Oecologia (2011) 166:265–272
DOI 10.1007/s00442-011-1937-9

ECOSYSTEM ECOLOGY - ORIGINAL PAPER

The balance between facilitation and competition in mixtures of *Eucalyptus* and *Acacia* changes as stands develop

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Received: 27 May 2010 / Accepted: 3 February 2011 / Published online: 23 February 2011

Abstract The balance between facilitation and competition is likely to change with age due to the dynamic nature of nutrient, water and carbon cycles, and light availability during stand development. These processes have received attention in harsh, arid, semiarid and alpine ecosystems but are rarely examined in more productive communities, in mixed-species forest ecosystems or in long-term experiments spanning more than a decade. The aim of this study was to examine how inter- and intraspecific interactions between *Eucalyptus globulus* Labill. mixed with *Acacia mearnsii* de Wildeman trees changed with age and productivity in a field experiment in temperate south-eastern Australia. Spatially explicit neighbourhood indices were calculated to quantify tree interactions and used to develop growth models to examine how the tree interactions changed with time and stand productivity. Interspecific influences were usually less negative than intraspecific influences, and their difference increased with time for *E. globulus* and decreased with time for *A. mearnsii*. As a result, the growth advantages of being in a mixture increased with time for *E. globulus* and decreased with time for *A. mearnsii*. The growth advantage of being in a mixture also decreased for *E. globulus* with increasing stand productivity, showing that spatial as well as temporal dynamics in resource availability influenced the magnitude and direction of plant interactions.

Keywords Growth dynamics · Individual tree models · Neighbourhood indices

Introduction

The development of plant communities is strongly influenced by the balance between competitive and facilitative interactions. The spatial and temporal variability of resource availability and other environmental conditions results in dynamic relationships within and between species (see Callaway 2007). According to the stress-gradient hypothesis, facilitative interactions are more likely to dominate competitive interactions towards more harsh ends of environmental gradients where one species or cohort can act as a nurse for another (Bertness and Callaway 1994; Callaway and Walker 1997; Brooker and Callaghan 1998). Many experiments, often in semiarid, arid and alpine environments, have backed up this hypothesis (e.g. Brooker and Callaghan 1998). In addition to these spatial effects, shifts between facilitation and competition have also been observed through time. These temporal dynamics result from changes in the relative sizes of co-occurring

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Communicated by Christian Wirth.

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cohorts or species, their influence on growing conditions and climate fluctuations (Rousset and Leopart 2000; Tielborger and Kadmon 2000; Gómez-Aparicio et al. 2005; Lloret et al. 2005; Miriti 2006; Schiffers and Teilbörger 2006; Sthultz et al. 2006; Reisman-Berman 2007; Armas and Pugnaire 2009). As with experiments dealing with spatial variability in facilitation and competition relationships, these temporal studies are also often conducted in semiarid, arid and alpine environments. However, facilitation can also be important in more productive communities and between tree species (Boyden et al. 2005).

Stand level studies in more productive forest ecosystems have provided insight into relationships between resource availability, stand level growth and growth trajectories of individual species (Binkley 2003; Pretzsch and Schütze 2009). However, studies of facilitative and competitive interactions in tree mixtures, let alone the temporal dynamics of these interactions, are rare (Callaway 1998; Sthultz et al. 2006). The long life span of trees increases their likelihood of experiencing variable climatic conditions, as well as significant changes in resource availability as stands develop and influence light availability as well as nutrient, water and carbon cycles. The temporal dynamics of competition and facilitation experienced by individuals, especially in tree communities, is under-explored but necessary for understanding the processes leading to community and stand level growth, mortality and structure.

A replacement series of *Eucalyptus globulus* mixed with the N_2-fixing species *Acacia mearnsii* provided a model system to examine the temporal changes in competition and facilitation. Earlier work in this trial showed that 1:1 mixtures of *E. globulus* and *A. mearnsii* produced about twice as much stand level aboveground biomass as *Eucalyptus* monocultures (Forrester et al. 2010). Corresponding measurements showed that this response resulted from improved availability, uptake, and/or use-efficiency of light, water and nutrients (Forrester et al. 2005, 2007, 2010).

Neighbourhood competition models were used to examine the interspecific and intraspecific influences on tree basal area growth as the stands developed. Inter- and intraspecific influences are net effects of many interactions that influence resource acquisition or other environmental conditions and may include both competitive and facilitative processes. Facilitative influences are often examined by comparing parameters such as the survival or growth of individuals in the presence of interspecific influences to that of individuals experiencing no inter- and intraspecific influences. Such comparisons are difficult in forests where individuals are rarely in situations without inter- and intraspecific influences. Therefore, in this study facilitation was considered to have occurred when interspecific influences were less negative than intraspecific influences on growth.

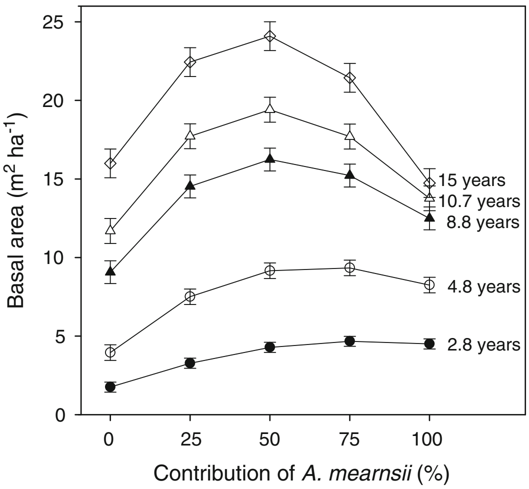

Fig. 1 Stand basal area development with increasing proportions of *Acacia mearnsii* trees per stand ($n = 4$). *Error bars* Standard errors of difference

Due to changes in the relative growth dynamics of each species and resulting changes in nutrient cycling and light availability, we expected that the balance between facilitation and competition would also vary through time. We hypothesised that (1) based on stand level trends (Fig. 1), interspecific competition experienced by each species would be more negative than intraspecific competition where the productivity of mixtures was greater than that of monocultures; (2) the difference between inter- and intraspecific influences would increase with time because competition would increase, and facilitation would decrease with time as (a) trees became larger and canopies became more crowded, and (b) rates of nitrogen (N_2)-fixation declined but *A. mearnsii* continued to compete for light, water and nutrients.

Materials and methods

Site description

The experiment was located 5 km southeast of Cann River, East Gippsland, Australia (37°35′S, 149°10′E). The long-term annual precipitation is 1,009 mm, distributed evenly throughout the year. The mean daily maximum temperature is 26°C in January and the mean daily minimum is 2°C in July. The trial was established in 1992, 1 year after clearing the dry sclerophyll forest, which was dominated by *Eucalyptus sieberi*. The soils are Mottled, Dystrophic, Brown Kurosol (Dy5.21) or Mottled, Mesotrophic, Brown Dermosol (Gn4.31) (Stace et al. 1968; Isbell 1998), characterised by a sandy loam A, AB or A2 horizon, a sandy clay loam B1 and B21 horizon above a light to medium clay B22 horizon. *Eucalyptus globulus* and *Acacia* *mearnsii* were planted in early July and early October 1992, respectively, in a randomised block design with four blocks. The proportion of *E. globulus* was 0, 25, 50, 75 or 100%. This replacement series was planted at two spacings, 2 × 3.3 m (1,515 trees ha^{-1}) and 3 × 3.3 m (1,010 trees ha^{-1}), in 23 × 28-m plots. In the mixed-species plots, trees were mixed within rows, resulting in a checkerboard arrangement. Plots were fertilised in November 1992 with 25 kg phosphate (P) ha^{-1} as superphosphate.

Growth models and statistical analyses

Tree diameters (at 1.3 m above the ground) and heights were measured at ages 2.8, 4.8, 8.8, 10.7 and 15 years and their positions mapped. Trees that died during these periods were also recorded. Growth, quantified as basal area periodic annual increment (PAI, cm^2 year^{-1}) was modelled as a function of initial tree size (basal area; cm^2), species-specific neighbourhood indices (NI), age and productivity. Growth is strongly correlated with tree size and its inclusion as an explanatory variable, rather than for modelling relative growth rate, can minimise spatial dependency in the models (Boyden et al. 2005). Age was included, in addition to tree size, because age-related changes in growth rates (Ryan et al. 1997) resulted in similarly sized trees having significantly different growth rates (Fig. 2). Growth, age, initial size and neighbourhood indices were all log-transformed to satisfy assumptions of normally distributed residuals and to remove heteroscedasticity for growth models. Growth and NI were ln (+1) transformed to satisfy the assumptions underlying the analysis and because it was necessary to add one prior to transformation to deal with the presence of values of zero.

The temporal dynamics of inter- and intraspecific interactions were examined by including age at the start of each growth period. The growth of *Eucalyptus* monoculture stands varied between replicates. Stand volume was 73, 108, 106 and 123 m^3 ha^{-1} at age 15 years in replicates 1, 2, 3 and 4, respectively. Therefore, to account for the effects of productivity on the inter- and intraspecific interactions, replicate was included in the model, such that productivity was low, medium and high for replicates 1, both 2 and 3 combined, and 4, respectively. The terms NI × age and NI × productivity were used to determine whether the influence of neighbours on focal tree basal area PAI was modified by age or productivity. Models containing all combinations of these variables and interactions were tested, and those with the lowest Mallow's CP (and highest R^2) were selected as the final models. To ensure that spatial dependency, such as microsite effects, had been removed (Fox et al. 2001), the effect of neighbouring trees on the diameter of each tree was examined by fitting a two-dimensional spatial model to the individual tree measurements using residual maximum likelihood analyses (REML). The first model assumed the variance structure to be uniform in both directions, whereas the second model assumed a power law to describe this variance structure. The power law was based on the distance between the trees, using the city block distance metric. The fixed effects for both models were the species proportion and spacing treatments. There was no evidence of any spatial dependency from this analysis or variogram plots. Replicate was included as a random effect using REML for all growth models but was insignificant in each case. Mortality rates were too low to model survival. All analyses were performed in Genstat (VSN Int, Hemel Hempstead, UK).

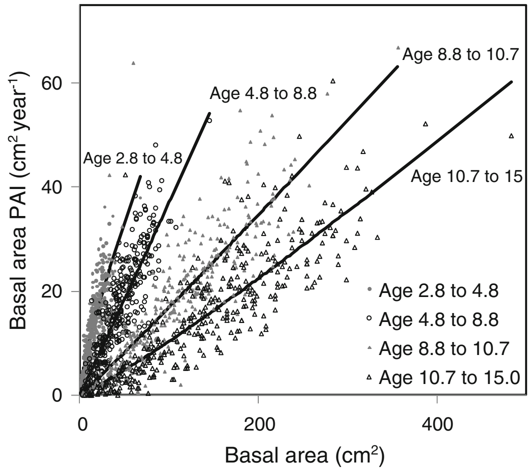

Fig. 2 Basal area periodic annual increment (*PAI*) against tree basal area for *Eucalyptus globulus* ($P < 0.001$, Adj $R^2 = 0.79$)

Neighbourhood indices

The competition experienced by a focal tree was quantified as a function of the size, proximity and species of the neighbouring trees. A simple distance-dependent summation equation was used that has been applied effectively in other *Eucalyptus* plantations (Boyden et al. 2005, 2008):

$$\mathrm{NI}_i = \sum_{j=1}^{n} \frac{\text{basal area}_j^{\alpha}}{\text{distance}_{ij}^{\beta}} \left(\frac{\text{basal area}_j}{\text{basal area}_i} \right)^{\gamma}$$

where NI_i is the strength of the interaction from all neighbouring trees experienced by the focal tree (i), from n neighbours (j), tree basal area is in square centimetres (cm^2) and distance is the distance (m) between the focal tree (i) and the jth neighbour. This equation assumes that the influence of a neighbour increases in proportion to its size and inversely with its distance from the focal tree. The importance of neighbour size and distance are controlled using the constants α and β, respectively. A size ratio divides the basal area of the neighbour with that of the focal tree, which alters the impact of the neighbour depending on its relative size. This indicates the asymmetry of competition, and its importance is controlled by the parameter γ. Trees with diameters (at 1.3 m height) less than 1.5 cm (<2% of trees) were excluded from the analysis because they appeared to be outliers that missed the fertiliser or were genetically inferior.

The optimum neighbourhood radius as well as the parameters α, β and γ was determined using least squares. The R^2 of the relationship between basal area PAI and NI_i (both log transformed) was regressed against each constant using the method described by Vanclay (2006) in Simile v4.7 (Simulistics; www.simulistics.com). The NI_i were recalculated along a continuous range of values of the given constant until the maximum R^2 was found. The neighbourhood radii were 6 m at most; therefore, trees within 6 m of the replicate boundaries were excluded from being focal trees to avoid edge effects.

Results

Tree growth and neighbourhood indices

Basal area PAI was closely related to tree size and age (Fig. 2). Tree basal area alone explained 38 and 1% of the variability in basal area PAI for *E. globulus* and *A. mearnsii*, respectively. Adding age increased this to 79 and 70%, respectively.

Between 52 and 60% of the variability in basal area PAI was explained by the neighbourhood indices (Table 1). The parameterisation of these indices varied with species. For *E. globulus*, α and β were zero while γ was 1. This indicates that competition was asymmetric and that the size of a neighbour relative to the focal tree was more important than the actual size of the neighbour or its distance from the focal tree. The size (α) and distance (β) parameters were important for *A. mearnsii*, indicating that the influence of their neighbours increases with neighbour size and decreases as the distance to the neighbour increases. Optimal neighbourhood sizes were 5 or 6 m for *E. globulus* and *A. mearnsii*, respectively.

Table 1 Parameter estimates of the neighbourhood index (NI) equation for each species

Species	Distance (m)	α	β	γ	r^2
E. globulus	5	0	0	1	0.52
A. mearnsii	6	1	1.5	0.8	0.60

Growth models

Tree basal area was excluded from *E. globulus* models because it was correlated with both the interspecific ($R^2 = 0.69$) and intraspecific NIs ($R^2 = 0.31$; all log transformed). This resulted from α and β constants of 0 in the NI equation and, hence, relatively simple calculations of NIs for *E. globulus* where focal tree size played a prominent role in calculations while other information, such as the distance to the neighbour, was not important ($\beta = 0$, Table 1).

The final growth models explained between 71 and 76% of the variability in individual tree growth for *A. mearnsii* and *E. globulus*, respectively (Table 2). Interspecific and intraspecific NIs were important in both models (Table 2). Intraspecific NIs usually had more negative influences on growth than interspecific influences (Fig. 3).

Table 2 Best models that described basal area PAI of each species as functions of tree basal area, neighbourhood influences from *E. globulus* ($\mathrm{NI_E}$) or *A. mearnsii* ($\mathrm{NI_A}$) and interactions with productivity and age

Parameter	Estimate	Standard error
Model of ln (*E. globulus* basal area PAI +1)		
Constant	4.6264	0.0348
ln ($\mathrm{NI_E}$ + 1)	−0.5889	0.0371
ln ($\mathrm{NI_A}$ + 1)	−0.3756	0.0312
Age 4.8 × ln ($\mathrm{NI_E}$ + 1)	−0.0748	0.0155
Age 8.8 × ln ($\mathrm{NI_E}$ + 1)	−0.1194	0.0165
Age 10.7 × ln ($\mathrm{NI_E}$ + 1)	−0.2642	0.0176
Medium productivity × ln ($\mathrm{NI_E}$ + 1)	0.1315	0.0399
High productivity × ln ($\mathrm{NI_E}$ + 1)	0.1329	0.0493
Medium productivity × ln ($\mathrm{NI_A}$ + 1)	−0.0722	0.0341
High productivity × ln ($\mathrm{NI_A}$ + 1)	−0.1055	0.0410
Model of ln (*A. mearnsii* basal area PAI +1)		
Constant	2.712	0.307
ln (basal area)	0.3362	0.0398
ln ($\mathrm{NI_A}$ + 1)	−0.2309	0.0397
ln ($\mathrm{NI_E}$ + 1)	−0.0055	0.0361
Age 4.8 × ln ($\mathrm{NI_A}$ + 1)	−0.0964	0.0283
Age 8.8 × ln ($\mathrm{NI_A}$ + 1)	−0.1128	0.0350
Age 10.7 × ln ($\mathrm{NI_A}$ + 1)	−0.1655	0.0370
Age 4.8 × ln ($\mathrm{NI_E}$ + 1)	−0.1140	0.0451
Age 8.8 × ln ($\mathrm{NI_E}$ + 1)	−0.1461	0.0444
Age 10.7 × ln ($\mathrm{NI_E}$ + 1)	−0.2529	0.0444

For the *E. globulus* model, the adjusted R^2, Mallows CP and number of observations were 0.76, 9.5 and 1,425, respectively, and those for *A. mearnsii* were 0.71, 10, and 1,460, respectively. For all parameters $P < 0.05$. Low productivity is used as the reference level for productivity in the *E. globulus* model and age 2.8 years is used as the reference level for age (starting age for a given growth period)

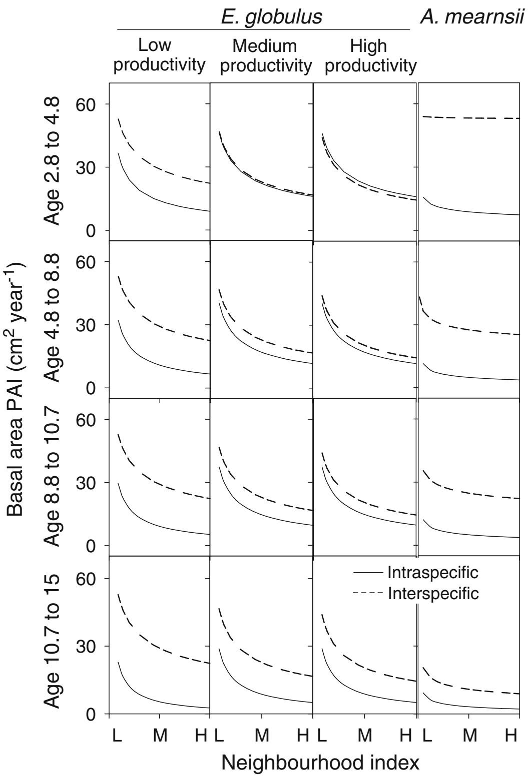

Fig. 3 Influence of intraspecific and interspecific neighbourhood indices (NI) on basal area PAI at low, medium and high productivity (not significant in the *A. mearnsii* model). For each graph, tree basal area is held constant as the average for that species and growth period. Interspecific responses are calculated with zero intraspecific competition and vice versa. A low NI (*L*) represents no neighbours within 5 m of the focal tree. A medium NI index (*M*) represents about six neighbours with an average diameter of 20 cm (*E. globulus*) or 15 cm (*A. mearnsii*) in relation to focal trees 10 cm in diameter. A high NI (*H*) is similar except there are 12 neighbours instead of 6

Age was also significant in both growth models and influenced growth through the inclusion of NI × age (Table 2). For *E. globulus*, only $\mathrm{NI_E}$ × age was significant, which intensified the negative effect of intraspecific influences ($\mathrm{NI_E}$) relative to interspecific influences ($\mathrm{NI_A}$) as the trees aged (Fig. 3). For *A. mearnsii*, both, $\mathrm{NI_A}$ × age and $\mathrm{NI_E}$ × age were significant, with $\mathrm{NI_E}$ × age having the more negative parameter estimate (Table 1). The resulting influence on the model was that as trees aged there was an increasingly negative effect of interspecific influences ($\mathrm{NI_E}$) and a reduction in the difference between interspecific and intraspecific influences.

Productivity did not significantly influence the growth as a main effect ($P > 0.05$). Nevertheless, it did influence *E. globulus* growth models by interacting with the NIs. The result of this interaction was that as productivity increased, the relative difference between interspecific and intraspecific influences decreased, particularly during the earlier stages of stand development (Fig. 3).

Discussion

The magnitudes and balance between competition and facilitation were dynamic and changed through time. Intraspecific interactions were usually more negative than interspecific interactions for both species. This is in agreement with Hypothesis One, which stated this would occur because, at the stand level, mixtures of *E. globulus* and *A. mearnsii* were significantly more productive than monocultures of either species. However, stand level results also suggested that these interactions were relatively consistent through time. In contrast, tree level analyses showed that the difference between interspecific and intraspecific influences varied depending on the species, stage of development and stand productivity. These dynamics can be explained by the timing of facilitative processes related to enhanced nutrition or reduced competition for light and water. Links between such growth trends and this range of directly measured processes and interactions is seldom reported.

Both inter- and intraspecific influences became more negative as the stands aged, which is consistent with our Hypothesis Two. For *A. mearnsii*, this meant that weak interspecific influences between ages 2.8 and 4.8 years developed into more negative competitive effects later on. Temporal shifts from net facilitative to competitive interactions have been found in plant communities of harsh environments (Miriti 2006; Schiffers and Teilbörger 2006; Sthultz et al. 2006, Reisman-Berman 2007; Armas and Pugnaire 2009). This trend is often observed for herbaceous plants and small woody plants that initially benefit from protection from harsh conditions or increases in resource availability but then experience and exert more competition as they develop or as conditions become more favourable for growth (e.g. during periods of higher rainfall) (Tielborger and Kadmon 2000).

The growth of mixed-species stands depends on the net effect of both inter- and intraspecific competition and, therefore, both need to be considered together. Such consideration indicates clear differences between *E. globulus* and *A. mearnsii*. While interspecific interactions were usually less intense than intraspecific influences, this difference—and hence the benefit of growing in mixture—increased as the stands aged for *E. globulus*, but decreased with age for *A. mearnsii* (Fig. 3). This is likely due to a decline in *A. mearnsii* growth rate with increasing age (Forrester et al. 2004), which lowers the rate at which $\mathrm{NI_A}$ increases. In contrast, the growth rates of *E. globulus* continued to increase with time (Forrester et al. 2004), thus increasing their competitive influence. These trends indicate an age effect on tree interactions per se and that the age effect is not simply due to increasing levels of competition resulting from the increasing average tree size and stand basal area as the stands develop.

The temporal dynamics were also driven by species effects on nutrient, light and water availability. The favourable influence of *A. mearnsii* on *E. globulus* was initially via increased N and phosphorus (P) availability due to N_2-fixation and accelerated rates of nutrient cycling (Forrester et al. 2005, 2007). The facilitative effect began as early as age 2 years after planting (Khanna 1997), and while rates of N_2-fixation may have declined as the stand developed (Khamzina et al. 2009), the faster N and P cycling remained (Forrester et al. 2005). The smaller difference between inter- and intraspecific effects on *E. globulus* between ages 2.8 and 4.8, despite favourable changes in nutrition, is likely due to competition for light as the *A. mearnsii* overtopped the *E. globulus* until about age 5 years (Forrester et al. 2004).

Thereafter, *E. globulus* overtopped *A. mearnsii* and benefitted from both improved nutrition and reductions in light competition (Forrester et al. 2004). This is consistent with the increasing difference between inter- and intraspecific influences on *E. globulus* as the stands aged (Fig. 3). As the stands developed further, the decline in the growth rates of *A. mearnsii* trees probably reduced their uptake of nutrients and water, and hence their competitive influence relative to *E. globulus* trees. For example, at age 15 years, growth of *A. mearnsii* was slow and soil moisture content was higher in monocultures of *A. mearnsii* than in those of *E. globulus* (Forrester et al. 2010). Thus, the increasing gap between the interspecific influences and more negative intraspecific influences on *E. globulus* growth as stands aged (Fig. 3) likely resulted from a slowing down of *A. mearnsii* growth rather than stronger facilitative effects of nutrient cycling or N_2-fixation. The improvements in light and nutrient availability did not only increase growth via structural changes (e.g. increased leaf area) but also resulted in physiological changes that increased water-use efficiency and the photosynthetic capacity of the crowns (Forrester et al. 2010) and altered the allocation of carbon from below to aboveground (Forrester et al. 2006).

We speculate that the facilitative influence of *E. globulus* on *A. mearnsii* could result from common mycorrhizal associations through which additional nutrients and carbon are passed to *A. mearnsii* (He et al. 2003). Both genera form symbioses with arbuscular mycorrhizal fungi when young (Gardner and Malajczuk 1988; Brundrett and Abbott 1991). Also, higher annual litterfall P contents in *A. mearnsii* (0.458 kg ha^{-1}) compared to *E. globulus* (0.741 kg ha^{-1}) monocultures and 166% higher rates of litter decomposition (Forrester et al. 2005) suggest that *A. mearnsii* may be a stronger competitor for soil P. Furthermore, prior to age 5 years, *A. mearnsii* trees were growing at their maximum rates and overtopping the *E. globulus* (Forrester et al. 2004). Even when *E. globulus* overtopped *A. mearnsii*, the former possess more vertical foliage and let a lot of light through to *A. mearnsii*, which has more horizontal foliage (Bauhus et al. 2004).

Few plant-level facilitation studies have included tree species, and those that have show contrasting trends depending on the environmental conditions. In semiarid woodland, facilitation from the shrub *Fallugia paradoxa* was important for *Pinus edulis* up to at least age 40 years on the more stressful sites (Sthultz et al. 2006). However, on less stressful sites, this interaction became more competitive as the *P. edulis* aged (Sthultz et al. 2006). In a subalpine ecosystem, the facilitative effects of *Pinus albicaulis* on *Abies lasiocarpa* stands were stronger at higher, more stressful, elevations. However, stronger facilitative effects were found for mature *A. lasiocarpa* than smaller individuals, probably because larger trees benefitted from protection from blowing ice and snow, while smaller individuals were protected by the snow pack (Callaway 1998). Soil nutrient availability influenced interactions between *Facaltaria moluccana* and *E. saligna*, such that the former facilitated the growth of *E. saligna* on sites with higher phosphorous availability (Boyden et al. 2005). In the same stands, *E. saligna* had a more competitive influence on *F. moluccana* growth as the N availability increased. These contrasting results illustrate the important site- and species-specific role that facilitation plays in the development of tree stands.

The facilitative influence of *A. mearnsii* on *E. globulus* declined as the productivity of *E. globulus* monocultures increased. This is consistent with the stress-gradient hypothesis (Bertness and Callaway 1994) where facilitative interactions are expected to become more common with increasing levels of abiotic stress. This is also consistent with 18- to 20-year-old mixtures of *E. saligna* and N_2-fixing *F. moluccana* where the competitive influence of *E. saligna* on *F. moluccana* increased from low to high soil N availability (Boyden et al. 2005); however, in that same stand, the facilitative influence of *F. moluccana* on *E. saligna* also increased from low to high soil P availability (Boyden et al. 2005). Further investigation would be required to link this reversal to dynamics in P and N availability. Nevertheless, small differences in site quality changed species interactions in ways that were not evident at the stand level (Fig. 1).

Conclusions

The magnitudes and relative differences between inter- and intraspecific interactions varied widely in these stands. The processes influencing these interactions occurred simultaneously and their net influence on growth changed through time, resulting in reversals in the ranking of inter- and intraspecific influences. This also resulted in a range of relationships that did not always support a simple existing ecological theory about plant interactions, age and productivity. The results of our experiment highlight the benefits of plant interaction studies that span several stages of stand development. The differences between blocks of contrasting productivity emphasise the influence of site quality and resource availability and that a wide range of interactions is likely rather than narrow generalisable patterns (Boyden et al. 2005).

The relative differences between interspecific and intraspecific interactions were not always consistent with stand level results, and temporal changes in the magnitude of these interactions were more evident at the scale of individual trees. This plasticity through time and space shows that the productivity of mixed forests is very variable, depending on the contrasting species growth dynamics, resource availability and the influence of silviculture on stand processes and species interactions. Successful management will require a good understanding of the mechanisms controlling the balance between facilitation and competition. If growth is effected so much by changes in resource availability due to site and age, then climate is also likely to modify these effects and warrants further study.

Acknowledgments David Forrester was funded by the Cooperative Research Centre for Forestry (Program 2) and an Alexander von Humboldt Research Fellowship. The experiment was established by the Commonwealth Scientific and Industrial Research Organisation, Division of Forestry, with the Department of Natural Resources and Environment, Victoria, providing the site and the Australian Centre for International Agricultural Research providing some financial support. We are also grateful to Partap Khanna, who established the experiment and provided early growth measurements. Three anonymous reviewers provided comments that improved the manuscript. Thank you also to John Collopy and Ben Smith who provided assistance in the field.

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