Aboveground interactions and productivity in mixed-species plantations of Acacia mearnsii and Eucalyptus globulus

Article *in* Canadian Journal of Forest Research · March 2004

DOI: 10.1139/x03-243

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Aboveground interactions and productivity in mixed-species plantations of *Acacia mearnsii* and *Eucalyptus globulus*

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Abstract: This study compared productivity in mixed-species plantations of *Eucalyptus globulus* ssp. *pseudoglobulus* (Naudin ex Maiden) Kirkpatr. and *Acacia mearnsii* de Wild with pure stands of each species and investigated how this might be explained by canopy stratification between species and changes in leaf characteristics of eucalypts. Investigations were carried out at a trial using the replacement series design, which consisted of the following combinations: 100% eucalypts (100%E), 75% eucalypts + 25% acacia (75%E:25%A), 50% eucalypts + 50% acacia (50%E:50%A), 25% eucalypts + 75% acacia (25%E:75%A), and 100% acacia (100%A). At 9.5 years, stem volume and biomass were highest in 50%E:50%A treatments. Canopy stratification occurred in all mixtures, with acacias in the lower and eucalypts in the upper canopy stratum. This and the increasing canopy light interception with increasing proportion of acacia in the mixture indicated that *A. mearnsii* is substantially more shade tolerant than *E. globulus*. Midcanopy foliage of *E. globulus* in the 50%E:50%A mixture had higher foliage nitrogen (N) but lower phosphorus (P) concentrations and lower light-saturated net photosynthesis rates (A_{max}) than those in the 100%E treatment. In addition, similar relationships between eucalypt crown volume and stem biomass across treatments indicated that eucalypt crowns were not more efficient in mixture. Our study indicates that the productivity gains in these mixtures may be partially attributable to aboveground niche separation between species.

Résumé : Cette étude visait à déterminer dans quelle mesure l'augmentation de productivité dans des plantations mixtes d'*Eucalyptus globulus* ssp. *pseudoglobulus* (Naudin ex Maiden) Kirkpatr. et d'*Acacia mearnsii* de Wild, comparativement à des peuplements purs de chaque espèce, peut s'expliquer par la stratification du couvert de ces espèces et les changements dans les caractéristiques foliaires des eucalyptus. Les travaux de recherche ont été réalisés dans un essais où avait été établi un dispositif contenant une série de remplacement composée des combinaisons suivantes : 100% eucalyptus (100%E), 75% eucalyptus + 25% acacia (75%E:25%A), 50% eucalyptus + 50% acacia (50%E:50%A), 25% eucalyptus + 75% acacia (25%E:75%A) et 100% acacia (100%A). À l'âge de 9,5 ans, la biomasse et le volume de la tige étaient les plus élevés dans le traitement 50%E:50%A. La stratification du couvert a été observée dans toutes les combinaisons : les acacia occupant la strate inférieure et les eucalyptus la strate supérieure. Ce fait et l'interception croissante de la lumière par le couvert avec la proportion croissante d'acacia dans le mélange indiquent qu'*A. mearnsii* est une espèce beaucoup plus tolérante qu'*E. globulus*. Le feuillage d'*E. globulus* situé au milieu du couvert dans le mélange 50%E:50%A avait une concentration plus élevée de N mais plus faible de P et un taux de photosynthèse nette à saturation lumineuse (A_{max}) plus faible que dans le traitement 100%E. De plus, des relations semblables entre le volume de cime et la biomasse de la tige de l'eucalyptus, quel que soit le traitement, indiquent que les cimes d'eucalyptus ne sont pas plus efficaces en mélange. Cette étude montre que les gains de productivité dans ces mélanges pourraient être partiellement attribuables à la spécificité de la niche épigée de ces deux espèces.

[Traduit par la Rédaction]

Introduction

Many problems currently attributed to plantations are associated with large-scale, industrial plantations established to supply a uniform resource such as fibre for pulp or sawlogs for milling (Hartley 2002). Concerns, in particular in relation to monospecific and short rotation plantations, include the export and depletion of nutrients (primarily nitro-

Received 6 May 2003. Accepted 9 October 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 23 March 2004.

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 doi: 10.1139/X03-243

gen (N) and phosphorus (P)), depletion of soil organic matter, soil erosion and compaction, lack of biodiversity, and pest or disease outbreaks (FAO 1995).

Mixed-species plantations have the potential to address some of the above-mentioned concerns whilst providing other benefits such as increased biodiversity, diversification of products, improved risk management, improved tree form for shade-adapted species (Keenan et al. 1995), increasing biomass production (Montagnini et al. 1995), and increasing carbon (C) sequestration (Kaye et al. 2000). Of particular interest have been the combinations of N-fixing and non-N-fixing tree species, which may maintain soil fertility at a higher level with reduced inputs of mineral fertilizers. Whether or not the productivity of mixed-species stands is superior to that of respective monocultures depends to a large extent on the design of the mixture and the availability of resources (Fridley 2002). Experimental plantations showing a synergistic effect of combining N-fixing with non-N-fixing species have been described by Bauhus et al. (2000), Binkley et al. (1992, 2000), Binkley and Ryan (1998), and Khanna (1997).

Based on a review of a small number of studies, Rothe and Binkley (2001) have speculated that N fixation in mixed stands increases linearly with the proportion of N-fixing species. However, the response of biomass in mixed-species stands to increasing proportions of N-fixing species deviates regularly from a linear pattern, which suggests that the relation between N fixation and biomass response is complex and that other factors may be responsible for increased biomass production in mixtures comprising N-fixing and non-N-fixing species. An overview of these potential factors has been provided by Kelty (1992).

A previous study reported a positive effect of *Acacia mearnsii* de Wild. on *Eucalyptus globulus* ssp. *pseudoglobulus* (Naudin ex Maiden) Kirkpatr. height growth in mixed treatments just 33 months after planting (Khanna 1997). This was explained by elevated levels of N in eucalypt leaves and fine roots and also by the stratification of fine roots between species in mixtures, where the acacias were shallow rooted and eucalypts were deep rooted. Revisiting the same plantations at age 6.5 years, Bauhus et al. (2000) investigated the hypothesis that increased productivity in mixtures was a result of belowground resource partitioning. However, fine-root biomass, root length density, vertical distribution of fine roots, and fine-root architecture were similar for both species in the top 30 cm of the soil profile, indicating that niche differentiation between fine-root systems was an unlikely contributor to increased productivity in mixtures. Bauhus et al. (2000) also found that the combined stem volume of eucalypts and acacias was greatest in the 50%E:50%A mixture (E = eucalyptus, A = acacia, numbers represent the percentage of each species in the given treatment). The authors proposed that the lower interspecific competition and increased productivity evident in mixed stands was also attributable to canopy stratification between species and increased light capture in mixed stands.

Kelty (1992) has described the mechanisms by which the mixture of shade-tolerant and shade-intolerant species may lead to increased stand productivity when compared with monocultures. In this study, we have followed up on this idea and examined canopy interactions between *A. mearnsii* and *E. globulus* in the same mixed-species plantation at age 9.5 years. In particular, two hypotheses were investigated in this study: (*i*) Canopy stratification in mixed stands increases stand-level light interception and consequently leads to greater levels of C assimilation than at similar densities in single-species plantations. This effect would result from combining the relatively more shade-tolerant *A. mearnsii* with the less shade-tolerant *E. globulus.* (*ii*) Increased availability of soil N and subsequent improvements of N nutrition in *Eucalyptus* in mixed stands results in photosynthetically more efficient eucalypt crowns.

Materials and methods

Site description and experimental design

The mixed-species plantation trial used in this study consisted of *A. mearnsii* and *E. globulus* ssp. *pseudoglobulus.* It was established in 1992 near Cann River (37°53′S, 149°15′E) in East Gippsland, Victoria, Australia. The eucalypts were planted at the beginning of July and the acacias at the beginning of October. Average annual rainfall at the closest meteorological station is 1009 mm and mean daily minimum and maximum temperatures are 7.8 °C and 20.5 °C, respectively. Bauhus et al. (2000), Khanna (1997), and Ryan et al. (1992) provide more detail about the site.

Plantations were established at two spacings: 2 m × 3.3 m (1515 stems·ha^{-1}) and 3 m × 3.3 m (1010 stems·ha^{-1}). Five proportions of the two species were planted following the replacement series proposed by de Wit (1960): 100% eucalypts (100%E), 75% eucalypts + 25% acacia (75%E:25%A), 50% eucalypts + 50% acacia (50%E:50%A), 25% eucalypts + 75% acacia (25%E:75%A), and 100% acacia (100%A). In mixed treatments, the two species were mixed within rows, so that every third or every second plant belonged to the admixed species. There were four replicates of each treatment arranged randomly within four blocks and each replicate plot was 23 m × 28 m in size. Detail about plantation establishment is documented in Khanna (1997).

Biomass determinations

To determine the standing biomass, we measured the entire trial at both spacings (1515 and 1010 stems·ha^{-1}). Diameter at breast height (DBH) was measured on all trees and the height (H) of four trees of each species in each replicate plot was measured using a Forestor Vertex Hypsometer® (Haglöf, Sweden). From these data, height models ($\ln(H) = a + b\ln(\mathrm{DBH})$) were developed to estimate the heights of all individual acacia and eucalypt stems. For *E. globulus*, aboveground biomass was calculated using the allometric function provided by Bennett et al. (1997).

$$[1] \qquad \ln(B) = -1.92 + 2.30\ln(D) \qquad (R^2 = 0.98,\ \mathrm{SE} = 0.095)$$

where B is biomass (kg), D is diameter at breast height (cm), and SE is standard errors of the estimates.

The biomass function for *A. mearnsii* was developed by Forrester et al. for the trees on site (2004).

$$[2] \qquad \ln(B) = -1.29 + 2.168\ln(D) \qquad (R^2 = 0.98,\ \mathrm{SE} = 0.145)$$

Variables are the same as defined in eq. 1.

Assessment of canopy stratification

To assess canopy stratification between acacias and eucalypts in mixed stands, we followed the suggestion by Parker and Brown (2000) to measure not only tree heights but also environmental variables, such as light attenuation, that are related to canopy functions. Green crown length was measured from the highest to the lowest extent of the living green crown. The crown percent was calculated from the ratio of green crown length to total tree height. Crown width was measured as the average of two diameters perpendicular to each other using a crown projection prism (Jackson and Petty 1973) and measuring tapes. The crown volume of eucalypts was calculated assuming that crowns have the shape of cones. Since the foliage in the lower part of acacia crowns was very sparse, crown volume would not have been a meaningful surrogate of leaf area in acacias and was therefore not calculated.

Light attenuation was quantified by comparing the amount of light available in the open, equivalent to above the canopy, with that occurring at different heights within the stands. Similar methods have been developed and used widely for quantifying the availability of diffuse light to understorey species and regenerating seedlings (e.g., Parent and Messier 1996; Montgomery and Chazdon 2001). The open sensor for photosynthetically active radiation (PAR_{open}) was at a height of 8 m in a local opening adjacent to the trial plots. To ensure compatibility of the two sensors (PAR_{canopy} and PAR_{open}), the PAR_{open} sensor was within 300 m of all locations where canopy light measurements were taken. In both locations, we measured light using a point quantum sensor (LI-COR, Lincoln, Nebr.). The PAR_{open} sensor was connected to a datalogger (Data Electronics Pty. Ltd., Rowville, Australia, model DT500), recording PAR every second and averaged every 10 s. The open readings were later time matched with canopy light readings to an accuracy of ±10 s. Measurements were taken in uniform overcast conditions over the period of 1 week (Nicotra et al. 1999). If the maximum difference between readings recorded by the PAR_{open} sensor during the measurement of vertical light profiles was greater than 20 µmol photons·m^{-2}·s^{-1}, the entire profile was considered too unstable and was removed from analysis. Canopy light readings were measured by attaching a quantum sensor to a 15-m telescopic height pole and handheld multirange PAR meter (LI-185B). PAR readings were taken at 1-m intervals from 15 to 2 m above ground, which was below any tree foliage.

The following formula was used to calculate light transmittance within the canopy.

$$[3] \qquad \%T_h = (PAR_{canopy}/PAR_{open}) \times 100$$

where $\%T$ is the percent transmission of diffuse light through the canopy at height h (m), PAR_{canopy} is light measured in the canopy, and PAR_{open} is light measured in the open.

Three vertical light profiles were measured in each treatment replicate for the 3 m × 3.3 m spacing. These measurements were taken at locations that represented the particular species combinations through the distance to the nearest four trees. For example, in the 50%E:50%A mixture, the measurement point would be located in the centre of a rectangle, where the corners would consist of two eucalypts and two acacias. A light attenuation curve was fitted for the light values between the crown base and the top height of the telescopic pole, or in the case of the 100%A treatment, the top height of the canopy, which was 11 m.

Assessment of leaf characteristics

Physiological and morphological measurements were conducted to determine possible effects of increased N supply on eucalypts in pure (100%E) and mixed stands (50%E:50%A). Focussing on these two treatments allowed us to assess whether N-fixing acacias influenced the nutrition and consequently photosynthesis of eucalypts.

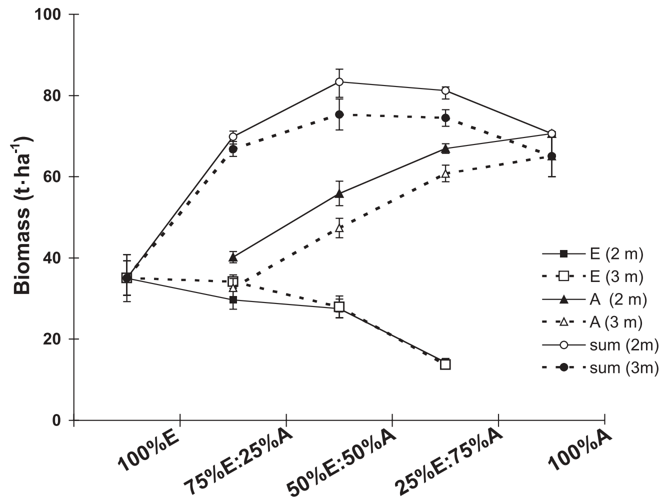
Specific leaf area (SLA), leaf area per unit of leaf ovendry mass, was determined to investigate whether there were differences in leaf structure between eucalypts in mixed and monospecific stands. Up to six branchlets (minimum of three) were collected from at least three randomly chosen trees in each of the 100%E and 50%E:50%A treatments. Branchlets were harvested from the midcanopy level. This was the highest canopy level that could be accurately sampled from the ground using lines to pull and break the branches. To ensure that leaves sampled for nutrients, gas exchange, and SLA were of similar age, we used only the youngest, healthy, and fully expanded leaves from each branchlet. A leaf area meter was used to determine the surface area of leaves. Leaves were dried at 45 °C for 28 days before weighing. To determine N and P concentrations, we ground and dried leaf material and digested this in digestion acid (potassium sulphate dissolved in concentrated sulphuric acid) and hydrogen peroxide (modified from Heffernan 1985). Analysis was performed with a Technicon AutoAnalyser II (Technicon Industrial Systems, Tarrytown, N.Y.) using an ascorbic acid – ammonium molybdate method for P and nitro-prusside method for N.

Gas exchange of midcanopy eucalypt leaves in the 100%E and the 50%E:50%A mixtures were measured using a LI-6400 (LI-COR) portable gas exchange analysis system. A light response curve was developed to determine the light saturation point for *E. globulus*. It was estimated that light saturation occurred at 2500 µmol photons·m^{-2}·s^{-1} of PAR or at lower light intensities. There was no evidence of photoinhibition at this light level. A minimum of two photosynthesis measurements were taken on separate leaves from each branchlet harvested, providing a minimum of six measurements per replicate. Branchlet collection and measurements took place between 0800 and 1100. The base of branches was immediately placed in water, where the ends were recut to ensure that embolisms did not occur within the vascular tissues (Ellsworth and Reich 1992). Branches were allowed 20 min to adjust to the new water balance before photosynthesis measurements. Measurements were taken when leaves had reached saturated photosynthetic and stable transpiration rates (CV of <1% for both variables). In most cases, this was between 10 and 15 min. Measurements were conducted at leaf temperatures between 22.1 and 34.4 °C. Relative humidity in the chamber ranged from 55.2% to 64.2%, and CO_2 concentrations were between 338.3 and 385.7 ppm.

Statistical analyses

Mixed models were used for the statistical analysis of treatment differences for foliar nutrient content (N and P), SLA, A_{max}, crown dimensions, and light beneath the canopy (at 2 m above ground). The mixed models incorporated treatment type as a fixed component and the block in which the treatment replicate occurred as a random component. Where only two treatments were compared, the standard error of differences was calculated. To compare several treatments, we calculated the least significant difference. A mixed model was also used to model the relationship between SLA and the foliar N and P. Chi squared probability P values were used to indicate the significance of regressions. Statistical significance was assumed at $P < 0.05$. Models for light attenuation were fitted for light values measured between the base and the top of the tree canopy. This removed possible effects that naturally regenerating vegetation may have had below the *A. mearnsii* and *E. globulus* canopy. To examine the effects of treatments on the relationship between crown volume and biomass of eucalypts, we performed an analysis of covariance.

Fig. 1. Total aboveground biomass at age 9.5 years in mixed and pure stands of *Eucalyptus globulus* (E) and *Acacia mearnsii* (A) with 3- and 2-m spacing within rows. Thin bars represent SE of the mean.



Results

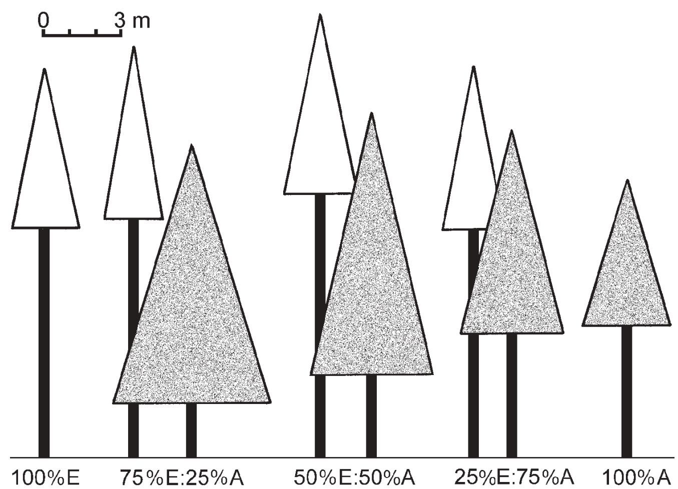
Tree biomass

The replacement of eucalypts by acacias did not result in a proportional decline in eucalypt biomass (Fig. 1). The reverse applies for replacement of acacias by eucalypts. Consequently, all mixtures showed synergistic effects at age 9.5 years, and stand-level tree biomass at age 9.5 was highest in the 50%E:50%A mixture, with 75.3 $t{\cdot}ha^{-1}$ for the wider spacing and 83.4 $t{\cdot}ha^{-1}$ for the narrower spacing. These values were significantly higher than those in the monocultures of each species. At the higher stand density, biomass in the 25%E:75%A mixture was also significantly higher than that in the monocultures. Biomass was lowest in the 100%E treatment, 35 $t{\cdot}ha^{-1}$ for both spacings. Whereas the biomass of acacias was always higher at the narrow spacing when compared with the wide spacing, this did not apply for the eucalypts that had almost identical biomass for both spacings in all treatments except the 75%E:25%A mixture. As a consequence, the combined biomass production of both species was higher in all mixtures at 2-m spacing.

Canopy stratification

Eucalypts were taller than acacias in all treatments and trees of both species were tallest in the 50%E:50%A mixture (Table 1, Fig. 2). However, significant height differences occurred only between acacias in the 100%A and 50%E:50%A treatment. The crown percent (percentage of tree height occupied by the green crown) was similar for eucalypts across all treatments. However, it increased in acacias with decreasing proportion of acacias in the mixture from 100%A to 50%E:50%A. There was no difference in acacias crown percent between the latter treatment and the 25%E:75%A mixture. Interestingly, the variability in crown percent also increased with increasing proportion of acacia in the mixture. Eucalypt crown diameters were greatest in the 50%E:50%A mixture, but the differences between treatments were insignificant. The pattern of acacia crown width across treatments mirrored that observed for crown length. However, in this case, greatest crown diameter was observed in the 25%E:75%A mixture. These differences in height and

Fig. 2. Scale diagram of crown distribution in mixtures and monospecific treatments. Crown dimensions are to scale (stems are for illustration only and not to scale). *Eucalyptus globulus* (E) crowns are in white and *Acacia mearnsii* (A) crowns are in grey.



crown dimensions resulted in canopy stratification between eucalypts and acacias in all mixtures (Fig. 2). The vertical overlap between acacia and eucalypt crown length was between 3.0 and 3.9 m across the different mixtures. Tree diameters and biomass in eucalypts were largely a function of crown volume (Table 1, Fig. 3). An analysis of covariance demonstrated that the species combination had no significant influence on either the intercept or slope of that relationship (Fig. 3), indicating that there was no difference in crown efficiencies, or tree biomass per unit of crown volume, between eucalypts from the different mixtures.

Canopy light attenuation

Canopy light transmission measured 2 m above the ground decreased with the proportion of acacias in mixtures

Table 1. Average tree heights, crown dimensions, and stem diameters of acacias and eucalypts in pure and mixed stands at 9.5 years.

	Species	100%E	75%E:25%A	50%E:50%A	25%E:75%A	100%A	LSD
Tree height (m)	A	—	12.4 (0.4)	13.6 (0.4)	12.8 (0.3)	10.8 (0.6)	1.60
	E	15.3 (0.8)	16.2 (0.6)	17.5 (0.6)	15.4 (0.7)	—	2.60
Crown percent (%)	A	—	83.4 (1.4)	76.6 (2.1)	62.1 (3.8)	51.5 (5.1)	8.68
	E	44.3 (1.8)	44.1 (1.4)	40.7 (1.6)	41.4 (1.4)	—	4.36
Crown diameter (m)	A	—	6.2 (0.2)	4.8 (0.1)	3.9 (0.2)	3.4 (0.3)	0.81
	E	2.5 (0.1)	2.3 (0.2)	2.9 (0.2)	2.3 (0.2)	—	0.60
DBH (cm)	A	—	17.5 (1.0)	16.9 (0.9)	16.0 (1.1)	12.2 (1.2)	3.71
	E	11.4 (0.9)	11.4 (0.9)	13.5 (0.9)	12.2 (0.9)	—	3.30

Note: n = 16; SE of mean is provided in brackets. E, *Eucalyptus globulus*; A, *Acacia mearnsii*. Crown percent = green crown length / tree height × 100; DBH, diameter at breast height; LSD, least significant difference.

Fig. 3. Relationship between crown volume and biomass of eucalypts in the different species mixtures. E, *Eucalyptus globulus*.

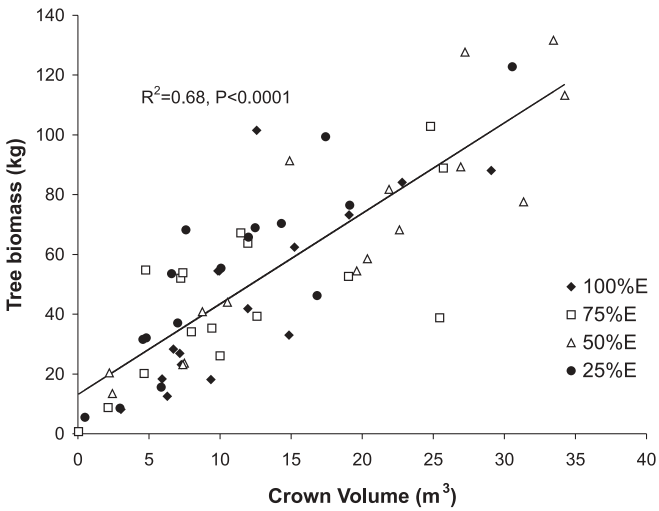
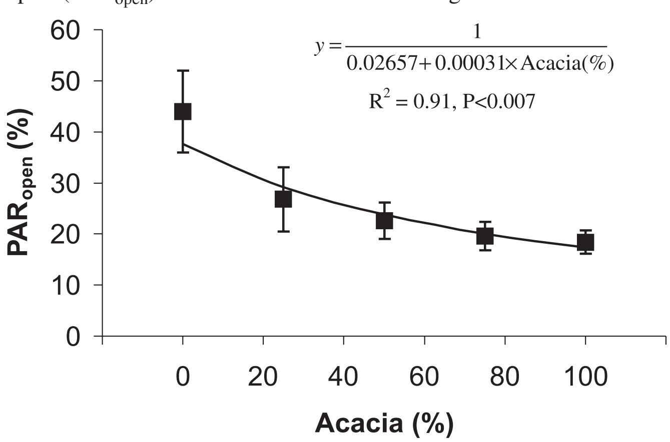
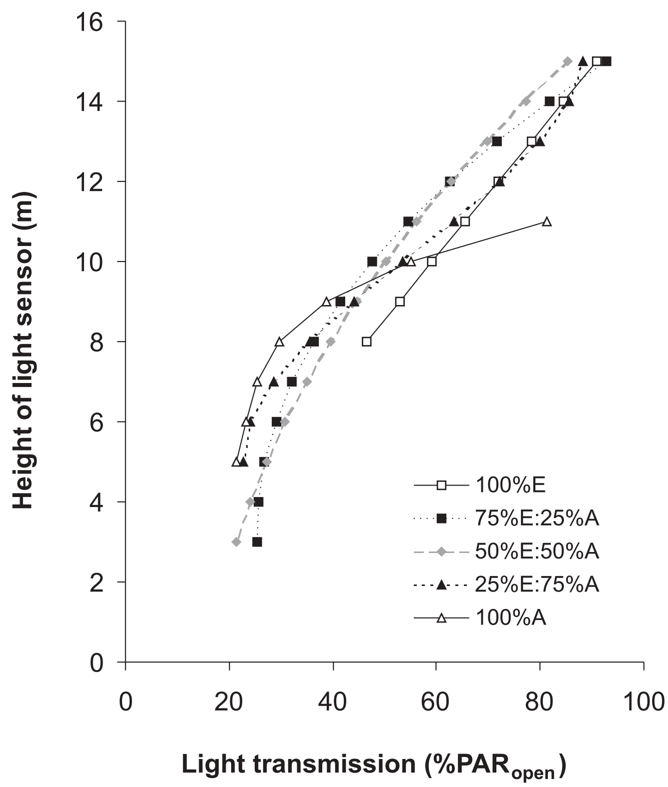


Fig. 4. Relationship between the percent acacia in mixture and the percent of diffuse photosynthetically active radiation in the open (PAR_{open}) measured at 2 m above the ground.



from a maximum of 44% diffuse PAR in the open (PAR_{open}) in the 100%E treatment to a minimum of 18.5% PAR_{open} in the 100%A treatment (Fig. 4). When the percent PAR_{open} at 2 m above the ground was compared between the different treatments, only the pure eucalypt stand was different from all treatments containing acacias, but there was no significant difference between stands containing acacias.

Fig. 5. Vertical attenuation of light as a percentage of diffuse photosynthetically active radiation in the open (PAR_{open}) measured at 1-m intervals vertically in the canopy of three treatments at the 3 m × 3.3 m spacing. E, *Eucalyptus globulus*; A, *Acacia mearnsii*.



For all treatments except 100%A, the mean height of eucalypts was greater than the maximum height at which data were collected for light attenuation models. Models were fitted to a maximum height of 15 m (Fig. 5). Mean tree heights therefore exceeded model height by 0.26, 1.12, 2.4, and 0.33 m in the 100%E, 75%E:25%A, 50%E:50%A, and 25%E:75%A, respectively. Vertical light attenuation within the canopy of eucalypt and acacia monocultures followed distinctly different patterns. Light attenuation in the 100%E treatment was linearly related to canopy depth. Models for other treatments were quadratic (75%E:25%A and 50%E:50%A) and cubic (25%E:75%A and

Table 2. Light transmission functions for height ranges determined by canopy measurements.

Treatment	Height range (m)	Constant	Term 1	Term 2	Term 3	P
100%E	8–15	68.7	6.35 (h=11.5)	—	—	<0.001
75%E:25%A	3–15	48.3	–3.18 (h=9)	0.448 (h^2=95)	—	<0.001
50%E:50%A	3–15	48.0	1.01 (h=9)	0.240 (h^2=95)	—	<0.001
25%E:75%A	5–15	54.4	–29.7 (h=10)	3.86 (h^2=110)	–0.26 (h^3=1300)	<0.001
100%A	5–11	39.3	44.8 (h=8)	–7.215 (h^2=68)	0.401 (h^3=608)	0.006

Note: Response is $\%PAR_{open(h)}$, where h is height (m) within the canopy. E, *Eucalyptus globulus*; A, *Acacia mearnsii*. P values are for the last (highest order) term in the model.

100%A) (Table 2). The extent to which light attenuation functions of the mixtures were significantly different from each was not examined here.

Leaf-level effects

Mean light-saturated net photosynthesis rates (A_{max}) of *E. globulus* expressed on a leaf area basis was significantly higher in monospecific stands (14.6 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) than in the 50%E:50%A mixture (11.2 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) ($P$ = 0.001). This difference was also apparent when photosynthesis rates were expressed on a foliage mass basis (0.053 μmol $CO_2 \cdot g^{-1} \cdot s^{-1}$ for the 100%E treatment and 0.040 μmol $CO_2 \cdot g^{-1} \cdot s^{-1}$ for the 50%E:50%A treatment), since the SLA was not significantly different between these treatments. The SLA in the 100%E and the 50%E:50%A treatment was 36.53 $cm^2 \cdot g^{-1}$ and 35.77 $cm^2 \cdot g^{-1}$, respectively. SLA was positively related to foliage P content ($P < 0.001$). The relationship between leaf N concentration and SLA was not significant (P = 0.07).

The mean leaf N concentration of *E. globulus* was significantly higher in the 50%E:50%A treatment (1.24%) than in the monospecific treatment (1.09%). In contrast, mean leaf P of *E. globulus* was significantly lower in the 50%E:50%A treatment (0.044%) than in the monospecific treatment (0.051%).

Discussion

The results of this study suggest that the increased productivity in mixed *E. globulus* and *A. mearnsii* plantations cannot be explained only by improved N nutrition of the eucalypts. Additionally, increased use of light resources must be considered important.

Biomass production

This study confirmed results from earlier growth stages in the same plantations (Bauhus et al. 2000, Khanna 1997), which showed that the most productive treatment was the 50%E:50%A mixture for both stand densities. The relative differences between mixtures and monocultures were of similar magnitude or greater than those reported by others for combinations of N-fixing and non-N-fixing tree species (e.g., Binkley et al. 1992; Wichiennopparat et al. 1998). The pattern of tree biomass across species combinations suggests that competition decreased for individuals of both species with increasing proportions of the other species. This effect was more pronounced in acacias, which is reflected in the greater change in crown size in this species. The greater plasticity of acacias is also indicated in the biomass increase at higher stand density, while there is no difference for the eucalypts between the two stand densities.

Light attenuation and canopy stratification

Despite maximum yield in the 50%E:50%A mixture, light attenuation was not greatest here but in the acacia monocultures. Assuming that light attenuation is closely related to canopy leaf area in cases where leaves are randomly distributed (Gower and Norman 1991), this study indicated that the increased productivity of mixtures when compared with monocultures cannot be explained by a maximum in leaf area for the 50%E:50%A mixtures. While the mixtures intercept more light than the eucalypt monoculture, the difference in light interception between the mixtures and the acacia monoculture, which produced less biomass than the 50%E:50%A mixture, was negligible. Leaf area in the 50%E:50%A mixtures was not greater than that in stands with a greater proportion of acacia, but the mixed canopy might still have been more effective in transforming the light intercepted into C. The combined length of the green crowns of both species in the 50%E:50%A mixture was greater than that in other stands. Although this has not translated into greater interception of diffuse light, it may be important under conditions of direct light, which was not measured in this study, to reduce the level of self-shading within the canopy. While the mature leaves of *E. globulus* are mostly oriented vertically (James and Bell 2000), the bipinnate leaves of *A. mearnsii* are oriented mostly horizontally, when not folded. James and Bell (2000) showed that light interception in mature *E. globulus* leaves was greater in absolute and relative terms in the morning at low sun angles than during midday at high sun angles. The reverse will be true for acacias with horizontal foliage. Some evidence for this comes from light extinction coefficients in mixed stands of *Eucalyptus nitens* and *Acacia dealbata*, which are closely related and very similar in appearance to the species used in this study. The light extinction coefficient measures the fraction of incident photons absorbed by a unit of leaf area (Beadle 1997). In these mixed stands, the light extinction coefficient of 0.65 was substantially greater than that normally used for eucalypt canopies (0.5) (Hunt 1998). Thus, over the course of a day, interception of direct and diffuse light might be optimized in the mixtures. This could not be described by our measurements. The species may also have different photosynthetic abilities in term of fixing C in low light and using short sunflecks. Total C fixation could be increased if acacias have higher photosynthesis rates than eucalypts at low light levels, which would allow them to utilize the light filtered through the eucalypt canopy. This is indicated by the maintenance of acacia foliage at relative light intensities that are substantially lower than those for eucalypts.

If the vertical layering of foliage in plant canopies is homogenous, light extinction can be modelled using a negative exponential equation in accordance with the Lambert–Beer Extinction Law (Monsi and Saeki 1953). Attenuation of light in the 100%E treatment, however, was best described using a linear function, which indicates that foliage density decreases with decreasing tree height. As the proportion of acacias in treatments increased, the shape of the light interception curves became more complex, such as the cubic function describing light attenuation in the 100%A treatment. This is indicative of an even distribution of foliage found for shade-tolerant species. For example, light attenuation curves fitted for a stratified tropical rainforest canopy (Yoda 1974) were most similar in shape to the cubic curve fitted to the 100%A treatment. The different light attenuation curves between pure eucalypt and acacia stands are thus good indicators of the difference in shade tolerance between the species, which is further evidenced by the differences in relative light levels at the base of the canopy. The shape of the light attenuation curves for treatments intermediate between the two monospecific treatments appear to be a direct result of combining the two monospecific treatments in varying proportions. However, without further analysis of foliage distribution, a combination of two static canopy types cannot be separated from a possible change in leaf distribution within species.

Crown morphology of acacias was substantially more plastic than that of eucalypts, as evidenced by crown percent data. Trends for increasing crown size of acacias in mixed-species treatments may be attributed to decreases in intraspecific competition as the proportion of acacias decreased. This suggests that aboveground niche differentiation occurred between the two species. Similarly, Hunt (1998) found that voluntary recruits of *A. dealbata* occupied codominant positions in 4-year-old plantations of *E. nitens*, then became subdominant in 8-year-old stands.

Crown efficiency of eucalypts

The average light-saturated net photosynthesis rates of 11.2 and 14.6 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ were similar to those obtained in other field measurements for *E. globulus*. Henskens et al. (2001) reported A_{max} rates between 8.4 and 11.6 (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) for the midcanopy of block-planted trees, and Battaglia et al. (1996) reported rates at optimum temperatures for different times of the year between 12.6 and 14.4 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$.

Despite the increase in foliar N concentrations, the light-saturated photosynthesis rates of *E. globulus* in mixture were lower than those in monoculture. This may be the result of reduced P concentrations in the leaves of *E. globulus* in mixtures, which may have been limited by enzyme concentrations. Foliar P concentrations of 0.04%–0.05%, as have been documented in this study, are clearly below the range for adequate nutrition of *E. globulus* (Dell et al. 2001). Our data indicated an increasing trend of A_{max} with increasing foliar P concentrations, but this was not significant ($P < 0.11$).

Küppers (1996) found that *Eucalyptus delegatensis*, when grown adjacent to *A. dealbata*, had higher foliar N concentrations, whereas protein and Rubisco concentrations were not significantly increased. When *Eucalyptus pauciflora* grew adjacent to *Acacia melanoxylon*, protein and Rubisco concentrations decreased with no significant effect on foliar N (Küppers 1996). This points to the potential competition for soil P by leguminous trees (Binkley et al. 2000; Kaye et al. 2000).

Alternatively, the difference might have resulted from sampling in different parts of the canopy within the 100%E and 50%E:50%A treatments. Although branches were collected from the midcanopy, it is conceivable that these were from a somewhat lower crown position in the mixtures, where trees were taller, than in the monocultures. Henskens et al. (2001) have demonstrated how A_{max} in *E. globulus* declines with decreasing canopy position as a result of self-shading.

Photosynthesis measurements were carried out once only, and therefore the differences between *E. globulus* in the 100%E and 50%E:50%A treatments reported here may not persist over the entire year. However, the results do suggest that admixture of *A. mearnsii* does not increase photosynthetic efficiency in *E. globulus*. This is consistent with the absence of differences in eucalypt crown efficiencies across mixtures. However, for a full assessment of the effect of mixtures on photosynthesis and leaf morphology in eucalypts, a more detailed study would be required. This should include measurement of photosynthetic activity and leaf attributes at varying heights and light levels within the canopy, as well as determination of the leaf area index of the different mixtures. In addition, photosynthesis measurements should include acacias, which might saturate at lower light levels, but may be better at utilizing sunflecks and may have a better induction than eucalyptus at low light. This would require photosynthesis measurements on intact branches within the crown, for which we were not equipped in this study.

The fact that eucalypts in mixture showed no increase in photosynthetic capacity does not indicate that facilitation through N fixation did not take place. Eucalypts in mixture had larger crowns and thus more N per tree than those trees in monoculture and consequently produced greater stemwood biomass per tree.

Other reasons for increased productivity in mixtures

In addition to the aboveground niche separation suggested by this study, other factors might have contributed to the increased productivity in mixtures. Bauhus et al. (2000) have shown that distribution and architecture of fine roots is very similar across the different species combinations and that belowground niche separation is therefore unlikely. However, improved N nutrition for eucalypts in mixtures (see also Bauhus et al. 2000) may lead to a reduction of fine-root turnover (Burton et al. 2000). This could lead to a shift in C allocation within trees to a proportionally greater growth in aboveground components of trees in mixed stands. To confirm this hypotheses, direct or indirect assessments of fine-root turnover would be required.

Implications for management of mixed eucalypt–acacia stands

This study has shown that shade-intolerant eucalypts can be combined with more shade-tolerant acacias when the growth rates of the two species are compatible, i.e., the shade-intolerant eucalypts can match the initially rapid height growth of acacias to overtop them eventually (see also Forrester et al. 2004). In this case, the shade-tolerant acacias, which were planted 3 months later than the eucalypts, have not reduced the crowns in eucalypts. For a species combination or under different site conditions, where acacias would be able to overtop the eucalypts, the mixture would be destined to fail or require frequent interventions. Problematic species combinations of this sort have been reported for mixed *Acacia auriculiformis* and *Eucalyptus camaldulensis* plantations in Thailand (Snowdon et al. 2002). To avoid this problem, acacias might be planted under established eucalypt stands. However, we are not aware of a documented example for this.

This study also shows that even if a plantation grower is interested in eucalypts only, these could be grown without production losses when mixed with 25% of acacias and considering the additional benefits of the secondary species. However, establishment costs might be somewhat higher in this case.

Acknowledgements

We greatly appreciate the use of the experiment, which was established by the Commonwealth Scientific and Industrial Research Organization (CSIRO Forestry and Forest Products, Canberra, Australia) with funding from the Australian Centre for International Agricultural Research. Aaron van Winden received Honours scholarships from Forestry Tasmania and the Co-operative Research Centre for Greenhouse Accounting. Dr Ann Cowling, Australian National University, assisted with statistical analysis. We are grateful for field assistance by John Smith, David Forrester, Amber Pares, Tom Halliday, and Lucy Nash. John Marsh carried out chemical analysis of foliage. We are thankful for critical comments by Robin Chazdon, Christian Messier, and Partap Khanna, as well as three anonymous referees. This helped to improve the manuscript substantially.

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