

Growth and species interactions of Eucalyptus pellita in a mixed and monoculture plantation in the humid tropics of north Queensland

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ABSTRACT

This study investigated whether mixed-species designs can increase the growth of a tropical eucalypt when compared to monocultures. Monocultures of Eucalyptus pellita (E) and Acacia peregrina (A) and mixtures in various proportions (75E:25A, 50E:50A, 25E:75A) were planted in a replacement series design on the Atherton Tablelands of north Queensland, Australia. High mortality in the establishment phase due to repeated damage by tropical cyclones altered the trial design. Effects of experimental designs on tree growth were estimated using a linear mixed effects

model with restricted maximum likelihood analysis (REML). Volume growth of individual eucalypt trees were positively affected by the presence of acacia trees at age five years and this effect generally increased with time up to age 10 years. However, the stand volume and basal area increased with increasing proportions of E. pellita, due to its larger individual tree size. Conventional analysis did not offer convincing support for mixed-species designs. Preliminary individual-based modelling using a modified Hegyi competition index offered a solution and an equation that indicates acacias have positive ecological interactions (facilitation or competitive reduction), and definitely do not cause competition like a eucalypt. These results suggest that significantly increased in growth rates could be achieved with mixed-species designs. This statistical methodology could enable a better understanding of species interactions in similarly altered experiments, or undesigned mixed-species plantations.

Keywords: Eucalyptus pellita; Acacia peregrina; mixed-species plantations; growth and yield modelling; competition; Hegyi index.

INTRODUCTION

Despite the well-recognised desire of small-scale forest growers to plant timber species in mixed-species designs (Herbohn *et al.* 1998), few publications support the popular contention that growing timber trees in mixtures is better than monocultures. Mixtures have been established to maximise positive ecological interactions (facilitation and competitive reduction) and to minimise negative interactions (competition) (Kelty 1992, Forrester *et al.* 2005, Forrester *et al.* 2006). Studies of mixed vs. pure plantations have shown that mixtures have the potential for greater

production of biomass (DeBell *et al.* 1997, Forrester *et al.* 2004), more diversified products (Keenan *et al.* 1995, Piotta *et al.* 2004), improved nutrient cycling and soil fertility (Binkley *et al.* 1992, Bauhus *et al.* 2000, Binkley *et al.* 2000, Montagnini 2000), and improved risk management and reduced incidence of pest and diseases (Montagnini *et al.* 1995, Nichols *et al.* 1999, Piotta *et al.* 2004). However, our understanding of the silvicultural requirements of these designs is generally poor and the appropriate design and management regimes for mixed species plantations are not well-established (FAO 1992, Forrester *et al.* 2005).

In north Queensland, government programs such as the Community Rainforest Reforestation Program (CRRP), which ran from 1992 – 1999, encouraged private, small-scale forest grower's interest in establishing plantations of tropical hardwoods. This program fostered the establishment of plantations of a range of species on cleared private land for timber production, conservation, water quality improvement and community employment, and has resulted in establishment of approximately 1870 ha of mostly mixed species plantations in the humid tropics of north-eastern Australia (Erskine *et al.* 2005).

Since the mid 1990s, the main hardwood species planted in this region of north Queensland has been Eucalyptus pellita (F. Muell). Less than 100 hectares are currently established in monocultures however E. pellita was the most planted species in the CRRP (Lott *et al.* 2005). Historically the profitability of eucalypt plantations in Queensland, as measured from plantings established over 25 years ago, has been marginal. Productivity has been variable, ranging from 6 to 30 m³ha⁻¹ merchantable

mean annual increment (MAI), depending on species and site characteristics, but averaging approximately 15 m³ha⁻¹ MAI in moist areas (Ryan 1993).

A replacement series experiment (Kelty 1992, Jolliffe 2000) was designed to examine the effect of mixtures on the establishment and survival of planted trees; the production and value of commercial timber produced from E. pellita and Acacia peregrina (M.W. McDonald & Maslin). The reasons for including an acacia in this trial were twofold; to assess the facilitation effect of its potential for nitrogen fixation on the growth of the eucalypt, and also to potentially produce logs of a second timber species. The objectives of this paper are to examine the growth and interactions up to age 10.1 years by: (a) relating the designed experimental effects to the growth of individual E. pellita and A. peregrina trees in an altered mixed-species experiment, and (b) evaluating the effect of inter- and intra-specific competition on growth of each species.

METHODS

Site characteristics

The trial (Experiment 757 Atherton) is located on the Atherton Tablelands (17°S 145°E) in north Queensland, Australia. The site was cleared of original vegetation in the 1940's, converted to pasture for dairy grazing for a short time (probably 15 years), and subsequently abandoned. Immediately prior to establishment the site was degraded tropical pasture. The original vegetation was wet tropical sclerophyll forest of Acacia aulacocarpa, A. crassicarpa and Eucalyptus pellita with understorey of rainforest species. The site is about 760 m above sea level on flat terrain. The soil is a humic gley, Carrington Series from alluvium parent material derived from granite and

rhyolite (Laffan 1988). The average annual rainfall in the nearby town of Atherton is 1413 mm, distributed seasonally with a dry winter and a wet summer. The mean daily minimum and maximum temperatures are 14.5 °C and 26 °C, respectively, frosts are rare, but can occur in the drier winter months (Bureau of Meteorology 2005).

Experimental design

Eucalyptus pellita and Acacia peregrina were planted as a replacement series with five relative densities: 100% E. pellita (100E), 75% E. pellita + 25% A. peregrina (75E:25A), 50% E. pellita + 50% A. peregrina (50E:50A), 25% E. pellita + 75% A. peregrina (25E:75A), and 100% A. peregrina. The trees were planted at 1000 stems per hectare (5 m x 2 m). Plots were arranged in a randomised complete block with two replications. Plot size was 35 m x 24 m including the single row of buffer trees. Excluding the buffer trees there were 50 trees per plot. In the mixed-species plots species were planted in alternating rows, with every second row mixed within the row in the 75:25 and 25:75 mixtures.

Site preparation and planting

The site was cultivated by mounding tree rows (about 60 cm height) in September 1994 followed by ripping these mounds in January 1995. Grasses and other germinants were removed with glyphosate one month before, and twice again immediately prior to planting (mid January and early February 1995). E. pellita seedlings were from a local, upland north Queensland provenance (Kuranda) and were planted in mid February 1995. A. peregrina seedlings were an Australian Tree Seed Centre seedlot (B17873) collected by villagers between Wipim – Oriomo in Western Province, New Guinea, in 1990 from 10 trees. This seedlot has mistakenly

been known as New Guinea Acacia aulacocarpa, however it was recently reclassified as Acacia peregrina (McDonald and Maslin 2000). Acacia seedlings were inoculated in the nursery with rhizobium (strain 311/1) and planted in the field in mid March 1995. No fertiliser was applied at planting, but in mid June 1995, 52 kg P ha⁻¹ as superphosphate was applied as a surface application approximately 30 cm from the base of the trees.

The trees were damaged by a tropical cyclone (TC) in March 1997 (TC Justin), and again in February 1998 (TC Rona) when the trees were age 2 and 3 years respectively. The trial design was considerably altered, with substantial but uneven mortality across the site and as a result planned thinning has not been required.

Growth measurements

To assess the effect of mixture on growth, tree height (Ht) was measured at ages 0.6, 1.7, 4.4 (eucalypts only), 5.6, 7.8, 8.7 and 10.1 years after planting. Diameter at breast height (1.3 m) over bark (DBH) was measured at age 4.4 (eucalypts only) 5.6, 7.8, 8.7 and 10.1 years. Stem volume (over bark) was estimated as:

$$\text{Stem volume (m}^3\text{)} = (\text{BA} \times \text{Ht})/3 \quad (1)$$

where BA is the basal area of individual trees in m².

Statistical techniques

Initial summaries of survival, individual tree and stand basal area were considered at the plot-level using analysis of variance. Because high mortality altered the design and confounded intraspecific and interspecific-tree competition for some treatments, a mixed effects regression model was used to examine the significant effects on tree

growth. An individual tree distance-dependent competition index (Hegyi 1974, Vanclay 1994, Vanclay 2006) was used to examine species interactions and density dependency.

Using the repeated measures on individual trees a linear mixed model of growth from age 5.6 to 10.1 years after planting was developed to test experimental effects, with a two-level sampling structure of trees and measure occasion nested within trees. The model was estimated using REML, and tested with maximum likelihood fit using MLwiN (Rasbash *et al.* 2004).

RESULTS

Survival

At age 10.1 years survival was higher for *E. pellita* (47%) than *A. peregrina* (39%) (Table 1), but this difference was not significant ($P = 0.231$). Natural mortality in establishment phase changed the stocking, species proportions and design treatment structures (Tables 1 and 2). There was high mortality in the years 2 -5 caused by cyclones at age 2 and 3 years, and to a lesser extent, in the year after planting, and for the acacia only in years 9-10 (Table 2). Mortality was not related to species proportions. Because uneven mortality altered the relative stocking in treatments, hereafter we refer to 41:0, 41:8, 18:26, 11:19, 0:48 stems/plot. These correspond to 100:0, 83:17, 41:59, 37:63, 0:100 % E : A respectively (Table 1). The former notation is used in this paper because it also conveys stocking information.

[Tables 1 & 2 near here]

Growth

The mean annual diameter increments across all treatments for E. pellita and A. peregrina are 2.6 cm yr⁻¹ and 1.6 cm yr⁻¹ respectively; mean size characteristics are shown in Table 3. At age 5.6 years the monocultures are producing the larger diameter stems, but by age 10.1 years the largest stems of both species are in the mixed-species plots (Figure 1). This figure illustrates that the largest diameters are around the 50:50 mixtures, however due to altered designs, the precise mix is not clear. The differences between monocultures and mixed-species are increasing steadily with each measurement occasion, but are not significant. The altered design is further illustrated by size relative to stocking (Figure 2). For instance, the plot with the large outlier acacias in Figure 1 might appear questionable; however by comparison with Figure 2 it is clear that this plot has a low stocking. Similarly the larger eucalypts appear to benefit both from 50:50% species mix and low stocking. Figure 2 also illustrates that the optimum stocking for the acacia reduces with age.

[Table 3 near here. Figures 1 & 2 near here, side-by-side]

The largest trees are also in the treatments with the fewest surviving trees leading to decreased stand basal area in the mixtures with lower proportions of the larger species, E. pellita (Figure 3). The cumulative line in Figure 3 indicates there were no species interactions. If a plot falls on the line, then there is no benefit of planting 2 hectares in a mixture versus 1 ha each in a monoculture. If a plot falls below the line, it is better to have monocultures. The few plots which are above this line suggest that a small proportion of acacia may be beneficial. The effect of the mixed treatments on the growth of both species is confounded by the size of the larger species (the

eucalypts) and the stocking of component species (within treatment) as shown by a comparison of the lines in Figure 4. If we consider mean tree volume we conclude that mixtures are more productive; but consider total stand volume and conclude that mixtures are slightly less productive. The previous figures explain this is because of stocking differences. The addition of eucalypts to any A. peregrina treatment increases the total stand volume compared with the acacia monoculture.

[Figures 3 & 4 near here]

Assessing treatment effects

Treatment effects from the original replacement series design were examined using the natural log of individual stem volume ($\ln V$) as the response variate in a mixed-effects model, and tested using random effects maximum likelihood (REML), in MLwiN. The strategy adopted in model-building was to commence with a nested two-level sampling structure with individual tree growth and measure occasion within tree, and then progressively add other effects. Different models were evaluated using the likelihood ratio test (LRT) for nested models, the change in the $-2\log$ likelihood statistics between models, or the Akaike Information Criteria (AIC) for alternative sets of effects (Fang and Bailey 2001, Zhao *et al.* 2005). The final model had both random intercepts and random slopes, implying that trees of the same component species (cs) will not only have different sizes over time, but will also grow at different rates (Table 4).

The equation of the final model is:

$$\ln(V_{ij}) = \text{constant}_{ij} + \alpha_i + \delta_i + \tau_j + (\delta\tau)_{ij} + \Omega_{ij} \quad (2)$$

where V is volume measured in m^3 . Where $\ln(V_{ij})$ = natural logarithm of tree volume of i^{th} tree on k^{th} measurement occasion; constant = component species 1 on occasion 1; α_i = block effect (fixed and treated as an attribute of the tree); δ_i = component species effect (fixed – dummy variables representing deviations from the constant); τ_j = measurement occasion effect (random – dummy variables representing deviations from the constant); $(\delta\tau)_{ij}$ = interaction of component species and measurement occasion (fixed – dummy variables representing deviations from the component species and occasion main effects); Ω_{ij} = variance-covariance matrix of random effects of occasion within tree. There are no ε_{ij} (random effects), as they are absorbed into Ω_{ij} because each tree is modelled exactly on each occasion.

[Table 4 near here]

The model was developed in a series of steps with each step tested using the likelihood ratio test from ML fits for significance, with the last three steps (labelled 1, 2 and final) shown in Table 4. Step 1 establishes the full fixed effects model, with the intercept (constant; i.e. eucalypt monoculture, at 5.6 years), the two-level structure: tree within experiment and measure occasion within tree, the replicate and component species (cs). The significance of the parameter estimates are assessed with P values. The estimates for cs2 and cs6 are not significant but have been retained in the model as the interaction effects of these component species and occasion of measurement were of interest. Step 2 shows that adjustment for random slopes on the measure occasion, implying that stem volume changes with measure occasion at different rates for the different component species. The models in steps 1 and 2 have different

random effects and are compared using an Akaike Information Criteria ($AIC = -2\log(L) + 2p$, where L is the likelihood and p is the number of parameters in the model). The model with the smaller AIC is preferred (Fang and Bailey 2001). The final model, compared with model 2 using a likelihood ratio test (LRT) using maximum likelihood estimates, illustrates a significant interaction term between measure occasion and component species. Table 4 shows which effects and interactions are significant. A model constructed for predictive purposes might remove the not significant estimates. This model is simply to compare effects and interactions, and therefore we suggest that removing the not significant estimates would only increase the significance on an already highly significant overall model ($P < 0.0005$). The variance-covariance structure of the standardised residuals (y ; the random slopes effects collected in Ω_{ij} , standardised) are shown on the diagonal of Table 5, illustrating that the trees that were larger on average at measure occasion 1 grew slower on average between occasion 1 and the subsequent occasions 2, 3 and 4. The standardised residuals plots do not reveal any observable patterns (Figure 5).

[Figures 5 and Table 5 near here]

Tests designed to answer the original design questions indicates that size of the E. pellita at age 10.1 years does not appear to be related to the designed treatment effect. In contrast, A. peregrina grown in the 11:19 mix are significantly larger, or nearly significantly larger (18:26 – 11:19, $P = 0.06$), than acacias grown in any other treatment, pure or mixed. Eucalypt monocultures (41:0) are growing significantly slower (71%) when compared to those in 18:26 ($P = 0.001$), and acacia monocultures are growing at significantly slower rates ($P = 0.04$) than those in the 11:19 mix.

However not all mixtures produce a positive growth effect, and eucalypts in the 41:8 mix have growth rates significantly less than those in monocultures ($P = 0.004$).

Earlier figures illustrate a significant stocking effect, but the effects of stocking were not assessed using this model because the plot level variables for overall stocking, or component species stocking, would not converge in the presence of the variables already in the model.

Competition

The random effects model (2) is useful for diagnosis, but not for prediction or for simulating alternative outcomes (Vanclay 2006b). To assist in drawing practical inferences from the experiment, an individual tree growth equation was developed, based on a spatially-explicit competition index that could accommodate local variation in stocking within the plots. Of many point-based density indices that have been proposed (Rivas *et al.* 2005), Hegyi's index (1974) was found to offer the best correlation with individual tree diameter increments. Better estimates were obtained by refining this index to search a surrounding neighbourhood defined by tree height, rather than by a constant distance. Our variation of the index estimates competition experienced by tree i as the sum of the relative heights divided by the distance:

$$C_i = \sum_j (\text{Height}_j / \text{Height}_i) / \text{Distance}_{ij} \quad (3)$$

for all trees j ($j \neq i$) where $\text{Distance}_{ij} \leq (k_s \text{Height}_i + k_s \text{Height}_j)$, where k_s takes the value 0.3 for E. pellita and 0.5 for A. peregrina. These estimates of k_s provided the best least-squares estimates in equation 5 (below; Vanclay 2006a).

This appears to be one of the largest reported search radii reported for Hegyi's index (Table 6). Transformations of height and distance offered little improvement to this basic form. Four partial competition indices, C_{is} , were calculated representing competition experienced by a tree of species i caused by all trees of species s within its neighbourhood. A preliminary equation was fitted using ordinary least squares regression:

$$\Delta d = 0.3111 S_e + 0.1453 d - 0.0020 d^2 - 0.3950 C_{11} + 0.0792 C_{12} - 0.1284 C_{21} - 0.1743 C_{22}$$

(4)

(s.e. 0.1051	0.0078	0.0002	0.0363	0.0644	0.0228	0.0268
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$\sigma=0.5937, df=1139)$

where Δd is the annual diameter increment, d is diameter over bark at 1.3 m above ground, and S_e is a binary variable which takes the value 1 for eucalypt trees. Parameter estimates are significant at $P \leq 0.01$ (except C_{12} which has $P = 0.2$). Parameters C_{21} and C_{22} do not differ significantly, and may be combined, leading to the following equation:

$$\Delta d = 0.3494 S_e + 0.1414 d - 0.0019 d^2 - 0.3948 C_{11} + 0.0778 C_{12} - 0.1449 C_{2*}$$

(5)

(s.e. 0.1028	0.0075	0.0002	0.0363	0.0644	0.0207	$\sigma=0.5942,$
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$df=1140)$

in which parameter estimates are significant at $P \leq 0.001$ (except C_{12} which has $P = 0.2$).

[Insert Table 6 near here]

The first three terms in equation 5 are unremarkable, describing a simple but realistic growth pattern with maximum growth at $d = 37$ cm and a maximum attainable size of $d \approx 75$ cm, both beyond the range of the present data. It is the last three or four terms

of equations 5 and 4 respectively, that are of interest. *A priori*, we expected all of these parameters to be negative, with intra-specific competition (C_{11} , C_{22}) more intense than inter-specific competition (C_{12} , C_{21}). Counter to expectation, the acacias seem to facilitate rather than compete with the eucalypts, as indicated by the positive parameter for C_{12} , and the increasing growth (solid line) with increasing competition shown in Figure 6a. This plot also illustrates the strong intra-specific competition within eucalypts (dashed line, Figure 6a). Figure 6b illustrates that acacias do not discriminate between inter and intra-specific competition, with both trend lines atop one another, and that all competition has a negative effect on growth. Estimates of competition were stable, and interaction terms between competition and measurement occasion (based on measurements at 5.6, 7.8, 8.7 and 10.1 years) and between competition and tree diameter were not significant ($P > 0.2$). Vanclay (2006b) illustrated some of the implications of this equation.

[Figure 6 near here]

DISCUSSION

Growth dynamics

Since the eucalypts grow faster than the acacias, the eucalypt monoculture should, in the absence of species interactions, provide the greatest yields. However, after 10.1 years the 11:19 mixture produces the largest *E. pellita* stems (ns $P = 0.29$), growing at rates faster than those evident in the eucalypt monoculture (ns, $P = 0.6$), grown in a mixture with significantly larger *A. peregrina* stems ($P=0.01$), with growth rates significantly faster ($P = 0.04$) than those evident in the acacia monoculture. In some instances, fewer eucalypts combined with additional acacias, lead to larger individual

E. pellita stems and faster growth rates. If these growth rates were to continue, E. pellita grown in mixtures would reach harvestable size earlier, with larger stems potentially producing more timber, than if it were grown in monocultures. The total stand volume (and that of the eucalypt component) increased with increasing proportions of eucalypts.

Growth of E. pellita in this trial was comparable with early growth rates of this provenance from other trials (2.2 – 2.8 cm yr⁻¹ up to age 3.2 years, Harwood *et al.* 1997); better than the average growth recorded for unknown provenances used in the CRRP (2.2 cm yr⁻¹ to age 8 years, Bristow *et al.* 2005); but slower than growth reported for trials of New Guinea provenances (2.8 – 4.2 cm yr⁻¹ up to age 3.2 years, Harwood *et al.* 1997). This provenance of E. pellita would no longer be recommended for this upland site as the growth of this species has been shown to be negatively correlated with cooler temperatures (Bristow *et al.* 2005). Less growth data exists for A. peregrina, however the continuing mortality between ages 9 - 10 years suggests this species may not be suitable for long-term timber production at this site. The natural distribution of this species is on the wet (1500 - 3400 mm) tropical lowlands (10 - 90 m.a.s.l.) of New Guinea (McDonald and Maslin 2000). Ongoing mortality of the acacias might be associated with climatic events over the life of the trial. The worst frosts in 15 years were experienced on the Atherton Tablelands in May-June 2000, and well below average rainfall (59% of mean for Atherton) was experienced in 2002, five and seven years after planting respectively (Bureau of Meteorology 2005). Canopy stratification with the eucalypts over-topping the acacias, leading to competition for light could also be contributing to the decline of this typically taller growing species (Forrester *et al.* 2006).

Analysis techniques

Plot level analysis of this replacement series yielded little new information about growth of eucalypts in mixed-species stands. It is difficult to determine whether changes in yield are due to changes in density of each species, or changes in proportion of component species. Growth functions and yield-density relationships in monocultures of E. pellita are unknown, and the added problem of uneven natural mortality, typical of long-rotation forest plantations, confounds any traditional analysis techniques such as ANOVA (Jolliffe 2000, Zhao *et al.* 2005).

Two techniques were used to understand growth and species interactions in this trial; firstly a mixed effects model was developed to test for effects of experimental design, and then distance-dependant competition was assessed to determine interactions and competition between and among the two species. The linear mixed effects model helped to establish the significant effects and interactions in spite of the considerable changes to the design, but was unable to resolve whether monocultures are better than mixtures as there does not seem to be a practical way to discriminate between the effects of species composition and stocking using a plot-level variable.

The traditional analysis of replacement series experiments is further compromised where the design is altered prior to canopy closure and the onset of between-tree competition (Jolliffe 2000), as with this trial, creating different growth environments than intended. Growth of individual trees in a plantation is not independent (in a statistical sense), but is correlated with species, plantation design and position within it (i.e. treatment, plot and replicate), historic growth rates, and the survival and growth

of neighbours and competition for the resources in the stand. To explain the uneven, and as yet unaccounted, changes to density a second methodology was used to consider the competition between trees using a variation of Hegyi's distance-dependent competition index (Hegyi 1974, Tome and Burkhart 1989). Discriminating between inter- and intra-specific competition by using partial sums contributed to a better understanding of competition. The results suggest that a eucalypt would 'prefer' to be adjacent to an acacia rather than an empty space. Whether this is because the acacia fixes nitrogen (Forrester *et al.* 2006), or because the acacia suppresses grass and other weeds, or both needs to be determined. Other terms reveal that intra-specific competition within the eucalypts is much stronger than within the acacias, and that the competition experienced by an acacia seems to be similar, irrespective of the species (eucalypt or acacia) of the competitors (C_{21} and C_{22} are not significantly different).

Mixed-species designs

The success of other eucalypt and acacia mixtures studies have been contingent on increased biomass production of one or both species in the mixture (Binkley *et al.* 1992, Kelty 1992, Parrotta 1999, Montagnini 2000, Forrester *et al.* 2004). With the exception of Keenan *et al.* (1995) and DeBell *et al.* (1997) few mixtures studies have considered increases in solid wood production as success criteria, and none where the objective is for both species to produce valuable, sawn timber. For a variety of social and perceived environmental reasons most of the small-scale private forest growers in the higher rainfall regions of east coast of Australia plant their woodlots in mixed-species designs (Erskine *et al.* 2005). To compete with industrial forestry, these small-scale growers of long rotation timbers must target high-value low-volume markets (Herbohn and Harrison 2004). Timber for these markets will come from silvicultural

regimes that allow the maximum volume growth on the fewest stems per hectare since larger stems yield more sawlog, with a higher value. This study shows that by growing E. pellita and A. peregrina in mixed-species stands significantly larger individual trees, and presumably higher value stems, of both species can be grown.

CONCLUSIONS

Results from a classic replacement series analysis of this experiment are ambiguous as the greatest basal area is attained in the eucalypt monoculture, while the largest individual stem volumes are obtained in mixed-species. However, individual-based modelling using a spatially-explicit competition index has revealed that eucalypts derive a positive growth stimulus from the presence of acacias. For growers of plantation mixtures this could potentially lead to increased production, and larger, more valuable trees. It is premature to extrapolate these early results to rotation age, but the potential exists for plantation growers to realise significant productivity gains by growing E. pellita in mixed-species designs.

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Table 1

Mean 10.1-year survival by treatment and species.

Designed treatment percentages (E%A%)	Percent survival			Post-mortality treatment proportions (E:A)
	<u>E. pellita</u>	<u>A. peregrina</u>	Total	
100:0	41		41	41:0
75:25	52	39	46	41:8
50:50	43	46	44	18:26
25:75	50	25	37	11:19
0:100		48	48	0:48
average for species	47	39	43	

Table 2

Annualized survival by measure period. The high mortality during years 2 – 5 was due to tropical cyclones in 1997 and 1998.

Species	Survival period (years)				
	1	2-5	6-7	8	9-10
<u>E. pellita</u>	0.92	0.85	0.98	0.99	1.00
<u>A. peregrina</u>	0.90	0.85	0.96	0.99	0.95

Table 3

Characteristics for E. pellita and A. peregrina monocultures after 10.1 years of growth.

Parameter	<u>E. pellita</u>	<u>A. peregrina</u>
Predominant Height *(m)	23.9 (2.0)	15.2 (2.5)
Average Diameter (cm)	26.4 (6.0)	16.3 (3.3)
Individual stem volume (m ³)	0.4 (0.2)	0.1 (0.1)

*Predominant height is the average of the tallest 4 stems per species, per plot.

Standard deviations shown in parenthesis.

Table 4

Linear mixed effects model development, natural log of stem volume as response

variate.

Effect	Step 1			Step 2			Final Model		
	Estimate	S.E.	P-value	Estimate	S.E.	P-value	Estimate	S.E.	P-value
Fixed									
constant	-2.221	0.066	*	-2.215	0.066	*	-2.222	0.067	*
replicate	-0.161	0.057	*	-0.162	0.057	*	-0.163	0.057	*
cs [†] 2 (E75)	0.006	0.094	0.94	0.016	0.094	0.86	0.069	0.096	0.48
cs 3 (A25)	-1.840	0.150	*	-1.834	0.149	*	-1.760	0.153	*
cs 4 (E50)	-0.252	0.117	*	-0.292	0.117	*	-0.443	0.120	*
cs 5 (A50)	-1.424	0.103	*	-1.438	0.102	*	-1.425	0.104	*
cs 6 (E25)	0.145	0.140	0.30	0.142	0.140	0.32	0.114	0.143	0.42
cs 7 (A75)	-1.244	0.109	*	-1.262	0.109	*	-1.297	0.111	*
cs 8 (A100)	-1.471	0.087	*	-1.482	0.087	*	-1.447	0.089	*
occasion 2 ^s	0.635	0.011	*	0.635	0.010	*	0.640	0.022	*
occasion 3	0.830	0.011	*	0.830	0.010	*	0.846	0.027	*
occasion 4	1.216	0.011	*	1.215	0.012	*	1.197	0.037	*
cs 2 x occ 2							-0.051	0.032	0.12
cs 2 x occ 3							-0.105	0.038	*
cs 2 x occ 4							-0.149	0.052	*
cs 3 x occ 2							-0.104	0.053	*
cs 3 x occ 3							-0.140	0.064	*
cs 3 x occ 4							-0.111	0.052	*
cs 4 x occ 2							0.196	0.041	*
cs 4 x occ 3							0.261	0.050	*
cs 4 x occ 4							0.347	0.067	*
cs 5 x occ 2							-0.018	0.035	0.60
cs 5 x occ 3							-0.040	0.042	0.34
cs 5 x occ 4							0.036	0.057	0.52
cs 6 x occ 2							0.024	0.048	0.62
cs 6 x occ 3							0.069	0.058	0.24
cs 6 x occ 4							0.045	0.079	0.56
cs 7 x occ 2							0.075	0.038	*
cs 7 x occ 3							0.054	0.046	0.24
cs 7 x occ 4							0.143	0.063	*
cs 8 x occ 2							-0.048	0.030	0.10
cs 8 x occ 3							-0.064	0.036	0.08
cs 8 x occ 4							0.019	0.049	0.70
Random									
tree within experiment	0.300	0.022	*	0.298	0.022	*	0.318	0.023	*
occasion within tree	0.022	0.001	*	0.018	0.001	*	0	0	*
-2 log likelihood		81.41			36.258			-821.537	
AIC⁺		105.41			60.258				
LRT[^]								857.795	

[†] cs is the component species, i.e. the species within the original treatment structure, [§] four measure occasions are 5.6 (start), 7.8, 8.7 and 10.1 years after planting, ⁺AIC Akaike Information Criteria, [^]LRT Likelihood ratio test calculated with respect to model [step 2] with maximum likelihood estimation applied, *Estimate is significant at $P < 0.05$.

Table 5

Tree-level random effects variance-covariance matrix

	Occ 1		Occ2		Occ 3		Occ	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
Occ 1	0.318	0.023						
Occ 2	-0.020	0.006	0.034	0.003				
Occ 3	-0.026	0.007	0.038	0.003	0.050	0.004		
Occ 4	-0.036	0.009	0.047	0.004	0.062	0.005	0.092	0.007

Table 6

Search radii reported for Hegyi's index.

Author	Species	Search radii
Clinton <i>et al.</i> 1997	White pine (<u><i>Pinus strobus</i></u>)	6 m
Mailly <i>et al.</i> 2003	Black spruce (<u><i>Picea mariana</i></u>)	4 m
Piutti and Cescati 1997	Beech (<u><i>Fagus sylvatica</i></u>)	8 m
Canham <i>et al.</i> 2004	Hemlock (<u><i>Tsuga heterophylla</i></u>) & redcedar (<u><i>Thuja plicata</i></u>)	8 – 13 m
Beland <i>et al.</i> 2003	Jack pine (<u><i>Pinus banksiana</i></u>)	6 m
De Luis <i>et al.</i> 1998	Black pine (<u><i>Pinus nigra</i></u>)	3 – 4 m

(Clinton *et al.* 1997, Piutti and Cescati 1997, De Luis *et al.* 1998, Beland *et al.* 2003,Mailly *et al.* 2003, Canham *et al.* 2004)

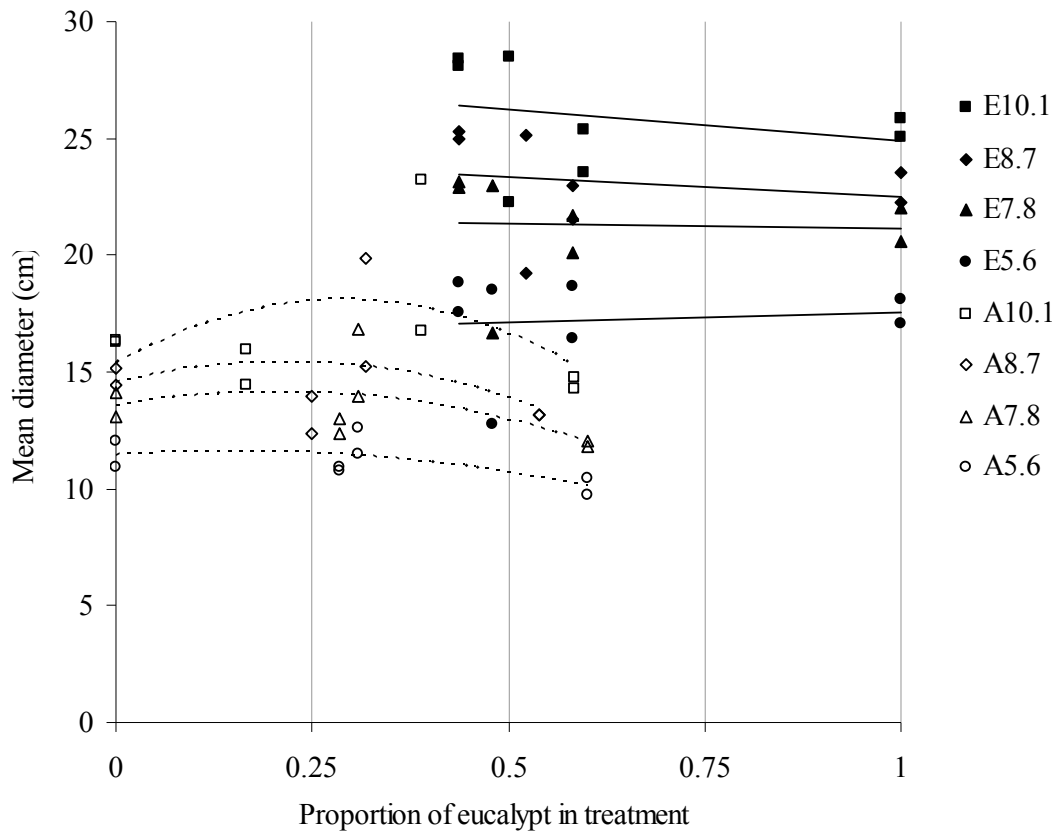


Figure 1

Mean diameters of *E. pellita* (solid symbols and lines) and *A. peregrina* (open symbols, dashed lines) as a proportion of eucalypt in treatment, at four measure occasions (5.6, 7.8, 8.7, 10.1 years after planting).

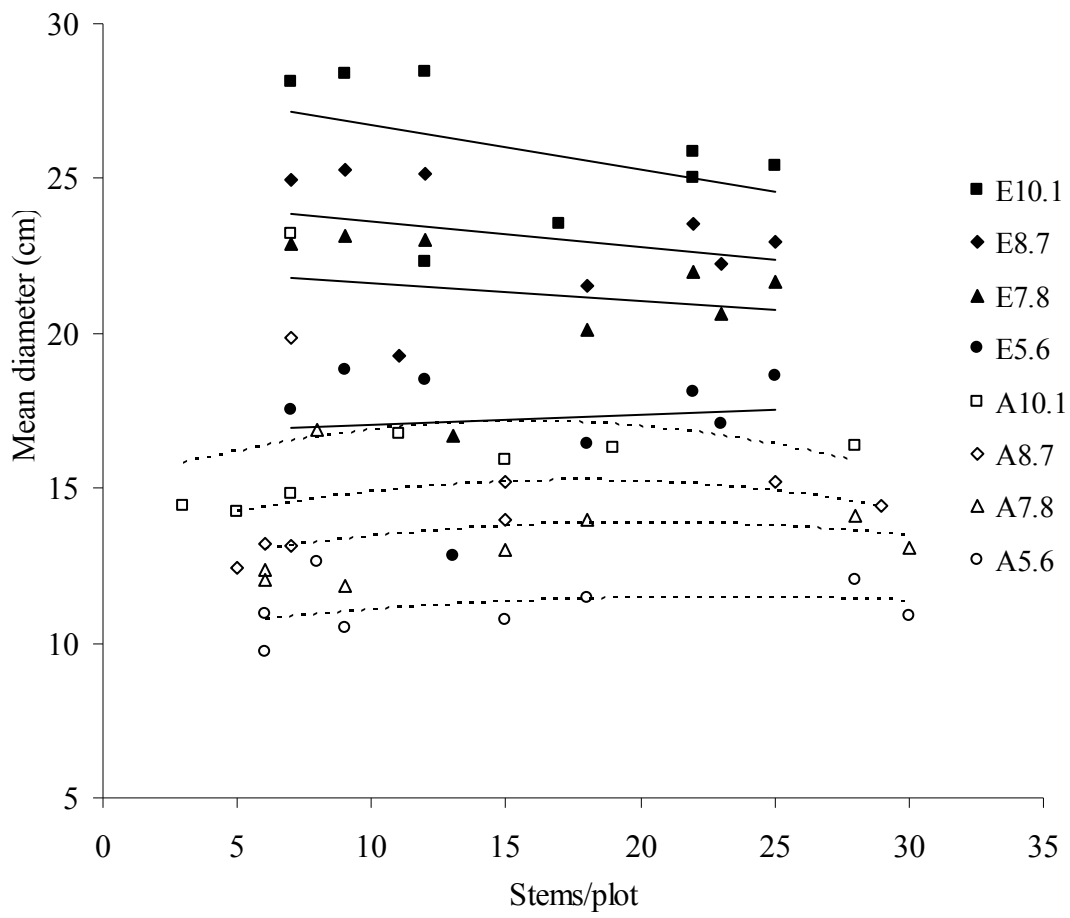


Figure 2

Mean diameters of *E. pellita* (solid symbols and lines) and *A. peregrina* (open symbols, dashed lines) versus the number of stems per plot, at four measure occasions (5.6, 7.8, 8.7, 10.1 years after planting).

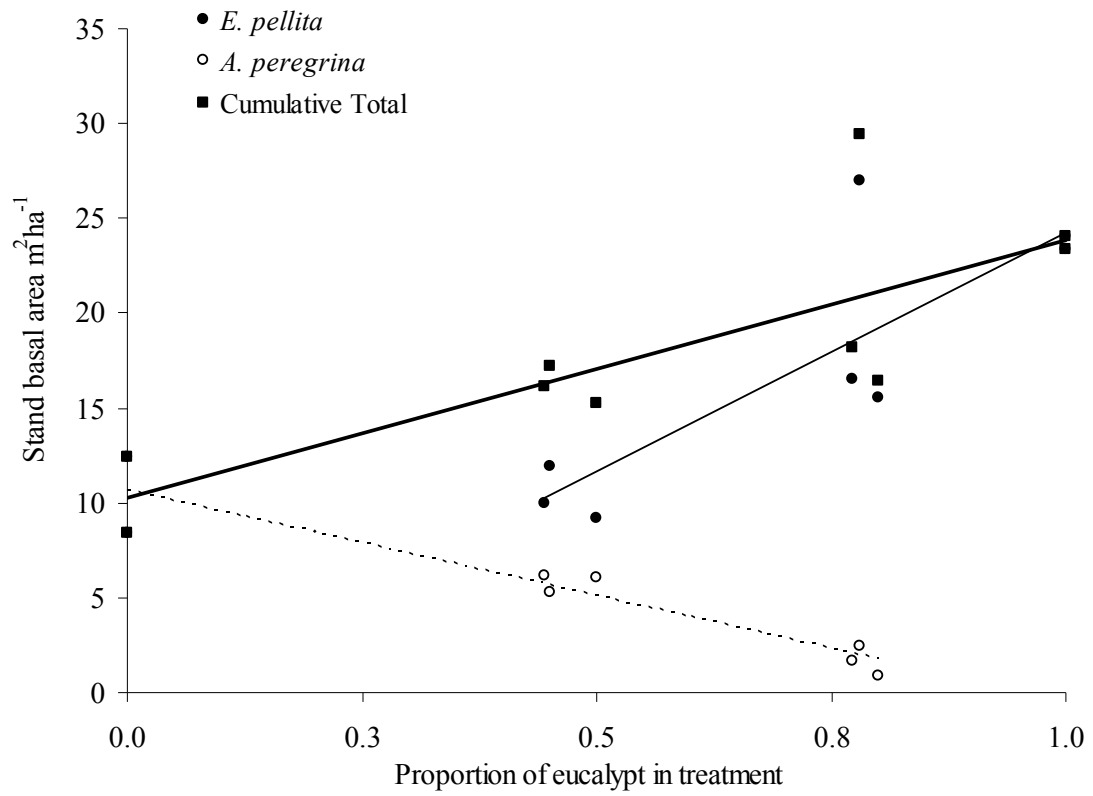


Figure 3

Stand basal area of *E. pellita* (solid circle, solid line), *A. peregrina* (open circle, dashed line) and cumulative total (solid squares, bold line) at age 10.1 years.

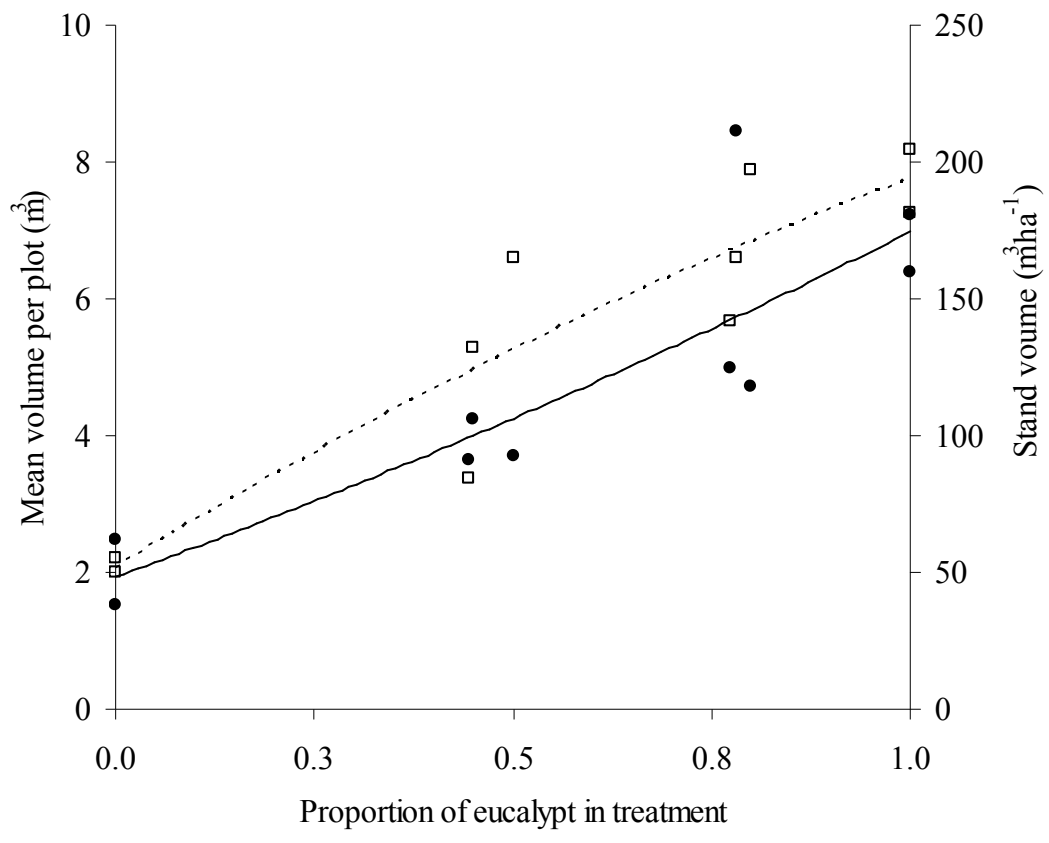
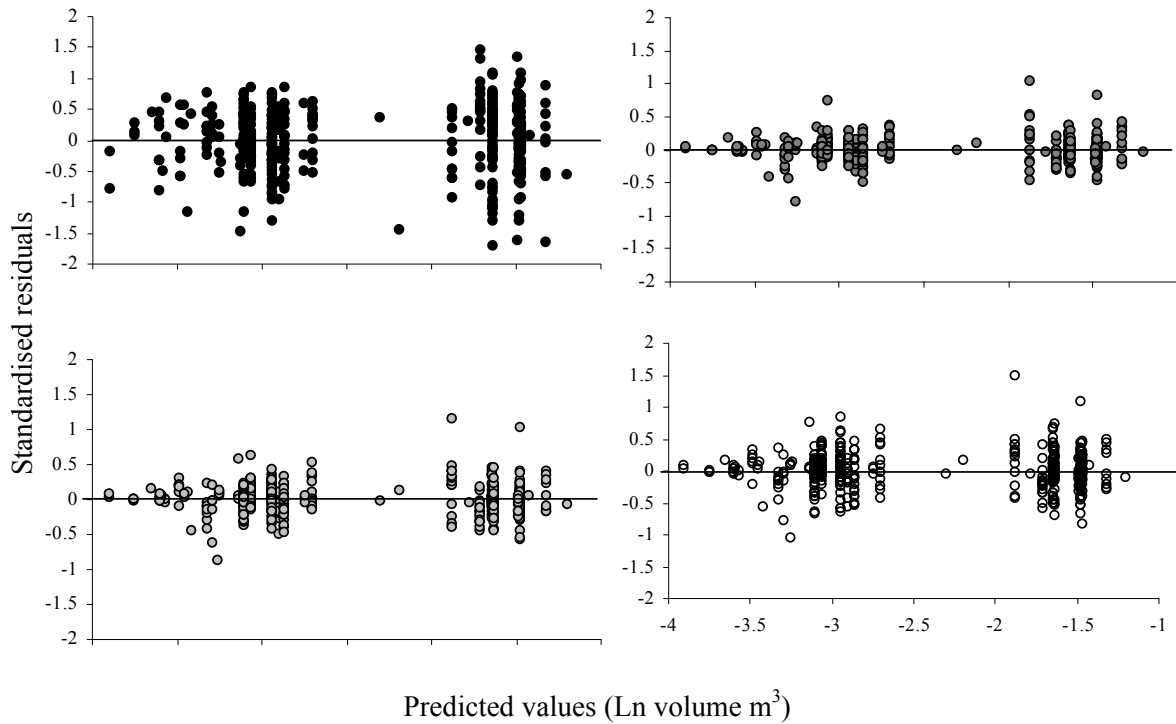


Figure 4

Mean tree volume per plot and mean stand volume per hectare relative to the proportion of eucalypts within treatments at age 10.1 years.



5 Figure 5.

Standardised residuals versus predicted values for model (Equation 2) at the four measure occasions (top left) predicted value of the constant (measure occasion 1), (lower left) predicted value of growth between the constant and occasion 2, (top right) predicted value of growth between measure occasions 2 and 3, and (lower right) predicted value of growth between

10 measure occasions 3 and 4.

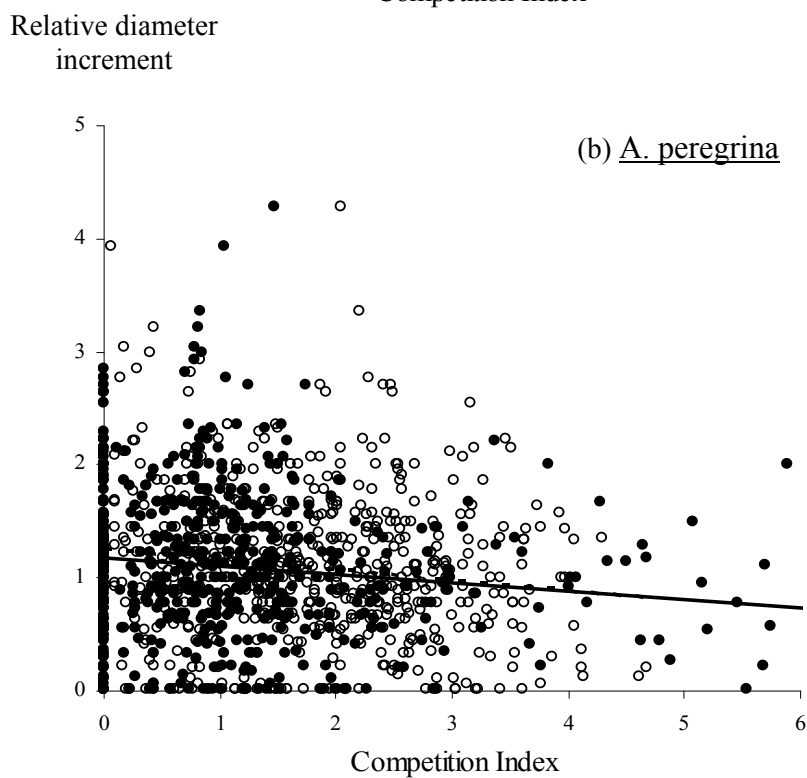
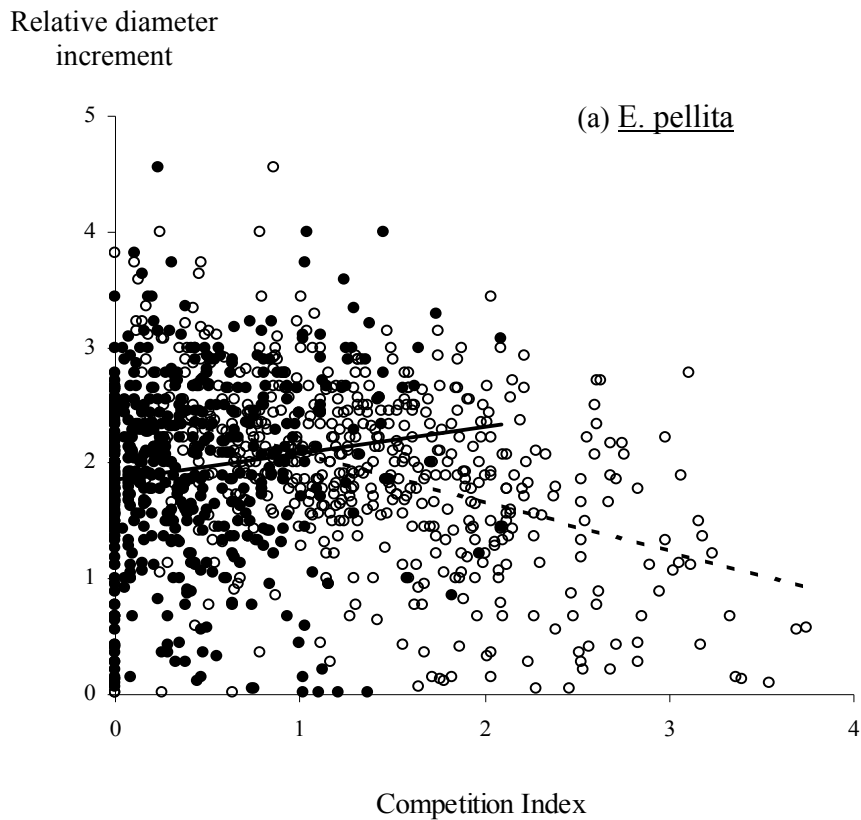


Figure 6a and b

15 Relative diameter increment ($\text{cm yr}^{-1}/\text{initial size (cm)}$) versus inter-specific (solid symbols, solid line) and intra-specific (open symbols, dashed line) competition for (a) E. pellita and (b) A. peregrina.