Spatially-explicit competition in a mixed planting of

Araucaria cunninghamii and *Flindersia brayleyana*

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Abstract

Context: A 20 year old Nelder wheel planted with hoop pine (*Araucaria cunninghamii* Aiton ex D.Don) and Queensland maple (*Flindersia brayleyana* F.Muell.) in 18 spokes and 8 rings represents nominal point densities of 3580, 2150, 1140, 595, 305, 158, 82 and 42 stems/ha and offers an opportunity to examine competition and spatial interaction between these two species.
Aims: To evaluate the intra- and inter-specific competition between two contrasting tree species, and determine the distance over which competition can be observed.
Methods: Competition was estimated using Hegyi's index, implemented using the Simile visual modelling environment, and calibrated using non-linear least squares with PEST.
Results: Interactions were detected between pairs of stems closer than $D_{ij} < 40(d_i + d_j)$ where D is distance (cm) and d is stem diameter (cm dbh). *F. brayleyana* trees surrounded by *A. cunninghamii* trees suffer negligible competition whereas *A. cunninghamii* surrounded by *F. brayleyana* trees experience strong competition.
Conclusion: Forty times diameter offers a useful guide to the extent of competition in even-aged stands planted with these species. Competition can be observed empirically when pairs of trees are closer than 40 times the sum of their diameters, but the intensity of the competition may vary considerably with species.

Keywords: *Araucaria cunninghamii;* Clinal spacing trial; *Flindersia brayleyana;* Hegyi index; Hoop pine; interspecific competition; Nelder wheel; Queensland maple

Introduction

Competition is a fundamental process that shapes plant growth and provides the basis for density management of tree plantations. Despite the importance of understanding competition in production forests, relatively few studies have reported details of inter- and intraspecific competition in mixed stands, and most publications deal with competition in a generic way by examining non-spatial measures (e.g., stand density as measured by stand basal area) and intra-specific competition in monocultural plantings (e.g., Mitchell 1975; Strub *et al.* 1975).

In recent years ecologists have begun exploring the potential of polycultures to increase ecosystem productivity (Yanai 1992; Tilman *et al.* 1997; Hooper *et al.* 2005; Jones *et al.* 2005; Bristow *et al.* 2006a; Erskine *et al.* 2006). Forest owners have also shown increased interest in the use of tree polycultures, because of their capacity to generate a wider range of goods and services than monocultures (Nichols *et al.* 2006; Lamb 2011). However, if the task of managing competition in a monoculture is difficult then it is even more so in mixtures, where there are many more ways in which competition can be manifested (Forrester *et al.* 2011). It is useful to recognise two broad categories of beneficial mixtures. In one such category, the dominant process is that of facilitation, such as when a nitrogen fixing species is planted together with a non-nitrogen fixer on an infertile soil. In this case, the growth of the latter species – and sometimes that of the whole stand – can be improved by the nitrogen-fixing species and the nitrogen it adds to the ecosystem (Forrester *et al.* 2006). In the second category, the species are complementary and occupy different ecological niches. This means they avoid or minimize competition and so increase overall productivity (Sheil *et al.* 2006; Pretzsch 2010). In such cases the key issue is finding truly complementary species and managing stands to maximize complementarity and minimize inter-specific competition.

This study seeks to contribute to an understanding of both intra- and inter-specific competition by examining spatial interactions in a two-species Nelder (1962) trial in the humid subtropics. Specifically, it seeks to calibrate the responses of the two species to intra-and inter-specific competition and the implications this has for the management of simple polyculture plantations.

Literature

Despite extensive literature on competition in plantation trees (e.g., Berger *et al.* 2008; Harrington *et al.* 2009; Binkley *et al.* 2010; Conteras *et al.* 2011; Weiskittel *et al.* 2011), relatively few studies have attempted to estimate inter-specific competition in binary mixtures in a spatially-explicit way (Mead 1979; Jones *et al.* 2005; Vanclay 2006b; Perot and Picard 2012). This is an important step to understanding competition in mixed-species plantings, and towards a paradigm of strong and weak competitors (Vanclay 1994, p.162). Much of the work on competition has focused on spatial indices

for monospecific plantings (e.g., Strub *et al.* 1975; Fox *et al.* 2007; Burkhart and Tome 2012) and non-spatial indices for complex forests (e.g., Vanclay 1994; Peltoniemi and Makipaa 2011), and relatively few publications deal with spatial indices in even-aged polycultures (e.g., Coates *et al.* 2009; Kaitaniemi and Lintunen 2010).

Many variants of forest competition indices have been proposed and tested (e.g., Strub *et al.* 1975; Martin and Ek 1984; Daniels *et al.* 1986; Pukkala and Kolstrom 1987; Tome and Burkhart 1989; Biging and Dobbertin 1995; Soares and Tome 1999; Ledermann and Stage 2001; Miina and Pukkala 2002; Radtke *et al.* 2003; Woodall *et al.* 2003; Stadt *et al.* 2007; Oheimb *et al.* 2011). A recent classification and review offered by Weiskittel *et al.* (2011) illustrates the utility of Hegyi-type indices (Hegyi 1974; Holmes and Reed 1991; Mailly *et al.* 2003; Vanhellemont *et al.* 2010) that rely on the relative size of potential competitors and the distance between them.

Many experiment designs offer a weak basis for testing competition indices because regular rectangular plantings provide a limited range of inter-tree distances (Vanclay 2006a), and unthinned stands may be confounded by the high correlation between size and competition. An analysis of species interactions in a mixed planting of *Acacia peregrina* and *Eucalyptus pellita* (Vanclay 2006b; Bristow *et al*. 2006b) demonstrated the ability of competition indices to reveal species interactions, but the blocked experimental design and the rectangular spacing employed in that trial created difficulties in establishing the spatial extent of competition. The present study draws on the wide range of spacing in a Nelder (1962) design to examine more closely the spatial extent of competition in mixed plantings. Vanclay (2006a) reviewed a variety of experimental designs of interest in studying competition, and whilst Nelder designs have been extensively studied (Stape and Binkley 2010; Parrott *et al.* 2012), the current trial retains interest because it is one of very few long-established mixed-species planting with a binary mixture.

The present study deals with Hoop pine (*Araucaria cunninghamii* Aiton ex D.Don) and Queensland maple (*Flindersia brayleyana* F.Muell.). These two species have been planted widely in Queensland (Vanclay 2006c; Manson *et al.* 2013), and hoop pine has become an important plantation species (Lamb *et al.* 2001). Elsewhere in southern Queensland, several *ad hoc* plantings with alternate row plantings have shown these two species can form a stable mixture over periods of up to 50 years (Lamb and Lawrence 1993). This apparent complementarity appears to be associated, at least in part, with the difference in canopy architecture (hoop having persistent branches and a deep crown, while maple has a shallow green crown). There is also some evidence that hoop pine has a deeper root system than maple (Lamb and Lawrence 1993). One of these alternate-row plantings exhibited increased height, bole length, diameter and smaller branch sizes in maple when compared with a monocultural planting of maple nearby, while hoop pine appeared similar to surrounding hoop plantation in respect of these and other mensurational parameters. This observation was part of the

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motivation to examine this apparent synergism using a Nelder design by arranging species in spokes to provide monocultural and polycultural comparisons. Earlier reports based on this trial include an examination of early growth pasture production within the Nelder plot (Lamb and Borschmann 1998; Woldring 1998), and soil and foliar analyses (Lamb and Borschmann 1998). This work showed that maple suppressed grasses more than hoop, even at relatively low densities (Costantini 1989; Woldring 1998; Xu *et al.* 2002), and that the height-diameter-density relationship remained stable over time (Vanclay 2009).

The physiology of both species was monitored between August 1992 and December 1994, and revealed that density effects on maximum photosynthetic rates were most apparent in maple, with greater rates occurring in trees planted at low tree densities ($\leq$158 stems ha^{-1}) than at high tree densities ($\geq$2150 stems ha^{-1}). In contrast, hoop had higher rates of photosynthesis at intermediate densities (305 - 1140 stems ha^{-1}) than at either high or low planting densities (Lamb and Borschmann 1998; Snell 1998). Hoop maintained high water potentials when surrounding individuals of maple displayed low potentials, apparently due to the deeper rooting system in hoop, which, when coupled with low stomatal conductance, contributes to greater drought resistance (Lamb and Borschmann 1998; Snell 1998). The ability of maple to compete for soil moisture either between individuals of the same species or with individuals of deeper rooted species is diminished when planted at high density during seasonal droughts (Lamb and Borschmann 1998).

Material and Methods

A Nelder trial with two species was established on a uniform one-hectare site at Mt Mee (27°S, 153°E) in south east Queensland, Australia, in June 1990. The site is former pasture on a deep kraznozem soil derived from basalt (Lamb and Borschmann 1998), and appears free of the variability that may confound productivity studies (Skovsgaard and Vanclay 2013). The two species, Hoop pine (*Araucaria cunninghamii* Aiton ex D.Don) and Queensland maple (*Flindersia brayleyana* F.Muell.), were arranged to allow an evaluation of monospecific growth as well as growth in mixed stands of various compositions (i.e., with alternate species on one or two sides, Figure 1). The design involved 18 spokes (each at 20 degrees) and 8 rings of trees at radii of 4.33, 6.2, 8.55, 11.9, 16.45, 23, 31.8 and 44.3 metres, creating nominal point densities (assuming the area tessellated in annular sectors) of 3580, 2150, 1140, 595, 305, 158, 82 and 42 stems/ha respectively. In addition, there were two internal 'buffer' rings with 6 and 9 trees, at radii of 0.7, 2.52 m, corresponding to 7400 and 3140 stems/ha – these were not part of the formal design, and did not involve the full complement of 18 spokes.
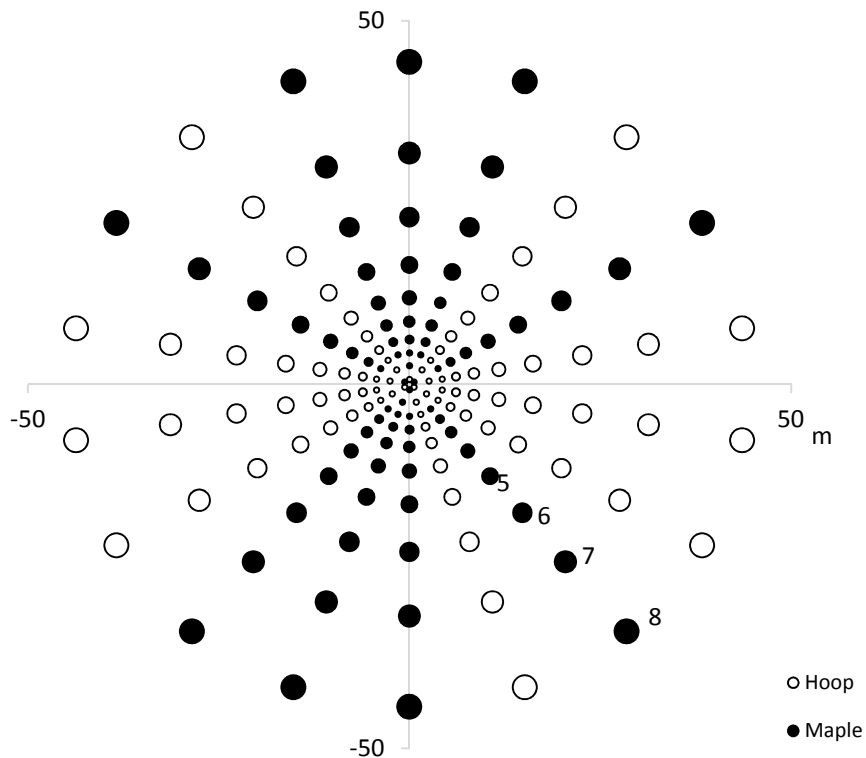
Figure 1. Mt Mee Nelder trial with hoop pine (*Araucaria cunninghamii*) and Queensland maple (*Flindersia brayleyana*). The innermost 2 rings (with 6 and 9 trees) are 'buffers', not part of the formal design. Symbol size is indicative of stem diameter. Ring numbers are shown for outermost four rings.

The plot was initially measured biannually during 1990-96, and then in 1997, 1998, 2002, 2003, 2005 and 2010. Diameter (either root collar or diameter at breast height of 1.3 m) was recorded at all measures, but tree heights were recorded less frequently and only in the early years. Only some of these measurements were used in this analysis: intervals were selected to attain diameter increments that were large relative to expected measurement precision. The seven measure dates chosen for use in subsequent analysis were 13 July 1992, 19 July 1993, 3 August 1995, 11 August 1998, 1 October 2002, 5 February 2005 and 9 July 2010. These dates provided intervals of 1, 2, 3, 4.1, 2.3 and 5.4 years. Analyses were based on stem diameter, because of the measurement frequency, because the precision of diameter measurement is generally greater than of height measurement, and because the diameter growth response to competition is more immediate than the height response (Richardson *et al.* 1999). Selected measurements were used to derive estimates of periodic annual diameter increment during the period immediately following these measures (except for the 2010 measure at 20 years after planting). Competition indices were estimated from potential competitor trees within the neighbourhood defined for each subject tree.

Figure 2. Google Earth image of Mt Mee Nelder trial, 20 July 2009 (© 2012 Google, © 2012 GeoEye, 27.096°S, 152.734°E), showing the two species, survival, and proximity of other plantings.

Competition was modelled using the simulation software Simile (Muetzelfeldt and Massheder 2003; Simulistics 2012), a generic modelling package that is well-suited to studying spatial interactions between individuals (Vanclay 2006b; Vanclay *et al*. 2006). Models were formulated and examined using Simile, and parameters were estimated by non-linear least-squares using PEST (Doherty 2005), which uses the Gauss-Marquardt- Levenberg method with Tikhonov regularisation (Doherty and Skahill 2006).

Although early survival of the plantings in the trial was good, eight trees were dead or missing by the 2010 remeasure (one in 2002, one in 2003, one in 2005, and five in 2010), and the proximity of adjacent plantings compromised the design slightly, as is evident in 2009 satellite imagery (Figure 2). The weak correlation (r=0.021, P=0.5) between tree size (dbh in 2010) of trees in the outer ring and the distance to adjacent plantings provides further support for the notion that these plantings compromise the design only slightly. Figure 2 illustrates the supplementary plantings in the vicinity of the Nelder planting, to the east and the south-west of the main Nelder design. These rectangular plantings were not always measured, so measurements taken in 2006 and 2010 were used to interpolate missing data. Interpolated diameters were used to calculate competition experienced by other trees, but were not used directly in any analysis.
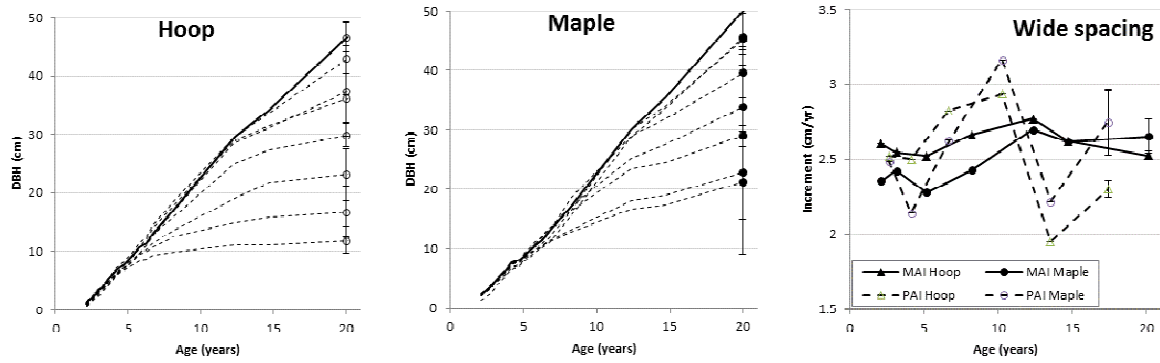
Figure 3. Mean diameter of the two species in the Nelder trial (left and centre), with lines representing the 8 different 'rings' in experiment. The rightmost graph shows the growth rates of trees at the widest spacing: the solid line is mean annual increment (MAI, dbh/age), dashed line is periodic annual increment (PAI, Δdbh/Δage). Vertical bars show ±1 standard error.

An established approach to estimating competition is to rely on the assumption that observed growth can be estimated as the product of potential growth modified by a competition index (e.g., Arney 1985; Vanclay 1994; Pretzsch and Biber 2010), typically

$$\text{Growth} = f(\text{tree size}) \times f(\text{competition experienced})$$

However, growth of the wide-spaced trees has been remarkably constant during these first 20 years for both species in these trials (Figure 3), so the size-related component of growth is subsumed within the constant term, and our analysis deals with the competition term.

Various approaches have been used to define the relevant neighbourhood. Many researchers rely on constant radii (e.g., 3 m by Hegyi 1974; 5 m by Kaitaniemi and Lintunen 2010; 6 m by Miina and Pukkala 2002; 8 m by Stadt *et al.* 2007; 11 m by Contreras *et al.* 2011) while a few define the neighbourhood in terms of tree size (e.g., proportional to crown radius, Lorimer 1983; or to tree height, Vanclay 2006b). Hegyi (1974) proposed an index $H_j = \Sigma_i(d_i/d_j)/D_{ij}$ where d_i is the diameter of the competitor i, d_j is the diameter of the victim j, and D_{ij} is the distance between trees i and j, for all trees where $D_{ij}<a(d_i+d_j)$. This index is analogous to the intuition used by field foresters who rely on relative size and separation of trees to gauge likely impact from potential competitors. An alternative index that was examined in some detail was proposed by Miina and Pukkala (2002): $M_j = \Pi_i\{1-\exp(-cD_{ij}{}^b/d_i)\}$, for all $h_i<ah_j$, where d_i and h_i are the diameter and height of the competitor i, and D_{ij} is the distance between trees *i* and *j*. Miina's index differs from most competition indices in that it indicates resource availability (cf. inverse of competition), depends only on the size and distance of potential competitors, can be computed for bare ground (Figure 4), and offers utility for understorey studies. In contrast, Hegyi's index is a classical competition index that can be computed only for competing pairs of trees. However, Miina's index is inherently constrained between zero and one, and may be ill-suited to situations where interacting species exhibit complementarity (e.g., Forrester *et al*. 2011).

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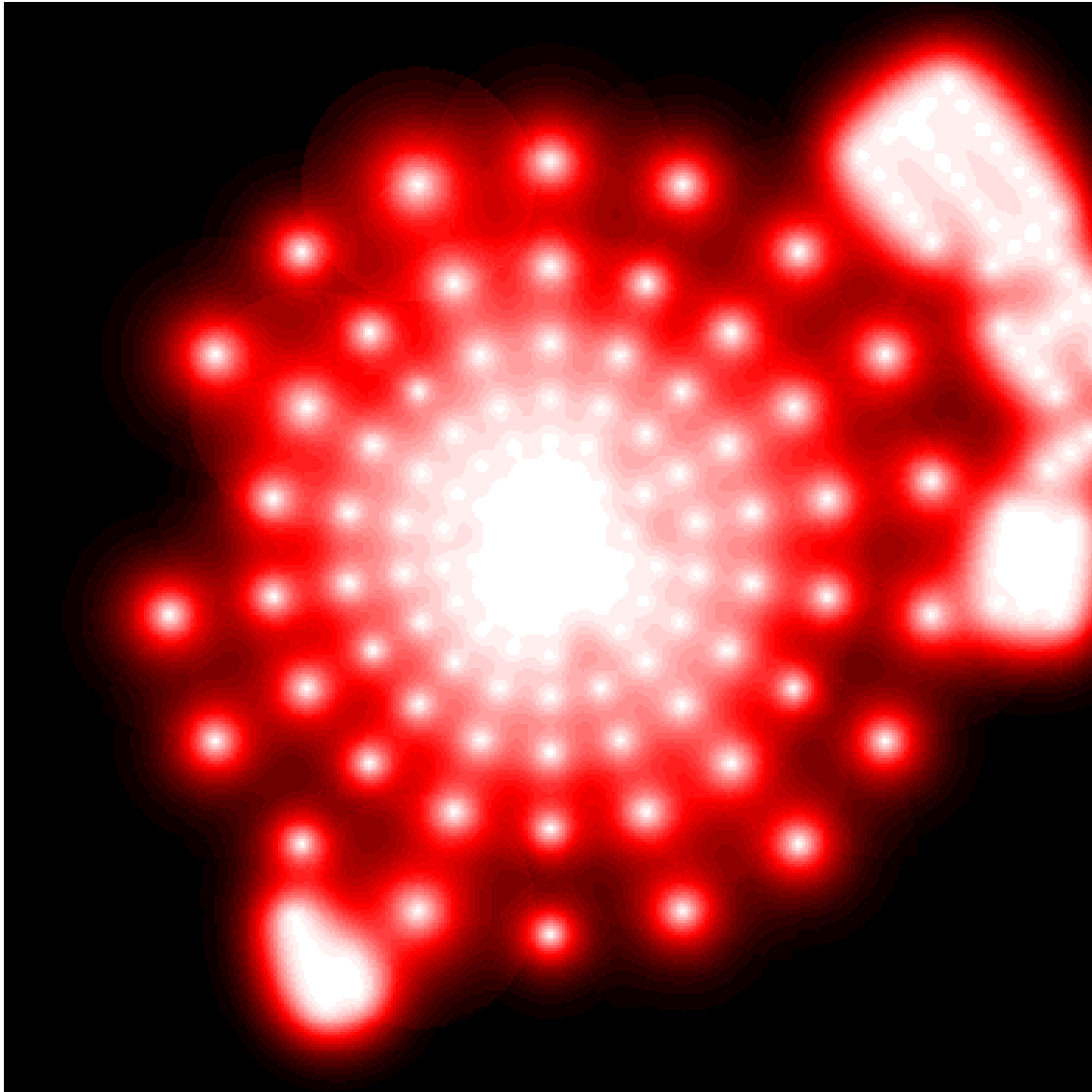
Figure 4. Indicative competition at age 20 based on the Miina index (black indicates high resource availability; white shows low availability). Competition from trees not part of the Nelder design is evident at top right and bottom left.

Empirical testing revealed that the Hegyi index performed better than Miina's index in the present study, and that the Hegyi index performed best when the search radius was expressed as a multiple of stem diameter rather than a fixed radius. There is little to discriminate between the two indices empirically: both are highly correlated with observed increments ($r \geq 0.76$) and with each other ($r=0.95$). However, the Hegyi index offered a stronger correlation, and avoided two drawbacks of the Miina index, namely the larger number of parameters to be estimated, and the multicollinearity (Belsley *et al.* 2004) that existed between these parameters.

Results

The non-linear model used to examine species interactions was:

$$(DInc_j)^{0.5} = \beta_0 + \beta_1 S + \beta_2 d_j + \beta_3 S d_j + \boldsymbol{\beta_4}\Sigma_i\{(d_i/d_j)/D_{ij}\}^{\gamma} \text{ where } D_{ij}<\lambda(d_i+d_j) \tag{1}$$

where $DInc_j$ is the periodic annual increment (cm/yr) of each tree j suffering competition, S is a dummy variable indicating species, and where $\Sigma_i\{(d_i/d_j)/D_{ij}\}^{\gamma}$ is a Hegyi index based on a partial sum for each species combination of all competitors i seen by victim j. The square-root transformation of $DInc_j$ was indicated by a Box-Cox (1964) test to stabilize variances. The terms $\beta_1 S$, $\beta_2 d_j$ and $\beta_3 S d_j$ were included to allow for any possible differences between the two species ($\beta_1 S$) and any size-related growth pattern ($\beta_2 d_j$) not explained by the Hegyi index. We considered the possiblity that the variables $\boldsymbol{\beta_4}$, γ and λ could represent vectors with up to four values: a single value to describe a universal trend, two entires to reveal species differences, or four entries to expose intra- versus inter-species responses within species; the bold notation for $\boldsymbol{\beta_4}$ emphasizes that this is a vector with four entries. However, poor estimates were obtained as a result of multicollinearity so the model was estimated more parsimoniously as:

$$(DInc_j)^{0.5} = \beta_0 + \boldsymbol{\beta_4}\Sigma_i\{(d_i/d_j)/D_{ij}\}^{0.5} \text{ where } D_{ij}<\lambda(d_i+d_j) \tag{2}$$

In Equation 2, $\boldsymbol{\beta_4}$ was initially estimated as a vector recognising intra- and inter-specific competition [β_{mm}, β_{mh}, β_{hm}, β_{hh}], with β_{mm} and β_{hh} indicating intraspecific competition in maple and hoop respectively, β_{mh} indicating competition exerted by maple on hoop, and β_{hm} indicating competition exerted by hoop on maple trees. There was no evidence to support the inclusion of the terms $\beta_1 S$, $\beta_2 d_j$ or $\beta_3 S d_j$ ($P>0.2$), so these were omitted from Equation 2. There was strong evidence for three entries in $\boldsymbol{\beta_4}$ ($P<0.001$), but the term β_{hm} was not significantly different from β_{hh}, indicating that hoop pine has the same competitive effect both within and between species. There was no evidence ($P>0.1$) to support multiple values for γ or λ, suggesting that the distance over which competition is experienced (λ) and the way it attenuates with distance (γ) either does not vary greatly between these two species, or cannot be estimated with the current database. Non-linear modelling suggested that attenuation (γ) was close to, and not significantly different ($P>0.4$) from 0.5, the value that may be expected for spatial diffusion in two dimensions. More flexible forms of the Hegyi index – such as $\Sigma_i\{(d_i/d_j)^{\varphi}/D_{ij}^{\psi}\}$ – were examined, but these contributed no significant improvement in residuals ($P>0.1$). The resulting parameter estimates are shown in Table 1.

Table 1. Parameter estimates for Equation 2, calibrated for the Mt Mee data.

| Parameter	Symbol	Estimate	s.e.	Student's t	P	Sig
Intercept	β_0	1.599	0.0106	151.4	<0.0001	***
Horizon	λ	40.06	0.0001	10116	<0.0001	***
Attenuation	γ	0.510	0.0356	14.3	<0.0001	***
Competition m-m †	β_{mm}	-0.0308	0.0097	3.2	0.0008	***
Competition m-h ‡	β_{mh}	-0.0149	0.0022	6.9	<0.0001	***
Competition h-*	β_{h*}	-0.0077	0.0053	1.5	0.07	-

† calibrated relative to β_{h*}, ‡ calibrated relative to β_{mm}, the intra-specific competition observed in maple.

The estimates from Equation 2 and Table 1 can be synthesised as

$$(DInc)^{0.5} = 1.599 - 0.0386H_{mm} - 0.0534H_{mh} - 0.0077H_{h*} \tag{3}$$

where H_{mm}, H_{mh} and H_{h*} are partial sums respectively of intraspecific competition in maple (H_{mm}), of interspecific competition caused by maple to hoop (H_{mh}), and of competition caused by hoop (H_{h*}), computed as $H_{mm} = \Sigma_j \Sigma_i \{(d_i/d_j)/D_{ij}\}^{0.5}$ for all $D_{ij} < 40(d_i + d_j)$ where i and j are both maple trees, etc. Whilst Equation 3 is a simple empirical summary of the observed increments, it offers a surprisingly good correlation (Figure 5), given that it spans a 20-year period and wide range of tree sizes (Figure 3) and stand density (42 – 7400 stems/ha).
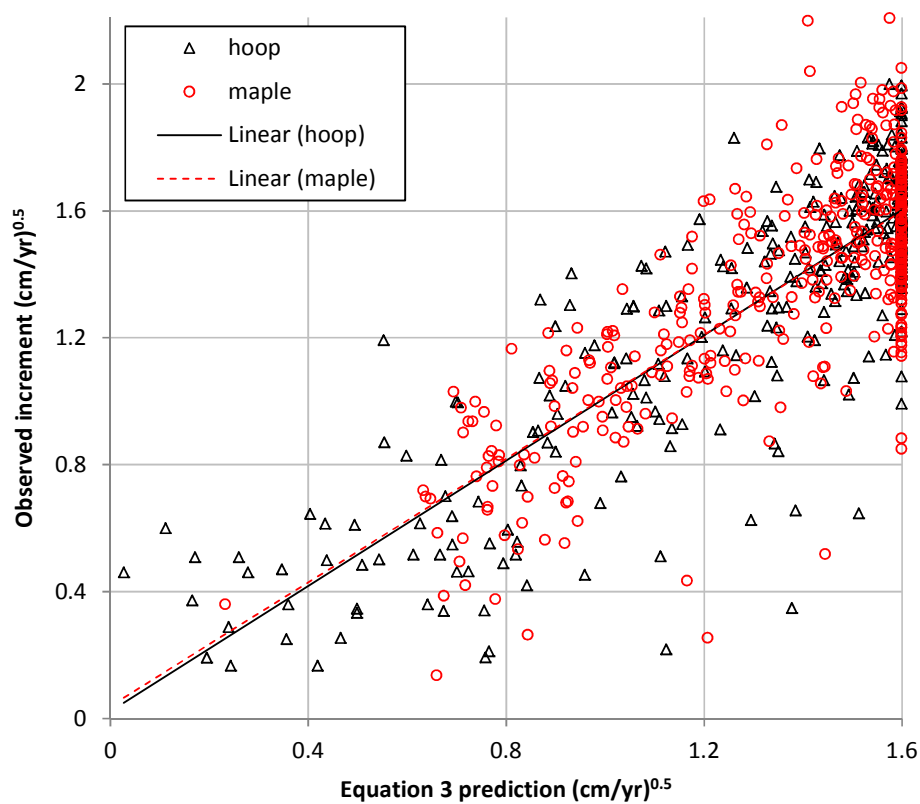
**Figure 5.** Observed and predicted increments from Equation 3.

Equation 2 allowed a thorough analysis of several formulations of competition, revealed the lack of statistical support for these formulations, and established that the parsimonious formulation for competition is Equation 3. No temporal or spatial pattern was evident in the residuals: spatial and temporal variables such as measure date, x,y coordinates and spoke identifier exhibited no trend with the residuals and were all statistically non-significant (P>0.1).

Table 1 reveals several important aspects about competition in the present study. A simple Hegyi index $\Sigma_i\{(d_i/d_j)/D_{ij}\}^{0.5}$ for all possible $D_{ij}<40(d_i+d_j)$ explains much of the variation (67%) in growth rate. There is no evidence that the parameter estimates $\lambda=40$ and $\gamma=0.5$ differ between these two species. The limit of competition $\lambda=40d$ corresponds approximately to three times the crown radius,consistent with the observations of Lorimer (1983). The limit of competition $\lambda=40d$ lies on a broad plateau, with a wide range $26<\lambda<52$ offering a coefficient of determination better than 66% (Figure 6). The spatial extent of this competition observed in these subtropical species is substantially greater than that commonly assumed in the computation of comparable indices for temperate species (e.g., Hegyi 1974; Kaitaniemi and Lintunen 2010; Miina and Pukkala 2002; Stadt *et al.* 2007).

The relationship β_c between the Hegyi index and observed tree growth ($DInc^{0.5}$) shows 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).

Discussion

As expected, the Hegyi index performed better than point estimates of stand basal area and the basal area of larger trees (BAL; Vanclay 1989, Biging and Dobbertin 1995). Basal area and BAL offered stronger correlations when the unit area adjustment was based on the distance between trees (D_{ij}) rather than (more conventionally) on the search area. However, in both formulations, total stand basal area performed better than BAL (Figure 6), indicating that two-sided competition (i.e., for water and nutrients) dominates in this planting, rather than one-sided competition for light. The optimal radius for the Hegyi index was 40 times stem diameter with an average of 29 neighbourhood trees. This distance is larger than those often reported in forestry studies, but is consistent with crown observations of Lorimer (1983), and with comparable work examining tree-crop interactions (e.g., Woodall and Ward 2002, who observed reductions in wheat yields up to 30 m from *Pinus radiata* trees). During the final measurement interval, the largest trees included in the analysis were 43 cm dbh, and the most distant pair of competitors were 33 m apart.
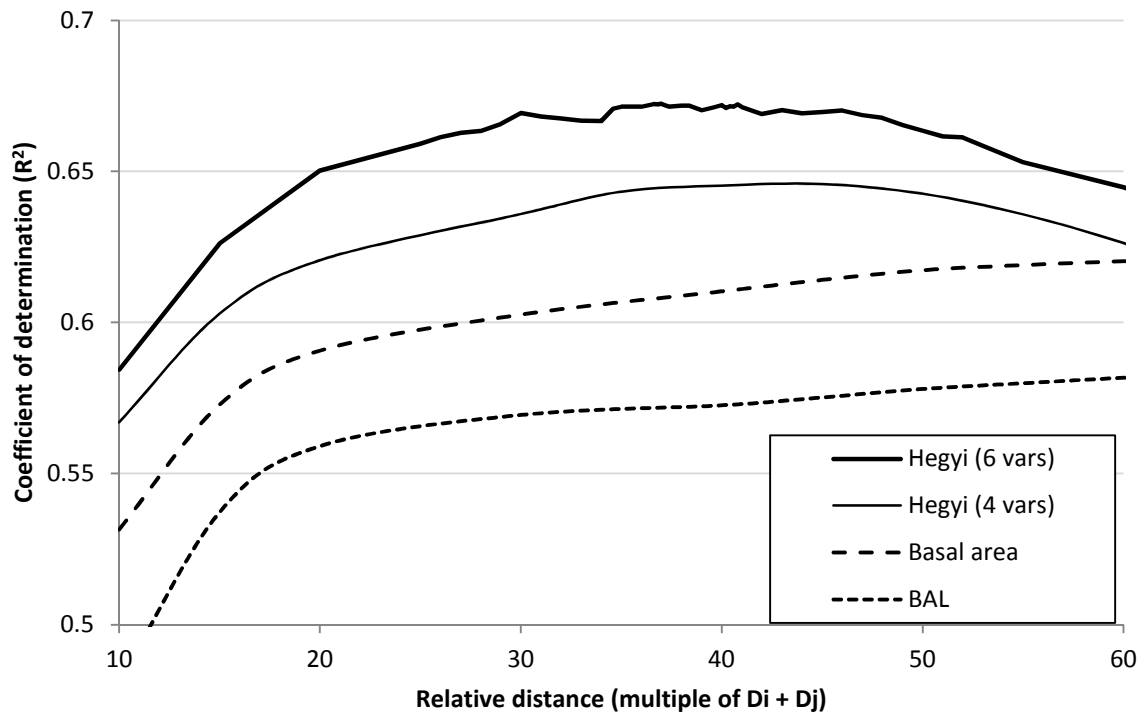
Figure 6. Relative efficiency of four measures of competition: Equation 2 using a Hegyi index with six estimated parameters, a generic Hegyi index with four parameters and no differentiation of species, conventional stand basal area (BA m^2/ha), and basal area in larger trees (BAL m^2/ha). BA and BAL were computed using distance to competitors (i.e., $\Sigma_i d_i^2/D_{ij}^2$) rather than using the usual fixed search area ($\Sigma_i d_i^2/r^2$ where r is the search radius) which results in weaker correlations.

Equation 3 describes the relative levels of competition observed in the trial, and is not intended for prediction or extrapolation. The square-root formulation of this equation confers desirable statistical properties, but limits the ability to extrapolate because extreme densities lead to problematic negative outcomes (not observed in the present data).

The strongly contrasting responses observed for interspecific competition (the effect of maple on hoop is seven times the effect of hoop on maple, Equation 3) is somewhat surprising and warrants careful consideration. One indicator suggesting a cautious interpretation is the high correlation (-0.8) between parameter estimates of interspecific competition: thus if maple-to-hoop competition is overestimated, hoop-to-maple competition may be underestimated. However, several indicators support the implication that hoop competes only weakly with maple. The most compelling indicator is that partial residuals after fitting Hegyi indices for intraspecific competition show a substantial unexplained trend for hoop revealing interspecific competition not yet accommodated, and a near-zero trend for maple reflecting the minimal effect that hoop has on maple growth. These competitive differences may be explained in part by the different growth habits of the trees: as with most gymnosperms (Pallardy and Kozlowski 2008), hoop pine demonstrates strong apical dominance and under the range of light

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conditions in the Nelder wheel they maintained conical tree form. Lower branches that were heavily shaded remained on the hoop pine even in the denser plantings. Conversely, maple demonstrated a great range of growth plasticity and rapidly shed branches that became shaded. This habit and a dense canopy near the top of the tree would have allowed the maple to shade surrounding hoop pines. Both hoop and maple can tolerate a broad range of light conditions (Thompson *et al.* 1988) but the plasticity of maple appears to be particularly advantageous when competing with hoop pine.

It is somewhat surprising that tree size (d_j) is not significant (P>0.2) in Equation 1, because it is well established that in general, tree size influences growth. The conventional suggestion that collinearity between tree size and competition precludes reliable estimates of both parameters does not apply in the present case, as weak correlations exist between competition and both tree size (0.13) and diameter increment (0.67), in contrast to the strong correlation with the Hegyi index (Figure 6). Nonetheless, is does seem likely that the co-development of tree size and competition hampers interpretation, and that it may be insightful to impose systematic thinning on a Nelder or other clinal spacing trial, to reveal further insights into the interplay between competition and tree growth.

Twenty years is a long time to await experimental results, but it is only at this point that the trial is about to exhibit density-related mortality. The twenty-year life of the trial has also provided a strong database for predicting plantation performance, as the current size of the widely-spaced trees approximates the sizes desired in commercial plantings. Earlier results (Lamb and Borschmann 1998) have been informative, but it appears that it is only now, near the twentieth anniversary, that the plot offers definitive insights regarding density-induced mortality. This highlights the need to re-examine the overall approach to forest research and the desirability of prioritising those studies requiring rigorous evaluation at the planning stage and long-term support throughout their life rather than what has become accepted as a standard 3-4 year term.

Conclusion

The Mt Mee Nelder trial provided a robust database that allowed an examination of inter- and intra-specific competition between hoop pine and Queensland maple in a polyculture. The mixture remained stable over 20 years but the analysis showed there were differences between the two species in intra- and inter-specific competition. Measurable competition was found to extend 40 times the diameter, with competition existing between pairs of trees for which separation $D_{ij}<40(d_i+d_j)$ where D is distance (cm) and d is stem diameter (cm).Maple was the more competitive of the two species and has high levels of intra- and inter-specific competition. In contrast intra-specific competition between hoop pines is modest and the competition experienced by maple from hoop competitors is negligible. This means the hoop and maple mixture at this site is not complementary and forms a win-lose

relationship rather than a win-win partnership. The combination of a long-established Nelder trial, coupled with individual tree modelling, has enabled new insights into the dynamics of these two species in mixed plantings.

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