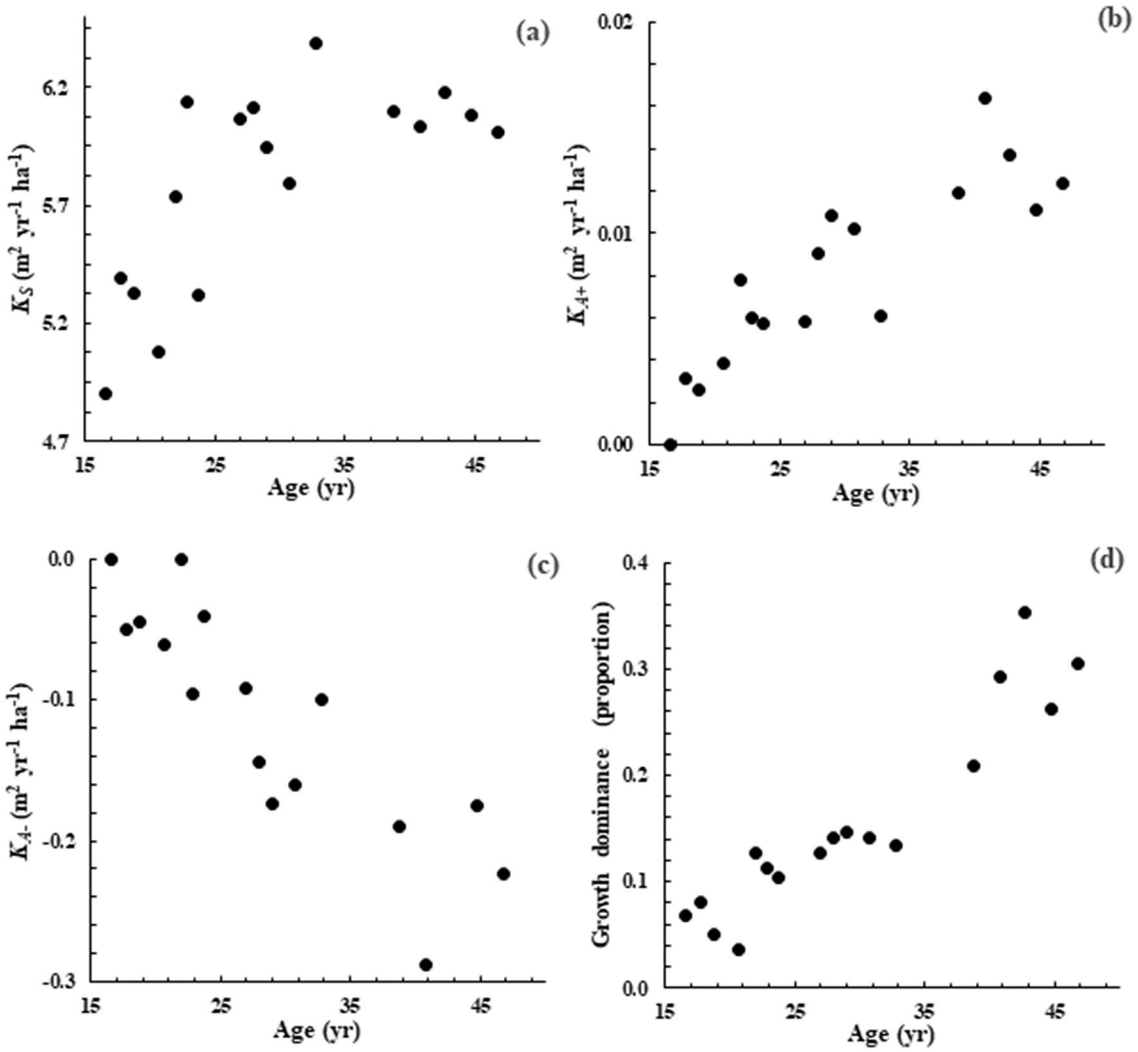


Fig. 4 Scatter plots showing the changes with age, at the start of each growth period of Plot 8, of pooled competition intensities **a** K_S, **b** K_{A+} and **c** K_{A-} and of **d** growth dominance

that its value tended to increase with age in Plot 8. That is, the tendency for larger trees to dominate growth increased with age, consistent with the tendency for K_{A+} to increase with age (Fig. 4b). However, it is important to compare the scales of (Fig. 4a–c); that makes it clear that that the intensity of symmetric competition was always far greater than that of asymmetric competition, consistent with the results of (Figs. 2d–f) and (Table 2).

Despite the much lower intensity of asymmetric competitive processes when compared with symmetric, as has been identified in this work, the results of (Fig. 5) make it clear that the asymmetric processes were quite sufficient to affect substantially the frequency distribution of tree sizes in the plot. Tree size inequality increased as the spread of the frequency distribution of sizes in a population became both wider and more even. Inequality is commonly assessed using the Gini coefficient, the value of which rose with age in Plot 8 (Fig. 5a); the use and computation of this statistic is described by West (2018). As well, both the skewness and kurtosis of the tree size distribution tended to increase with age (Fig. 5b, c), although becoming more or less constant at later ages. The net result of these changes can be seen by comparing the shape of the distributions at the first and last measurements of the plot (Fig. 5d). These changes reflect the long term effects of the asymmetric competitive processes in the plot.

Discussion and conclusions

There has been considerable discussion in the literature about how competitive processes between individual trees arise and whether they be symmetric or asymmetric in their operation (e.g., Schwinning and Weiner 1998;

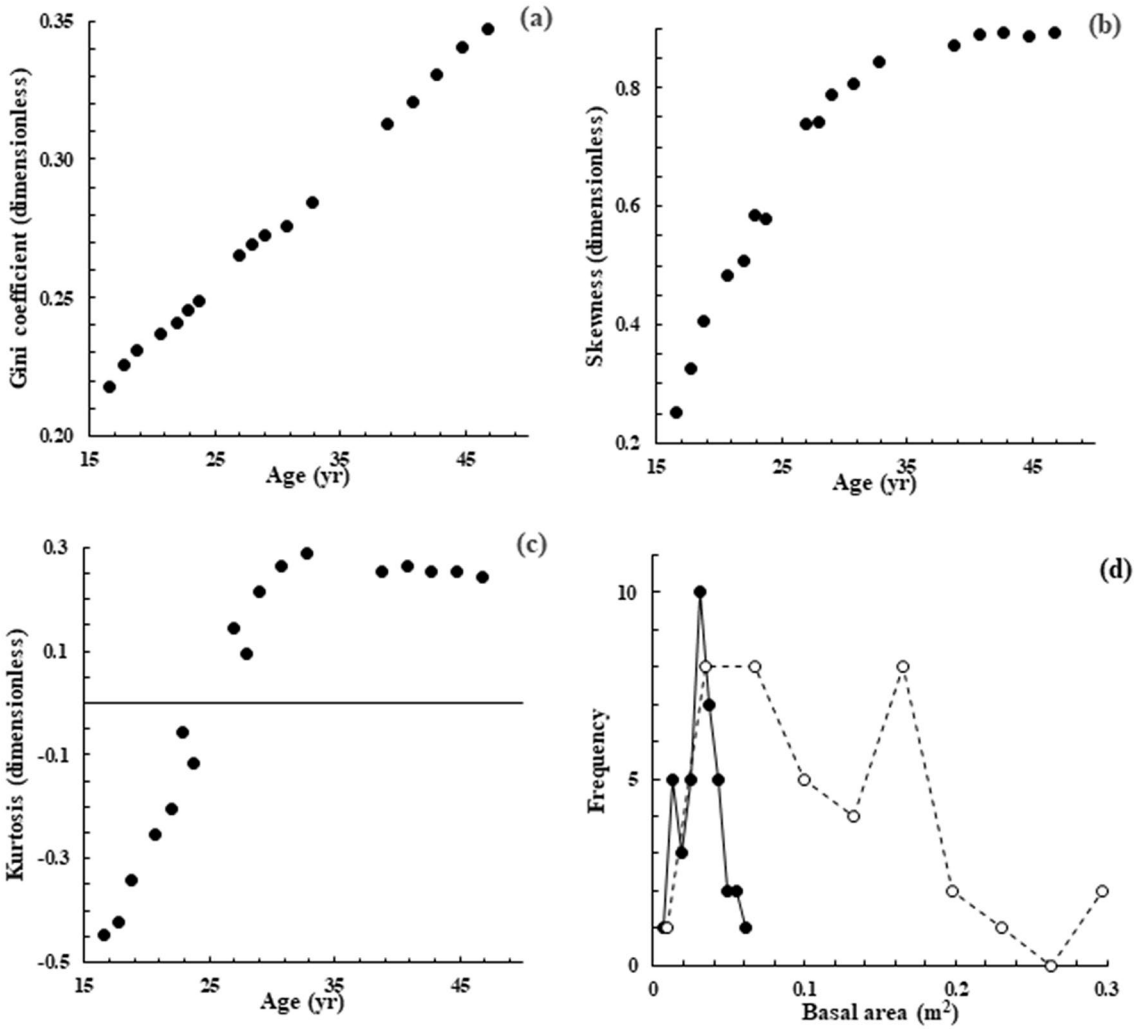


Fig. 5 Scatter plots showing changes with age, at the start of each growth period of Plot 8, of properties of the frequency distribution of tree basal areas, being **a** size inequality as measured by the Gini coefficient, **b** skewness and **c** kurtosis. Then **d** shows the observed distributions at the start of growth at 17 (•——•) and finally at 49 (O----O) years of age; the plot contained 42 trees at 17 years of age and two had died by age 49 yr

Fernández-Tschieder and Binkley 2018; Pommerening and Meador 2018; Forrester 2019; Forrester et al. 2022). Whilst it has often been considered that the principal cause of asymmetric competition is above ground competition for light, through inter-tree shading, and that of symmetric competition is below-ground competition for water and nutrients, through root uptake, there are various other biological processes that may contribute to the development of both forms of competition (see further discussion in the Appendix).

It is important to appreciate that the methods devised in the present work to assess quantitatively the intensity and importance of both forms of competition, in any one stand over any one growth period, are quite independent of the way(s) in which those competitive processes have arisen. They are based on the growth behaviour observed empirically, both under forest conditions when trees are assumed to be growing without any form of competitive inhibition (see Eqs. 1, 2) and when growing in stands in the presence of competing neighbours over any one growth period of no more than a few years (see Eqs. 3, 4, 5). In particular, competition in a stand is defined as only symmetric if observed tree growth rates are directly proportional to tree sizes (Eq. 5) and is defined to be involving asymmetric competition, with or without symmetric as well, if that is not so (Eqs. 3, 4). That is, these methods involve no assumptions as to how the symmetric or asymmetric competitive processes have arisen in the stand and whether they are operating above or below ground or both. No other work known to this author has assessed competitive processes in forests separately and quantitatively using these or any other methods.

At least for the even-aged, monoculture Australian blackbutt forests studied here, a rather unexpected finding was

that individual tree growth rates were determined principally by symmetric competitive processes and far less by asymmetric processes (Figs. 2, 4, Table 2). The part of the hypothesis advanced in the Introduction that symmetric processes are likely to be more influential at younger ages was supported (Fig. 4a). That increase with age was principally a consequence of the slope of Model (5) declining with age as stand growth rate declined with age in the plot being used as an example there. This is consistent with the well known behaviour for overall forest growth rates to decline progressively after a certain age (e.g., Ryan et al. 1997). Many theories have been advanced to explain this, but the most recent findings suggest it is a consequence of increasing respiratory costs, associated with increasing tree ages (that is, sizes), that reduce the overall metabolic efficiency of tree growth (West 2020, 2021); the effects of this are apparent in the shape of Model (1), as illustrated in Fig. 1).

However, the net effects of asymmetric competition on tree growth rates in a stand were independent of age and averaged close to zero (Figs. 2d–f, 4b, c, Table 2). But, as age increased, the positive effects of asymmetric competition on larger tree growth rates increased (Fig. 4b), whilst the negative effects on smaller tree growth rates declined (Fig. 4c). This is likely to have reflected a progressively increasing ability of progressively larger trees to shade smaller trees, with a concomitant progressively increasing incidence of asymmetric competitive processes, as reflected in the growth dominance index (Fig. 4d). These changes with age of the effects of competitive processes will be tempered by changes, from time to time, in the stocking density of a stand (Fig. 3), particularly as a consequence of management practices such as thinning.

It was clear also that whilst they were much less intense than symmetric competitive effects, asymmetric effects were sufficient to influence substantially the development of the shape of the distribution of tree sizes with time (Fig. 5); if symmetric competition only was applying, the spread of the distribution would be affected with time, but not its shape. The shape of the frequency distribution can be altered also as trees are lost through mortality. Normally trees that die come from amongst the smaller, suppressed trees in the stand. Extensive studies have shown how the shape of the growth rate function, the variation in tree growth rates and tree losses through mortality combine to alter the frequency distribution of tree sizes with time (e.g., Westoby 1982; Hara 1984a,b, 1986, 1992; West and Borough 1983; West et al. 1989; Yokozawa and Hara 1992; Masaki et al. 2006; West and Smith 2019).

Ultimately, the results imply that it is essentially the size of a tree at any time that is the prime determinant of its subsequent growth behaviour. This defines the extent of the spread of its root system below ground and the size of its canopy. In turn, these determine, firstly, the maximum possible amount of growth resources the tree can access from whatever resources are available on the site on which it is growing. Secondly, they determine the intensity of competition between it and its neighbours, competition that limits the proportion of the total resources on the site that are actually available to each tree. Of course, at any time the size of a tree reflects both the growth behaviour of the tree up to that time and the availability from the site of the resources it required for that growth. But then, its size at a particular time should be a good indicator of both its maximum potential for future growth and its competitive capabilities which will determine its growth rate in relation to its neighbours.

Recognition of this importance of tree size perhaps explains why the extensive past modelling work (described in the Introduction) has often found that competition indices, designed to quantify inter-tree competitive processes, make a relatively small contribution to explaining growth. West and Ratkowsky (2022a) examined some such models that tested the inclusion of competition indices designed to define separately the influence of both symmetric and asymmetric competitive processes. They found that the competition indices were correlated substantially with tree size and included tree size itself as part of their construction. Thus, the inclusion of tree size alone in a model often makes that model a reliable predictor of tree growth.

Others have claimed to develop models to predict tree growth that exclude tree size as a predictor variable. For example, Larocque (2002) used data from an experimental plantation of red pine (*Pinus resinosa* Ait.) in Canada. He omitted tree size directly as a predictor variable in a model to predict tree basal area growth rates. However, he included a competition index designed to describe asymmetric competitive processes that incorporated both tree crown size characteristics and tree basal area as part of its formulation. Thus, by default, Larocque did incorporate measures of aspects of tree size in the model while feeling that he had not done so. Brand and Magnussen (1988, p. 909) went so far as to say that "… growth rate is naturally related to tree size and its inclusion in models can confuse the expression of the effect of competitive stress". The present work suggests that the competitive status of a tree is determined by characteristics that reflect its size and so models to predict its growth will inevitably include size as a predictor variable and/or other variables that are related to its size.

Of course the relationships between growth and size may sometimes be rather more complex than those considered in the individual stand relationships dealt with here (Fig. 2a, b, c) and as used in other studies (e.g., West and Borough 1983; Wichmann 2001; Forrester et al. 2011; Glencross et al. 2016; West and Smith 2019). When data have been pooled over many stands of many ages and different site productive capacities and a model then developed to predict individual tree growth rates, tree sizes may

still form a primary predictor in the model. However, to get an adequate fit to the data in such cases, it may require more complex parameterisations of the model and transformations of the data than were considered here.

The present work dealt specifically with data from even-aged, monoculture forests. Many of the principles of inter-tree competitive processes will apply in the more complex uneven-aged and mixed species forests. However, the effects of these processes will be modified by the physiological differences between different species. For example, the effects on growth rates of shading will be affected by characteristics such as the shade tolerance of different species. Similarly, growth of a seedling that has regenerated below an established canopy of larger trees will be restricted by shading and below-ground competition of the bigger trees; its subsequent performance will then be influenced by this as well as by its shade tolerance characteristics. There are numerous studies of intra- and inter-specific interactions in these more complex forests (Biging and Dobbertin 1995; Vettenranta 1999; Uriarte et al. 2004a,b; Canham et al. 2004, 2006; Dolezal et al. 2009; Forrester et al. 2011; del Rió et al. 2016; Quiñonez-Barraza et al. 2018; Zambrano et al. 2019, 2020; Bongers 2020; Trogisch et al. 2021; Wambsganss et al. 2021; Bi et al. 2022). That of Coates et al. (2009) for mixed hardwood and softwood species of British Columbia, Canada, suggested that below-ground competitive processes tended to be appreciably more important in affecting growth than did above ground shading effects (their Fig. 5); the importance of shading effects varied between species over the range 0−30%, depending on their shade tolerances. Even genetic differences within the one species have been found to affect the level of competition between individuals (Pretzsch 2021b).

In conclusion then, the present work is perhaps unique in that it developed methods to separate clearly the effects of tree size and both symmetric and asymmetric competition on individual tree growth rates. Its findings that symmetric competitive effects were far more important than asymmetric were unexpected. However, it is important to appreciate that this conclusion was based on examples using information from even-aged, monoculture forests of one species in one part of the world. Much further work will be necessary to address the relevance of the approaches developed here for other tree species throughout the world and for the more complex, multi-species, uneven-aged forests.

Appendix

See Appendix Fig. 6

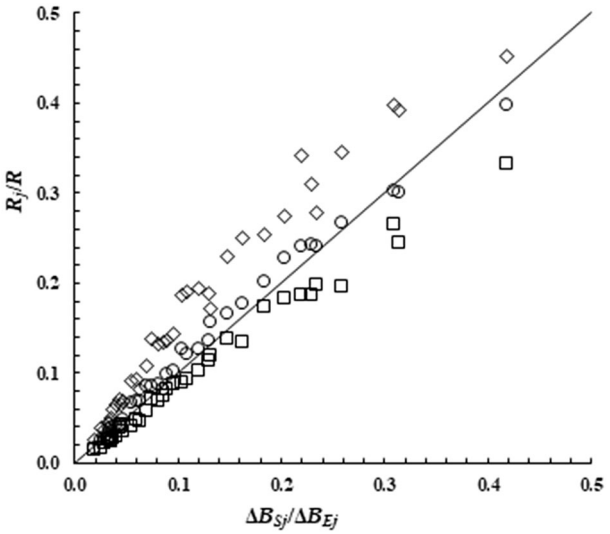


Fig. 6 For individual trees of Plot 1009, scatter plots of the average of 20 simulated estimates of R_j/R against values of $\Delta B_{Sj}/\Delta B_{Ej}$ (see Eq. 21) as determined with the number of trees making up a patch of competing trees being six (◇), eight (O) or 10 (□). Results are shown for a random selection of one third of the total of 109 trees in the plot or else too many values become super-imposed and the results become difficult to appreciate. The solid line is a 1:1 line on which all the points would lie if the agreement between the two ratios was perfect

Simulation study examining uptake of ground resources in relation to below-ground competitive processes

This study aimed to examine the relationship between tree growth rates and the ability of their root systems to take up the below-ground resources necessary for growth, water and nutrients, under varying levels of inter-tree competitive intensity. Such competition has often been assumed to be symmetric, where plants take up amounts of growth resources in proportion to their root biomasses, with consequent proportionality of their growth rates (Putz and Canham 1992; Weiner et al. 1997; Schwinning and Weiner 1998; Casper et al. 2003; Bartelheimer et al. 2008; Coates et al. 2009; Pommerening and Meador 2018). However, some circumstances have been found to give larger plants an advantage and led to some asymmetry of uptake. These have included spatial heterogeneity of resources in the soil or of litter layers (Casper and Jackson. 1997; Rajaniemi 2003; Hodge 2006; Forrester 2019; Garlick et al. 2021), conditions of low water availability (Forrester 2019; Forrester et al. 2022), development of ectomycorrhizal systems on roots (Franklin et al. 2014) and of inter-specific effects in mixed species populations (Putz and Canham 1992; van Noordwijk et al. 1996; Forrester 2019; Boyden et al. 2012; Forrester et al. 2022). Higher efficiency of water uptake by

smaller trees may even lead to inverse-symmetric competition (Meinzer et al. 2005).

It was clear from Fig. 2b, c that there are cases in the even-aged, monoculture forests being considered here that little or no asymmetric competition occurs over some growth periods. Presumably competition for below-ground resources is indeed symmetric only in those cases. For the present study, it was then assumed that this is the case for any growth period and that the incidence of some below-ground asymmetric competitive effects is generally restricted to circumstances that are in some respects atypical, as the discussion above implies. Given this assumption, an hypothesis was advanced for this study that, if inter-tree competition for uptake of growth resources from the soil is reduced, there will be corresponding and predictable increases in tree growth rates.

Suppose a subject tree is located alone at the centre of a circular patch in a stand and has no neighbours whose root systems would otherwise overlap its root system and compete with it for growth resources from the soil. Suppose there is some total amount R (its units are unimportant here) of those resources available in the patch that the subject tree takes up. The amount of those resources would reflect the environmental circumstances of the site on which the tree was growing.

Suppose now that other trees are introduced into the patch. Suppose they are close enough that their root systems overlap that of the subject tree and they compete with it, and each other, for the growth resources within the patch. Suppose there are then n trees in the patch, including the subject tree. Suppose that the ith tree in the patch takes up an amount of the resources, R_i, that is proportional to its size as represented by its stem basal area, B_i (m^2), that is, consistent with symmetric competitive processes. Assume that, between them, all the trees in the patch take up the total amount of the resources available from the patch. Thus

$$R = \sum_{i=1\ldots n} R_i = \lambda \sum_{i=1\ldots n} B_i \tag{19}$$

where λ is the constant of proportionality of the uptake by individual trees. The growth rate of the ith tree in the patch (ΔB_{Si}) would then be proportional to its size, that is, consistent with the form of Model (5) and the processes of symmetric competition.

Suppose now the jth tree of the patch is the subject tree. In the presence of the competitors, it takes up an amount R_j of the resources, where

$$R_j = \lambda B_j \tag{20}$$

Whether free of competition or not, its growth rate would be proportional to the quantity of growth resources available to it. Thus, it might be expected that the ratio of its growth rate when subject to competition from other trees to its growth rate when free of competition might be the same as the ratio of its resource uptake when subject to competition to its resource uptake when free of competition. That is, it might be expected that

$$\Delta B_{Sj}/\Delta B_{Ej} = R_j/R = \lambda B_j \Big/ \left(\lambda \sum_{i=1\ldots n} B_i\right) = B_j \Big/ \left(\sum_{i=1\ldots n} B_i\right) \tag{21}$$

where ΔB_{Sj} and ΔB_{Ej} may be predicted using Eqs. (6) and (2), respectively. If Eq. (21) can be found to hold for all the trees in a stand, when each is treated as a subject tree, it might be assumed that tree growth rates are reflected directly in their growth resource uptakes.

Numerous simulations based on this theory were carried out for the circumstances of Plot 1009 as they are shown in (Fig. 2a). In each simulation, the number of trees in a patch within which trees were assumed to be competing (that is, the value of n) was varied. Each tree in the plot was treated as a subject tree and the competitors with it in the surrounding patch were chosen at random from amongst the other trees in the plot. A total of 100 simulations were done for each tree in the plot, using five different values of n, ranging over 6−10), and 20 different sets of randomly chosen competitors. The estimates of R_j/R (Eq. 21) for the 20 sets of simulations for each value of n, were then averaged for the jth subject tree. A corresponding value of $\Delta B_{Sj}/\Delta B_{Ej}$ was obtained also for the jth subject tree.

Figure 6 shows scatter plots of R_j/R against $\Delta B_{Sj}/\Delta B_{Ej}$ for different trees of Plot 1009 and for simulations that were based on patches that contained six, eight or 10 trees. It was clear that a patch number of eight trees gave estimates of R_j/R that were closest to the values of $\Delta B_{Sj}/\Delta B_{Ej}$, that is, closest to the 1:1 line drawn on (Fig. 6). Of course, there were some 'residual' deviations of those plotted points from the 1:1 line; this is unsurprising since tree growth behaviour is not going to correlate exactly with uptake of growth resources from the soil, given that there are many physiological processes that occur between uptake and growth.

However, the results clearly infer that the removal of competition for growth resources from the soil will lead to good predictions of the increased growth behaviour that results when a tree is free to grow without such competition. That suggests it is indeed realistic to assume that symmetric competitive processes that are occurring in a stand may indeed be reflected in growth rates defined through Models (6−8). That is to say, the intensities of symmetric competition evident for the trees in Fig. 2d–f would seem to be realistic and it follows then that they are indeed generally far greater than the intensities of asymmetric competition.

Also, these results indicated that assuming a patch size of eight trees led to simulation results that were closest to the observed results of Fig. 2a, d. The stocking density of Plot 1009 at the start of the growth period concerned was 1420

stems ha^{-1}. Thus, eight trees in that plot are likely to occur in circular patches with radii of about 4.2 m. This is consistent with studies that have considered competitive processes between trees in a range of forest types and forest circumstances and concluded that competitors of trees generally occur within a range of 4–13 m away from it (e.g., Soares and Tomé 1999; Lederman and Stage 2001; Canham et al. 2004; Coates et al. 2009; Forrester et al. 2011, 2013; Luu et al. 2013; Zambrano et al. 2020; Bhandari et al. 2021a,b). This finding provides further evidence that the assumptions of this study were reasonable and reflect reasonably how symmetric competitive processes operate below ground in forests.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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