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Inter-tree competitive processes occurring over 24 years in a mixed-species Nelder trial

West, P.W.

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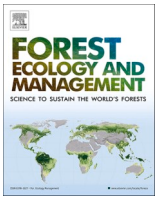
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Inter-tree competitive processes occurring over 24 years in a mixed-species Nelder trial

P.W. West

Faculty of Science and Engineering, Southern Cross University, Lismore, NSW 2480, Australia

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ABSTRACT

Development of symmetric and asymmetric inter-tree competitive processes was assessed to 24 years of age in a Nelder wheel experiment in Queensland, Australia. It contained a mixture of hoop pine (*Araucaria cunninghamii* Aiton ex D.Don) and Queensland maple (*Flindersia brayleyana* F.Muell.). The levels of these processes were assessed through the changes with age of the growth dominance statistic at different stocking densities at planting; this statistic is based on the relative contributions of larger and smaller trees to total stand growth. After 6 –11 years of age, asymmetric competition, probably for light, developed in hoop pine but had barely developed in maple by 24 years. As stocking density increased, hoop pine suffered progressively more intensive competition, but this did not occur in maple. Earlier work had examined tree stem growth rates and found that maple exerted more intense competition on hoop pine than on other maple trees. Hoop pine had much lower inter- and intra-specific competitive effects than maple. It is suggested these effects might be explained through architectural differences between the crown structures of the two species allowing maple to compete asymmetrically for light with hoop pine but not with itself nor hoop pine with maple.

1. Introduction

Reviews are available of the issues that affect neighbouring plants as they compete with each other for the resources they need for growth (e.g. Pommerening and Meador, 2018; Fernández-Tschieder and Binkley, 2018). Each neighbour has a root system, that occupies some below-ground volume, to take up water and mineral nutrients from the soil. It also has a canopy, that has an above-ground volume, to intercept sunlight from time to time during the day. Where their root or canopy volumes overlap, the neighbours will have to compete with each other to obtain the resources each needs.

If the amounts of those resources that either neighbour obtains from the overlapped volumes is proportional to its physiological needs for growth, as reflected by its size, competition between the two individuals is said to be 'symmetric'; the growth of each can then be expected to be directly proportional to its size. If one of the competitors obtains a disproportionately large amount of the resources than the other, the competition is said to be 'asymmetric'; its growth can then be expected to be disproportionately large relative to its size. If it is the smaller competitor that obtains the disproportionately large amount of resources, the competition is termed 'inverse asymmetric'.

Over the life of a forest stand, the influences of these competitive processes will vary through the various stages of stand development as described in a system proposed by Binkley (2004) and Binkley et al. (2006) (reviewed by West, 2024). Initially, as seedlings start to grow each may take up amounts of resources proportional to its size; competition is then believed to be largely symmetric and principally below ground for water and nutrients. Differences in growth rates of differently sized individuals then lead to differences in tree heights, when a new growth phase starts; that involves asymmetric competition for sunlight, when taller trees tend to shade smaller, in addition to the symmetric competition for water and nutrients that is already occurring. Asymmetric competition for below ground resources has been found occurring where distribution of soil resources is irregular (Hodge, 2006) and, in mixed species forests, where the species have different uptake capabilities depending on resource availability (Schenk, 2006) or where root growth behaviour of one species is affected by the presence of another, particular species (Leuschner et al., 2001; Lei et al., 2012; Rasmussen et al., 2019; Lak et al., 2020; Mekontchou et al., 2020; Sheng et al., 2020; Wambsganss et al., 2021). 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.

E-mail address: pwest@nor.com.au.

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Over many years and for many forest types around the globe, models have been developed to relate individual tree growth rates to the competitive processes between them and their neighbours. Major texts offer substantial reviews of such work (e.g., Weiskittel et al., 2011; Burkhart and Tomé 2012). Often in such work, tree biomass is used to describe growth. 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 (1.3 m above ground) usually correlates well with tree biomasse and is much easier to measure. It has most commonly been used in studies examining tree growth rates as affected by inter-tree competitive processes and is the characteristic that will be considered in the present work.

As discussed by West (2024), in even-aged, monospecific forests much of tree growth behaviour is determined largely by symmetric competition from neighbouring trees for below ground soil resources and, in later years as trees grow taller, this is supplemented by asymmetric competition above ground for light. Some evidence has suggested that symmetric competition has considerably more substantial effects on growth rates than asymmetric at all stages of forest development (West 2023a). In more complex, uneven-aged and/or mixed-species forests, interactions between individual trees that affect their growth rates can reflect a wide range of biological mechanisms that may include inter-tree competitive processes (Pommerening and Meador, 2018; Trogisch et al., 2021).

The present work aimed to examine tree growth behaviour and competitive processes in one type of more complex forest, in this case an even-aged forest with two species growing together. It used data from an experiment involving tree species, native to tropical east coast regions of Australia, the gymnosperm hoop pine (*Araucaria cunninghamii* Mudie) and the angiosperm Queensland maple (*Flindersia brayleyana* F.Muell.). These had been grown together for 24 years at a range of stocking densities, using the circular experimental design of Nelder (1962). The objectives of this work were (a) to determine if and how growth of either or both species was affected by intra- or inter-specific symmetric and/or asymmetric competitive processes and (b) how variations in age and stocking density across the experiment affected those processes. Such work is complementary to that undertaken with results of other Nelder trials which have looked at growth or physiological behaviour in mixtures of tree species with grasses or other agricultural species (Cole and Newton, 1987, 2019, 2023; Newton and Cole, 1991; Doran et al., 2001; Pachas et al., 2019; Ruano et al., 2022).

2. Methods

2.1. Experimental

The experiment considered here was established in June 1990 with one-year old seedlings on a fertile, 1-ha site near Mt Mee (27° 4′ S, 152° 46' E) in southeast Queensland, Australia. The area has a sub-tropical climate. Its average annual rainfall is around 1100 −1500 mm, most of which falls in the summer months. Summers are hot and humid with daily maximum temperatures around 30 −35°C. Winters have mild days and cool nights with maximum temperatures around 20 −22°C and minimums as low as 5 −10°C. The soils of the area are deep and well-structured ferrosols (Isbell, 2021) derived from basalts. The site was at an altitude of 400 m, had a slope of about 5°, a south westerly aspect and was sometimes exposed to strong south easterly and westerly winds. It would have originally carried rainforest, but had been cleared for agriculture for at least 100 years (Lamb and Borschmann, 1998).

The experiment used the circular design 1a of Nelder (1962) with eight circles and 18 radii, arranged at angles of 20°. The radius, r_n (m), of the nth circle was determined as $r_n = r_0\alpha^n$, where $r_0 = 3.1614$ m and $\alpha = 1.3914$. In addition, there were two inner circles which simply filled the centre region of the design and were not intended to be measured. One of those two circles had six trees planted at a radius of 0.7 m from the centre and the other had nine trees at a radius of 2.6 m. Nine of the radii were planted with hoop pine and nine with maple. Layout of the trees of both species in circles 1−8 of the design are shown in Fig. 1.

Trees were measured on 21 occasions from the time of planting until 24 years of age. Measurements were done at 4–6 monthly intervals until early 1997. They then became less frequent until 2014, being at 1 −5 year intervals, averaging 2½ years. Tree heights and/or stem diameters at breast height were measured, the latter not before a tree had reached breast height. Heights were not measured after 12 years of age. The present work used the data available from measurements taken during 1.8 −24 years of age from trees in circles 2 −7 only. At establishment, the stocking densities of trees in those six circles were 2150, 1140, 595, 305, 158 and 82 stems ha^{-1}, from innermost to outermost respectively. By the time of the last measurements used here, there had been some mortality with, at most, three hoop pine and one maple tree lost from the nine of each species in any one circle. Losses tended to be slightly higher in circles with higher stocking densities; none of either species was lost in the circle with the lowest stocking density.

2.2. Growth dominance statistic

Individual tree growth rates in stem basal area, relative growth rates and growth dominance were determined for each measurement growth period of each of circles 2 −7 of the experiment. Because the length of growth periods varied from time to time, age at the centre of a growth period was used in subsequent analyses to represent age of the trees at that time. Initially, each circle had 18 trees, half hoop pine and half maple (Fig. 1). Using the growth data of trees that survived a growth period, separately for each species, a measure of the extent to which inter-tree asymmetric competition was super-imposed on symmetric competition within each species was assessed using the 'growth dominance statistic' (Binkley, 2004; Binkley et al., 2006; Larocque et al., 2013; West, 2014, 2018, 2023a; Cordonnier and Kunstler, 2015). It is determined from growth data of individual trees that survive a growth period, usually of no more than a few years, in a stand (a circle of the experiment in the present case) in relation their sizes (West, 2018).

The statistic is based on a scatter plot of the proportional cumulative growth of successively larger trees in a stand against their proportional cumulative sizes; such scatter plots, and their interpretation as to the extent to which asymmetric competition is occurring, are illustrated in the examples shown in Fig. 2. Following Eq. (2) of West (2014), the growth dominance statistic (G, dimensionless) of the n trees that

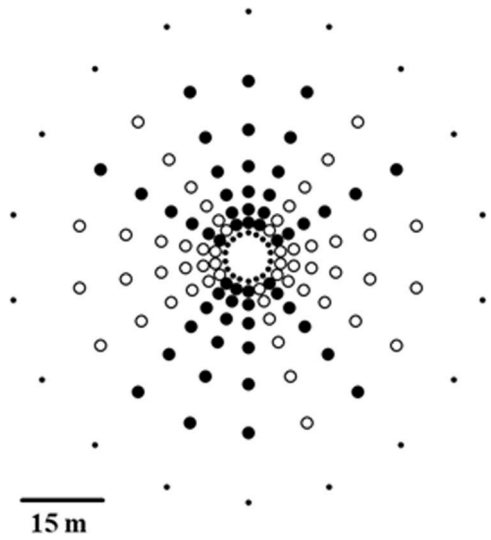


Fig. 1. The layout of the trees planted in eight circles of the Mt Mee Nelder trial. Tree species, and their positions in circles 2 −7, are shown as (O) hoop pine or (●) maple. Data (•) from trees in circles 1 and 8 were of corresponding species in each radius, but were not used in the analyses here.

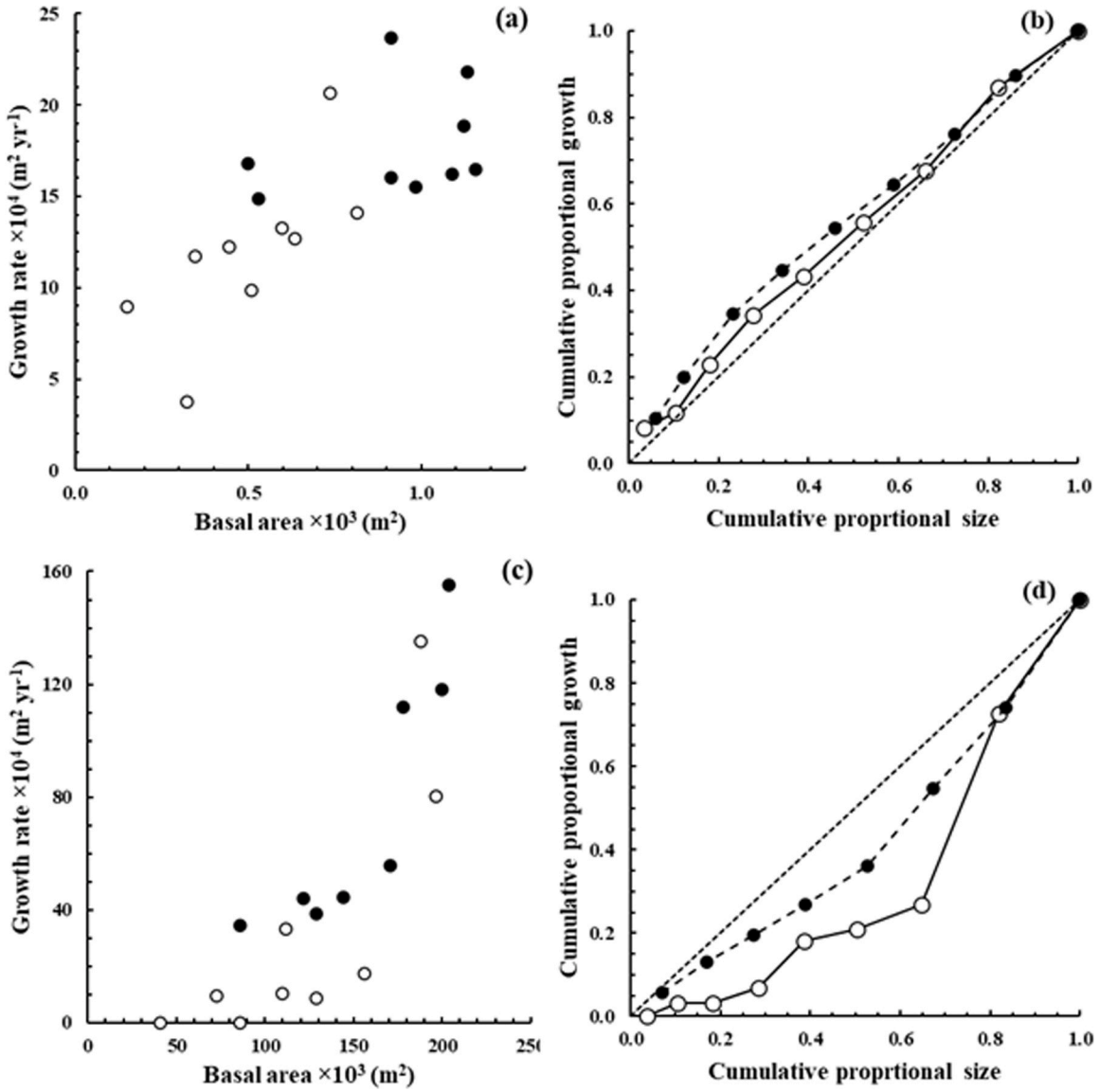


Fig. 2. Example scatter plots (a) at 2.4 −2.8 years of age, and (c) at 21.8 −23.8 yr, of individual tree basal area growth rates against tree basal area at the start of the growth period concerned for (O) hoop pine and (●) maple. Results are from Circle 6 of the experiment. Corresponding scatter plots (b,d respectively) show the cumulative proportional tree basal area growth rates against cumulative proportional tree basal areas for both species as used to determine growth dominance during the period concerned as discussed in the text. In these cases, growth dominances for hoop pine and maple, respectively, were (b) −0.070 and −0.121 and (d) 0.360 and 0.175.

survived the growth period concerned, of either of the species in a circle of the experiment, was determined as

$$G = 1 - \Sigma_{i=1\ldots n}\,(q_i - q_{i-1})\,(r_i + r_{i-1}) \quad (1)$$

where q_i was the basal area of the ith tree of that species in the circle at the start of the growth period, expressed as a proportion of the total basal area of the rees in the circle, and which had been arranged in ascending order so that $q_{i+1} \geq q_i$. Then, r_i was the corresponding growth in basal area, between a pair of successive measurements, of the ith tree of the circle, expressed as a proportion of the total growth of the trees in the circle, and $q_0 = r_0 = 0$.

Of course, all the trees in any one circle of the experiment will be subject to competitive interactions from trees of adjacent circles. All that competition will then be reflected in the value determined for growth dominance of the trees in that circle. But, the objectives of the present work were achieved by examining the difference in behaviour of the two species within particular circles. Others have used the development over time in the size distribution of trees in a stand to infer what competitive processes have been occurring (e.g. Weiner, 1990; Weiner and Thomas, 1986; Wyszomirski et al., 1999; Rasmussen and Weiner, 2017). However it appears the growth dominance statistic is a more reliable indicator because it is based on the short-term growth behaviour of individuals (Fernández-Tschieder and Binkley, 2018).

The growth dominance statistic reflects the relationship between the relative growth rates of individuals in a stand to their sizes. Suppose at some age, A, a plant is of size B. Its relative growth, R, is then defined as $R = (1/B)(\mathrm{d}B/\mathrm{d}A) = \mathrm{d}[\ln(B)]/\mathrm{d}A$, where $\ln(\bullet)$ denotes natural logarithms. If its size changes from B_1 to B_2 between ages A_1 and A_2, its relative growth rate over that period may then be approximated as $[\ln(B_2) - \ln(B_1)]/[A_2 - A_1]$. If inter-tree competition for site resources is symmetric, resource uptake and growth will be directly proportional to tree size and relative growth rates will be unrelated to tree sizes. If competition is asymmetric and larger trees are obtaining amounts of growth resources that are disproportionately large with respect to their sizes, relative growth rates will increase with tree sizes. If competition is inverse asymmetric and smaller trees are obtaining amounts of growth

resources that are disproportionately large with respect to their sizes, relative growth rates will decrease with increasing tree sizes.

2.3. Assessing competition

The first objective of the present work involved determination of the growth dominance statistic for both species. For each of the various measurement periods over the duration of the experiment and for its various circles, scatter plots were drawn of tree basal area growth rates against basal area at the start of the growth period concerned. Fig. 2(a,c) show examples of such scatter plots at two ages for trees in Circle 6, which had an initial stocking density of 158 stems ha^{-1}.

The growth dominance statistic was then determined through a scatter plot of the proportional cumulative growth of successively larger trees against their proportional cumulative sizes, consistent with Eq. (1). This has been illustrated using the growth data in Fig. 2(a,c) to give the respective cumulative growth results of Fig. 2(b,d). If such a cumulative growth scatter plot falls on a 1:1 line (the dotted lines shown on the Fig. 2b,d), trees of all sizes will be contributing growth to the overall growth of trees in the stand by an amount that is directly proportional to their sizes, tree relative growth rates will be unrelated to tree sizes and inter-tree competition will be symmetric. If the scatter plot falls above the line, the statistic will have a negative value. That implies that smaller trees are contributing to the overall growth of the stand by amounts disproportionately large relative to their sizes, their uptakes of growth resources are then disproportionately large with respect to their sizes and inter-tree competition is inverse asymmetric. If the scatter plot falls below the 1:1 line, the statistic will have a positive value. In that case, competition will also be asymmetric as larger trees in the stand grow and take up resources in amounts disproportionately large with respect to their sizes, most commonly by shading smaller trees.

For the second objective of the present work, models were sought to determine if the growth dominances observed for each species could be related to their ages of measurement and the stocking density at establishment of the circles of the experiment in which they occurred.

These procedures were followed and growth dominance results obtained for each of hoop pine and maple for 17 growth periods in circles 2 –7 of the experiment from 1716 observations of individual tree stem

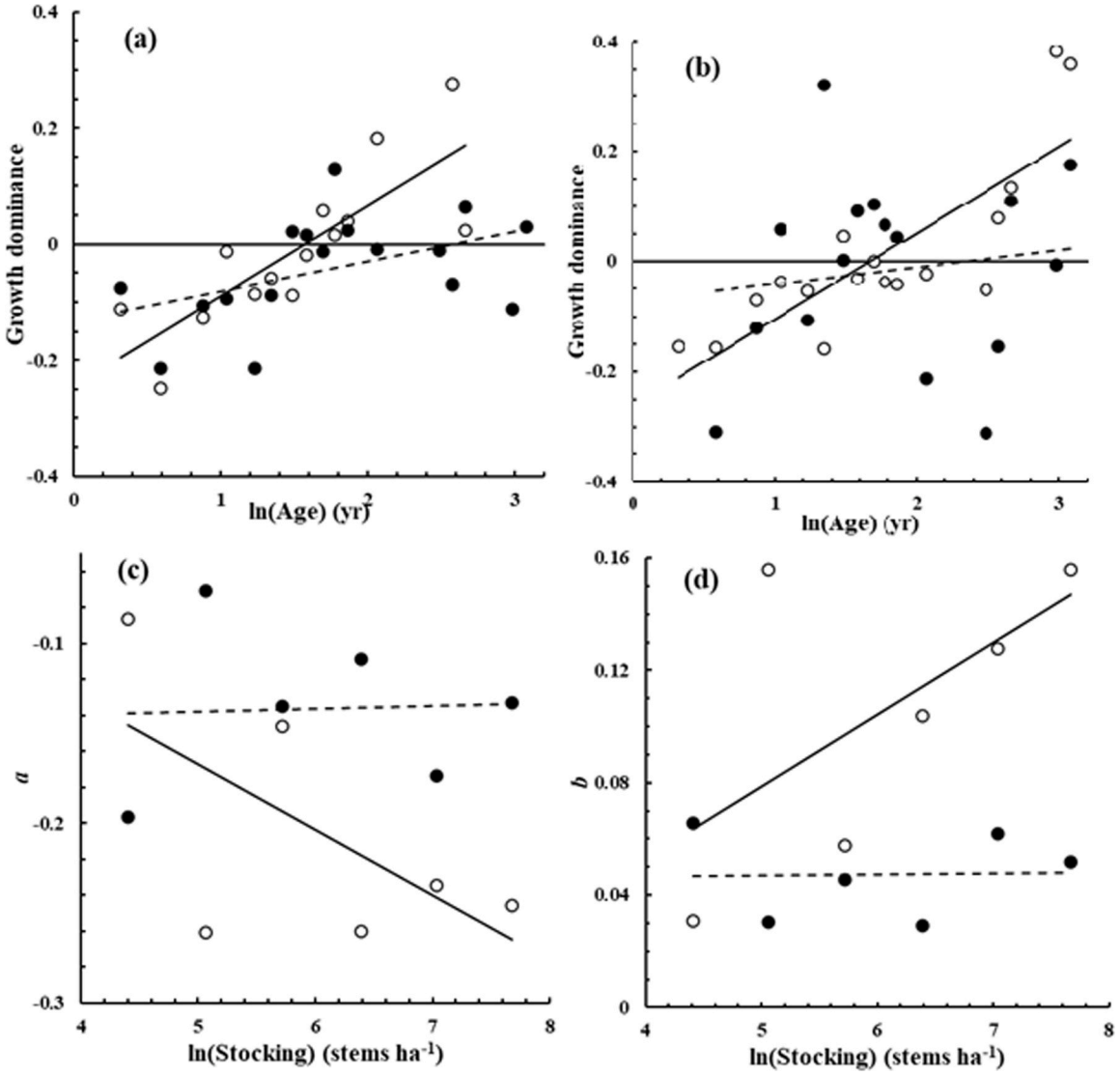


Fig. 3. In (a,b), scatter plots are shown of growth dominance against the natural logarithm [ln(•)] of age, at the midpoint of the growth period used to predict growth dominances, for (O,—) hoop pine and (●,– – –) maple in each of (a) Circle 2 (1250 stems ha^{-1} at planting) and (b) Circle 6 (158 stems ha^{-1}) of the Nelder trial. The lines shown are the ordinary least-squares fit of in each case of Model (2). In (c,d), scatter plots are shown of estimates of the parameters *a* and *b* from Model (2) against the natural logarithm of stocking density at establishment for the six circles of the experiment, with ordinary least-squares fits to the data in each case for Models (3a) or(3 b).

basal area growth rates. Some earlier publications have reported various aspects of the growth and development of the trees in this experiment (Lamb and Borschmann, 1998; Vanclay, 2009; Vanclay et al., 2013).

3. Results

As an example of the results obtained from these determinations of growth dominance, Fig. 2(b) suggest that in circle 6 at young ages, 2.4 −2.8 yr, there was a little inverse asymmetric competition affecting growth of both species, where smaller trees have the competitive advantage. However at later ages, 21.8 −23.8 yr, Fig. 2(d) suggests asymmetric competition was occurring with larger trees having the competitive advantage; this affect appeared to be greater in hoop pine than in maple.

The next stage of the analysis was to determine if the growth dominances observed for each species could be related to their ages of measurement and the stocking densities at establishment of the circles of the experiment in which they occurred. Fig. 3(a,b) show examples of the changes with age in growth dominance for both species and for two circles of the experiment. For all seven circles and both species, it appeared that this relationship could be described by the model

$$G = a + b\ln(A) \tag{2}$$

where G was growth dominance and A (yr) was age at the mid-point of the growth period between any two measurements, ln(•) denotes natural logarithms and a and b are parameters. Two examples of this relationship, for two of the circles of the experiment, are shown in Fig. 3 (a,b). This model was fitted to the data of each circle using ordinary least-squares regression analysis as shown on the Figure.

As a second stage of this analysis, scatter plots were drawn relating both a and b, as determined separately for each species and circle with Model (2), to circle stocking density at establishment. These scatter plots are shown in Fig. 3(c,d) for the same two circles. These suggested that possible second-stage models might then be

$$a = a_1 + a_2\ln(S) \tag{3a}$$

and

$$b = b_1 + b_2\ln(S) \tag{3b}$$

where S (stems ha^{-1}) was stocking density at establishment and a_1, a_2, b_1 and b_2 were parameters. The ordinary least-squares relationship shown fitted to the data of Fig. 3(c,d) suggest these relationships might fit reasonably for hoop pine, but barely at all for maple. Models (3a,b) were then fitted jointly using seemingly unrelated regression (SUR) as implemented in the procedure MODEL of the SAS® statistical package.[1] Note that SUR has been found convenient for use in two-stage models such as that here and takes account of the correlation amongst the residuals of the fitted model that may have occurred as a consequence of the repeated measurements in both a spatial and temporal sense in the present data set (West and Ratkowsky, 2024). Substituting Models (3a, b) back into Model (2) yielded a complete, two-stage model as

$$G = a_1 + a_2\ln(S) + b_1\ln(A) + b_2\ln(S)\ln(A) \tag{4}$$

Scatter plots of the residuals from this model against their fitted values, ln(S) and ln(A) showed little discernible pattern for either species. The SUR parameter estimates and their standard errors are shown in Table 1.

Fig. 4 shows how Model (4) predicts the change with age in growth dominance and how this varied in each of the six circles of the experiment. In the case of hoop pine (Fig. 4a) growth dominance was initially negative. That is, smaller trees in the stand were dominating growth initially, the effect progressively declining as growth dominance increased with age. Until about 4 −5 years of age, this inverse asymmetry was more pronounced (more negative) with higher stocking density. Thereafter, it was reversed and became greater with lower stocking densities until around 6 −11 years of age. At ages beyond 6 −11 years, growth dominance became positive, indicating that larger trees were dominating growth. This effect then increased progressively with age and was greater with higher stocking density. In the case of maple (Fig. 4b), stocking density had negligible effect on growth dominance at any age, as had appeared apparent in Fig. 3(c,d). However, as with hoop pine, there was progressively decreasing dominance with age by smaller trees until larger trees just began to take over dominance somewhere between 15 −16 years of age.

Table 1
Parameter estimates (and their standard errors in parentheses) of Model (4) as estimated fitting Models (3a,b) with SUR over all circles and ages for each of the two species under consideration here in the Mt Mee Nelder trial.

	Parameter			
	a_1	a_2	b_1	b_2
Hoop pine	0.0149	−0.0365	−0.0492	0.0255
	(0.1433)	(0.0233)	(0.1036)	(0.0168)
Maple	−0.1460	0.0016	0.0451	0.0004
	(0.1128)	(0.0183)	(0.0387)	(0.0063)

The initial negative growth dominance, with smaller trees dominating growth in both species (Figs. 2b, 4), implies that inverse asymmetric inter-tree competition was occurring during many of the earlier years of the experiment. As mentioned earlier, growth dominance by smaller trees in a stand occurs when their relative growth rates decline with increasing tree size over some growth period. Fig. 5 then shows how relative growth rates in stem basal areas of individual trees of both species, over all six circles of the experiment, changed with stem basal areas between (a) 1.8 −2.4 and (b) 22 −24 years of age. The tendency to decline with tree size is quite clear over the younger age period, consistent with the negative growth dominances apparent at younger ages in Fig. 4. The tendency to increase with tree size at the later age period is then consistent with the positive growth dominances apparent at later ages in Fig. 4. Possible reasons to explain the growth dominance by smaller trees during early growth of both species are explored later in the Discussion.

Examination was now made of tree height development with age. The aim of this was to determine if maple came to dominate hoop pine in height, perhaps then leading to asymmetric competition for light. Tree heights had only been measured until 12 years of age. The average heights of the trees of each species in each of circles 2 −7 of the experiment were determined at each of four, roughly equally spaced, ages, 1.8, 4.9, 7.9 and 12 yr. These data were then treated as a 6 × 2 factorial experiment with two main effects, six stocking densities at establishment and two species. This meant that, in essence, each of the six circles was treated as being made up of two experimental 'plots', which each contained one of the two species, and had been established at a particular stocking density. Using the procedure GLM of the SAS© statistical package, an analysis of variance was then carried out for the data of each of the four ages. Because there were no replicates in the 'experiment', this analysis could investigate the main effects only and not the species × stocking density interaction.

Fig. 6 shows the average heights, over all trees of both species, at the six different stocking densities for each of the four ages considered. The analysis found that at the youngest age, 1.8 yr, maple trees averaged slightly taller than hoop pine, 1.9 m against 1.6 m. At later ages, the difference between the two species was not significant.

4. Discussion

Using the same experiment, Vanclay et al. (2013) examined

[1] Documentation for the SAS statistical package is available at https://support.sas.com/en/documentation.html (accessed July 2026)

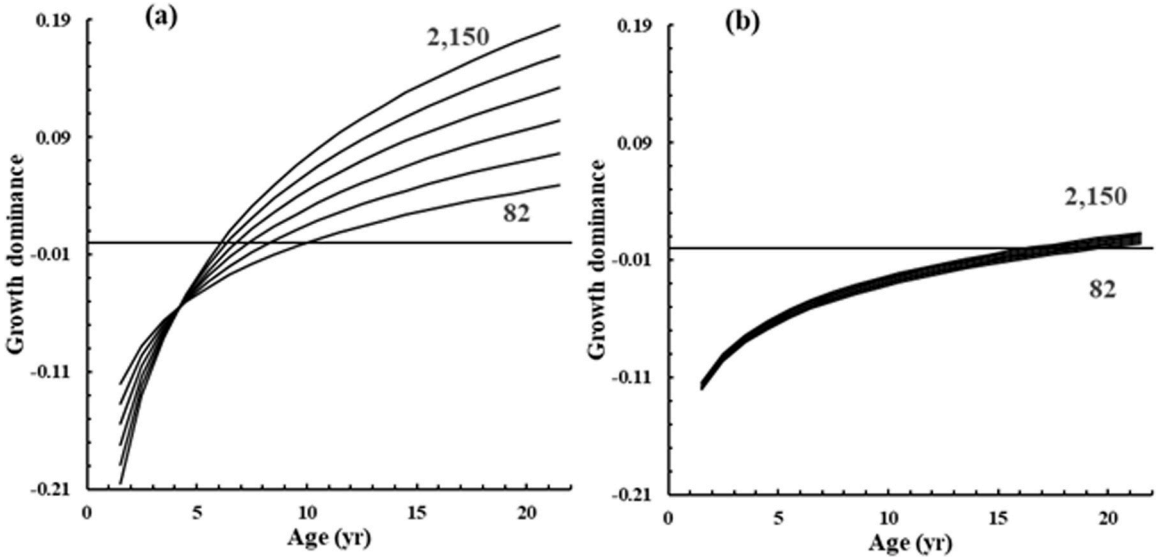


Fig. 4. Predicted change with age in growth dominance as predicted using Model (4), with parameter estimates as in Table 1, for each of the six circles of different stocking densities in the Mt Mee Nelder trial for trees of (a) hoop pine and (b) maple. The lines are drawn in successive order from the lowest to highest stocking densities (82 and 2150 stems ha^{-1}, respectively) as indicated.

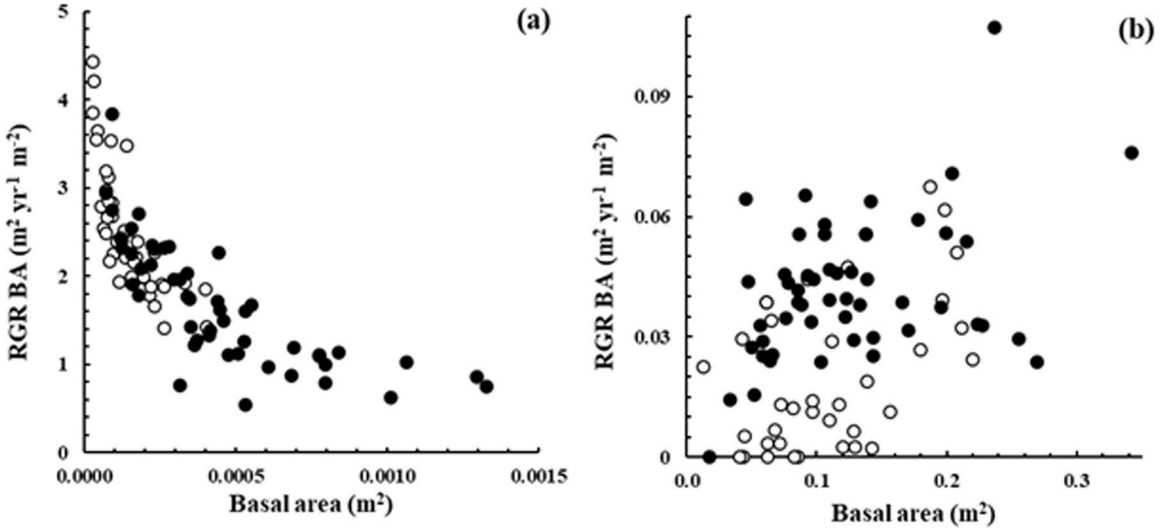


Fig. 5. Scatter plots of tree relative growth rates in tree basal area against tree basal area at the start of the growth period concerned for (O) hoop pine and (●) maple over all six circles of the experiment for growth periods of (a) 1.8 −2.4 and (b) 22 −24 years of age.

competition effects on stem diameter growth rates of individual trees between 2 −20 years of age. They developed a model that related growth rates of individual trees to indices based on their sizes of, and distances to, their neighbours; they found that competition became more intense as stocking density increased (see their Fig. 4), with consequent reductions in tree growth rates. Their work did not explore whether the competition occurring was symmetric or asymmetric; the methods they were using are problematic in that matter (West and Ratkowsky, 2022). The present work aimed to identify what competitive processes were occurring through use of the growth dominance statistic. That is based on growth rates of all trees in a stand at any given time, not on individual tree growth rates as Vanclay et al. used.

Present results apparent in Fig. 4 raised three issues, (a) increasing growth dominance with age, (b) stocking density effects on intensity of competition and (c) reversal of stocking density effects after 4 −5 years of age in hoop pine. These issues are discussed in the next three sections, where it is hypothesised that their occurrence can perhaps be explained through physiological phenomena involved with the growth behaviour of trees of different species as influenced by inter-tree competitive processes.

4.1. *Growth dominance increases with age*

As age increased from 1.8 to 24 years, growth dominance of both species increased progressively (Fig. 4). Further, it was negative initially, implying that smaller individuals of both species were dominating growth at young ages, consistent with the pattern of relative growth rates evident in Fig. 4(a). At 6 −10 years of age, growth dominance became positive for hoop pine, implying that larger trees were dominating growth and asymmetric competition was starting to occur. However, in the case of maple, this barely occurred at all, even up to the oldest age considered, suggesting there was little tendency for asymmetric competition to affect growth of that species, but inverse asymmetric competition was common, but declined with increasing age.

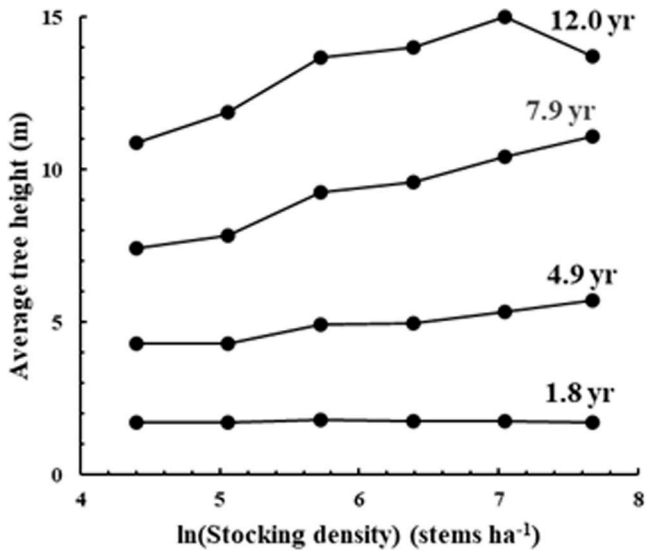


Fig. 6. Tree heights, averaged over all trees of both species, plotted against the six stocking densities [scaled as their natural logarithms ln(•) to make the figure easier to view] at which they were planted in different circles of the experiment at each of four different ages of the experiment at which heights had been measured.

The work of Schwinning (1996) suggested how differences between relative growth rates of two competing plants can be used to define the mode of competition between them. However, she recognised that some physiological factors might reduce relative growth rates with increasing tree sizes (e.g. Carl et al., 2018) and confuse this issue; such factors include differences between trees of different sizes in the proportions of their whole plant biomasses that is uptake tissue for growth resources (Schwinning, 1996), the need for larger plants to spend more on tissue maintenance respiration (e.g. Penning de Vries, 1975; Amthor, 1984, 2000; Thornley, 2011) or new tissue construction (West, 2020, 2023b, 2024) or the need for taller trees to develop their stem shape and size differently from shorter trees (West, 2024).

In the present experiment, if the only competitive factor affecting individual tree growth rates during the early years of growth had been inter-tree symmetric competition, below ground for water and nutrients, the growth dominance statistic would have taken zero values throughout that period, instead of the negative values that occurred here. Schwinning's work suggests that one or other of the various physiological factors mentioned above may have reduced the value of the statistic. These physiological factors may have then declined in importance as the trees grew older and larger, leading to the rising growth dominance with age, but with inter-tree competition remaining symmetric. As trees grew older and larger, the tendence for declining relative growth rates with increasing tree size may have vanished so that growth dominance tended to zero. After that, asymmetric competitive processes above ground may have led to positive values of growth dominance as evident, at least for hoop pine, in Fig. 4.

4.2. Stocking density effects on intensity of competition

Changes in stocking density had virtually no effect on the level of the competitive processes in maple at any age (Fig. 4b). In the case of hoop pine, immediately after 4 −5 years of age increased stocking density led to an increasing (but negative) growth dominance (Fig. 4a). After 6 −11 years of age, this effect of increasing stocking density in hoop pine led to increasing levels of asymmetric competition. The lack of effect in maple and strong effect in hoop pine suggests that maple trees might have progressively come to shade hoop pine, subjecting them to asymmetric competition for light.

However, shading of one tree by another suggests height differences between them. The results of Fig. 6 gave no indication of any substantial differences in height between the two species. At the youngest age shown there, stocking density showed no effect on average heights, but, at all three succeeding ages there was a significant effect. Average height increased progressively with increasing stocking density at ages 4.9 and 7.9 yr, the trend becoming steeper at the older age. But, at 12 years of age, height reached a maximum at a stocking density of 1140 stems ha^{-1} (where the natural logarithm was 7.04) and fell off progressively at stocking densities either side of that.

Such height growth behaviour is typical of the commencement of the 'wave phenomenon' or 'ripple effect' that is observed in Nelder experiments, where trees are taller (and larger) at progressively lower stocking densities as time passes (e.g. Krinard, 1985; Galiński et al., 1994; Lamb and Borschmann, 1998; Aphalo et al., 1999; Apahalo and Rikala 2006; Pachas et al., 2019). It is believed to be a consequence of a reduction in the ratio of red:far red light absorbed by the canopy as a result of greater leaf density within crowns of trees growing at higher stocking densities This leads to a physiological response that affects photosynthetic production and stimulates tree height growth (e.g. Ritchie, 1997; Aphalo et al., 1999; Aphalo and Rikala, 2006; Pierik,and Ballaré 2021). This effect has an interaction with age as trees grow larger, leading to the ripple effect.

However, whilst there appeared to be little differences in total heights of the trees of the two species in the present experiment at any stocking density, Vanclay et al. (2013) pointed out that hoop pine and maple have very different canopy architectures (see also Boland et al., 2006). Hoop pine has a lengthy, deep crown with persistent branches whilst maple has a much shallower, broader crown, held nearer the top of the tree. Fig. 7 shows satellite imagery of the present experiment, taken when it was 19 years of age; the image is oriented in the same way as the design in Fig. 1. The much broader spread of the maple crowns, when compared with the hoop pine, is very evident. Thus, it might be hypothesised that maple trees could shade much of the canopy of hoop pine trees leading to asymmetric competition of hoop pine, but hold their canopies too high for the reverse to occur. As well, perhaps there was insufficient differences in maple heights and canopy spreads that they were unable to shade each other, even in the denser stocking densities; that might explain why there was little evidence of asymmetric competition affecting maple.



Fig. 7. Satellite image of the experiment taken in July 2009 when it was 19 years of age. The layout is as in Fig. 1. The diameter of the outermost circle of the experiment was 89 m. The image was provided by Google Earth and includes data from Google Maxar Technologies.

4.3. Reversal of stocking density effects in hoop pine

In the case of hoop pine, increased stocking density reduced further the negative levels of growth dominance during 2 −4 years of age, an effect reversed thereafter as evident in Fig. 4(a). Perhaps at very early ages, the trees growing at low stocking densities were too far apart to suffer any competition from neighbours, symmetric or otherwise. Those at higher stocking densities might have been close enough that their growth was affected by symmetric competition from their neighbours. This may have reduced the possibility for smaller trees at higher stocking densities to show increased relative growth rates and so show lower growth dominance. Examination of this would require very detailed study of the growth and physiological behaviour of trees at these very young ages.

Interestingly, Schwinning (1996) applied her model system to examine growth behaviour over about two months of a short-lived, cereal plant Pearl millet (*Cenchrus americanus* (L.) Morrone, commonly known by the synonym *Pennisetum glaucum*) in field experiments in Arizona, USA. The site circumstances were such that light was considered to be the only growth resource for which plants might be competing. After several weeks, plants at low stocking densities displayed growth behaviour consistent with only symmetric competition for light whilst those at higher stocking densities appeared to displaying behaviour consistent with asymmetric competition (her Fig. 8 C). Of course, trees are far longer lived than plants like Pearl millet, but Schwinning's studies show what types of finely detailed studies can be undertaken at these young ages.

4.4. Comparison with other forest types

Models have been developed to predict individual tree growth in relation to inter-tree competitive processes for many forest types around the globe. Much of this work has investigated the use of different 'competition indices' to examine growth in relation to inter-tree competition and, through them, to identify if the competition occurring is symmetric or asymmetric. There are various reviews and examples of such model systems (e.g. Weiskittel et al., 2011, Chap. 2; Burkhart and Tomé 2012, Chap. 9; Szmyt, 2014; del Río et al., 2016; Acquah et al., 2025). Often, these have 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; West 2023a) whilst some have found both operating on trees of different sizes (Acquah et al., 2025).

These growth behaviour and competitive processes seem to operate quite clearly in even-aged, mono-specific forest growing on a particular site. The present results have examined the interactions in even-aged forest between two species in relation to their stocking densities. This led to hypotheses regarding their morphological and physiological characteristics that might have determined these interactions. However, it is clear that the factors controlling interactions between species in the more complex, uneven-aged and/or mixed-species forests, are determined by many different factors, including their spatial arrangement, genetic origins or physiological and morphological characteristics (such as shade tolerance, root or crown development or response to environmental circumstances) (e.g. Doran et al., 2001; Leuschner et al., 2001; Pretzsch and Biber, 2010; del Río et al., 2014; Cordonnier and Kunstler, 2018; Cole and Newton, 2019; Zhang et al., 2022). Thus, it is difficult to make *a priori* assumptions about how different species will behave under any particular forest conditions. Each case will need to be considered under its particular circumstances.

5. Conclusions

Using the present experiment, Vanclay et al. (2013) considered individual tree stem diameter growth rates, at various time over 2 −20 years of age, as they varied with stem diameter and the proximity and sizes of neighbouring trees. They concluded (p. 616) "… that maple exerts strong competition on both maple and hoop neighbours (1.4 times the intraspecific competition), but that hoop pine behaves quite differently, with less competitive influence (only 20% of the maple intraspecific competition)."

The present work has extended those results by showing that hoop pine trees become subject to asymmetric competition after about 6 −10 years of age (Fig. 4a). This had progressively increasing effects on growth behaviour at higher stocking densities, where the trees were closer together. By contrast, maple showed virtually no evidence of experiencing asymmetric competition at any stocking density, even after more than 20 years of age (Fig. 4b). There was little difference between average heights of trees of either species at any age (Fig. 6). However, their crown architectures differ quite markedly (Fig. 7), with maple crowns being much shallower than those of hoop pine. It was hypothesised that this difference might allow maple trees to shade hoop pine asymmetrically, but not do that for trees of its own species. Such a phenomenon might then explain why maple has stronger competitive effects on hoop pine stem diameter growth and not *vice versa*, consistent with Vanclay et al.'s conclusions.

Some hypotheses concerning physiological processes were advanced to attempt to explain the increases in growth dominance with age that were apparent for both species during early growth, before any asymmetric competition had started (Fig. 4). To assess the validity or otherwise of those suggestions would require detailed physiological studies of these phenomena in new experiments altogether. Such studies are likely to yield conclusions that are quite specific to the species used in this experiment and difficult to apply to other species and other forest circumstances.

CRediT authorship contribution statement

P.W. West: Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The authors do not have permission to share data.

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