Vertical structure and basal area development in second-growth *Nothofagus* stands in Chile

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Summary

1. Some studies have shown that mixed forest stands can develop more biomass or basal area than pure stands when the component species occupy different strata. It has been predicted that such additive effects are most likely in moist habitat sites where size-asymmetric competition controls stand development.

2. In south-central Chile, secondary succession often gives rise to vertically stratified mixed forest stands, with a *Nothofagus* overstorey overtopping lower tiers dominated by more shade-tolerant taxa. We examined the relationship between the degree of understorey development and total basal area accumulated by 83 second-growth *Nothofagus* stands aged 40–70 years. Basal area is defined as the cross-sectional area at breast height of all trees in a stand, per unit land area.

3. When age, overstorey leaf habit and geographical location were controlled by ANCOVA, stands with a heavy understorey ($> 6 \text{ m}^2 \text{ ha}^{-1}$) yielded $> 25\%$ more total basal area on average than stands with little or no understorey. The average basal area of the *Nothofagus* component did not differ significantly between stand structure categories.

4. The total basal area of stands dominated by evergreen *N. dombeyi* was nearly 50% higher on average than that of stands of similar age dominated by deciduous *N. obliqua* and/or *N. nervosa*, reflecting denser stockings in the former as a result of allometric differences. Although the percentage of total stand basal area contributed by the understorey was higher on deciduous-dominant plots, mean absolute basal area of understorey associates was similar beneath evergreen and deciduous *Nothofagus* overstoreys.

5. *Synthesis and applications*. The results broaden the evidence for additive effects in mixtures of species with complementary light use, suggesting that no significant advantage to overstorey wood production will be gained by eliminating a woody understorey in *Nothofagus* second-growth stands on mesic sites. Despite the minor contribution of the understorey to merchantable timber volume, other benefits and ecosystem services associated with subcanopy species in these stands can be regarded as additive to benefits obtained from the *Nothofagus* overstorey. Our findings are also consistent with the proposal that size-asymmetric competition controls stand development after canopy closure on mesic sites.

Key-words: complementarity, functional diversity, mixed forests, primary production, size-asymmetric competition, stratification

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Introduction

Over the last decade there has been renewed interest among ecologists in the influence of resource-use com-plementarity on productivity of plant communities (Naeem *et al.* 1994; Denslow 1996; Tilman, Wedin & Knops 1996; Huston 1997; Hector *et al.* 1999; Reich *et al.* 2001). This topic has been of long-standing interest to foresters and agroecologists, who have sought to determine when species mixtures are more productive than monocultures (Weidemann 1943; Assmann 1961, 1970; Vandemeer 1988; Kelty 1989; Liebman 1989).

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Vertical structure is a key aspect of resource-use differentiation in forests (Enright 1982; Terbough 1985; Enright & Ogden 1995) and is therefore likely to have important implications for the productivity of these systems. Stand productivity should be enhanced by an appropriate vertical arrangement of species that complement each other in light use, i.e. upper strata dominated by light-demanding fast-growing species, and lower tiers occupied by shade-tolerant taxa able to exploit low light environments (Kelty 1989). Analyses of European plantation experiments support this idea, reporting overyielding of various stratified mixtures but not of mixed stands in which both species differing in growth rate and shade tolerance occupied the same stratum (Assmann 1961, 1970).

Naturally regenerated second-growth stands provide opportunities for exploring the influence of vertical structure, and other aspects of functional diversity, on stand productivity, without the need to monitor production directly. In young aggrading stands of known age, losses to mortality can be assumed to be minimal, and so rates of biomass production can be roughly indexed from volume or basal area data. In one such observational study, Kelty (1989) showed that New England deciduous hardwood stands (mainly *Quercus* spp.) with a well-developed understorey of the shade-tolerant conifer *Tsuga canadensis* outyielded neighbouring stands that lacked such an understorey. The presence of the *Tsuga* understorey was associated with only a slight depression of overstorey production, which was more than compensated by the understorey contribution to total stand basal area and volume. Wood production by the two strata was therefore essentially additive. Kelty (1989) speculated that the difference in leaf habit between the two strata might favour understorey development, the evergreen habit of *Tsuga* permitting carbon gain in spring and autumn when the deciduous overstorey is leafless.

While overstorey phenology could influence the degree of understorey development, site water balance may mediate the influence that such development has on overstorey production. Whereas at least two studies have indicated that understorey development does not detract much from overstorey production on mesic sites (Kelty, Gould & Twery 1987; Kelty 1989), understorey removal in stands growing in drier climates has been shown to enhance overstorey growth significantly (Dale 1975; Oren *et al*. 1987). It has therefore been proposed that overstorey–understorey interactions are dominated by size-asymmetric competition for light on mesic sites, whereas size-symmetric competition for soil resources becomes important on more xeric sites (Kelty 1989; Coomes & Grubb 2000). Thus, additive effects on basal area development in stratified forests seem more likely on mesic than on xeric sites.

In this study we examined the effect of vertical structure on basal area accumulation in naturally regenerated, unthinned second-growth *Nothofagus* stands in mesic environments in south-central Chile. Basal area,

defined as the cross-sectional area at breast height of all trees in a stand, per unit land area, is a commonly used index of forest biomass or wood volume. *Nothofagus* spp., which are among the most important native Chilean timber species, dominate the forest overstorey during the early to middle stages of succession in most forest types in the region, undergoing gradual replacement by more shade-tolerant species in older stands (Veblen *et al*. 1996). Both deciduous and evergreen species of *Nothofagus* occur throughout the region, whereas all associated tree species are evergreen. *Nothofagus* spp. grow faster, attain greater heights and are less shade-tolerant than most other long-lived broad-leaved trees in south-central Chile (Veblen 1985; Veblen *et al*. 1996; C. H. Lusk & G. Hofmann, unpublished data). Stands therefore often show a marked vertical segregation, with *Nothofagus* overtopping other taxa.

We addressed the following questions. (i) Does development of understorey associates detract from (or is it additive to) basal area accumulation by the *Nothofagus* overstorey in stratified mixtures? (ii) Is understorey development greater beneath deciduous *Nothofagus* overstoreys than beneath evergreen ones?

Methods and materials

STUDY AREA

Stands were distributed between latitudes 37° and 41°S in south-central Chile, on sites ranging in altitude from 100 to 900 m a.s.l. (Fig. 1). A maritime temperate climate prevails throughout the region, with precipitation ranging from 1200 to 3500 mm (Di Castri & Hajek 1976). Total rainfall increases steadily from north to south, and a summer rainfall minimum attenuates along the same gradient. There are also important orographic influences on rainfall, with the highest figures reported from the seaward (western) upper slopes of the Andean and coastal ranges, and much lower annual averages in the central depression between the two ranges.

Three species of *Nothofagus* occurred on the study sites, the deciduous *N. obliqua* and *N. nervosa* (syn. *N. alpina*) and the evergreen *N. dombeyi*. The latter species tends to occur on moister sites than the deciduous species (Weinberger 1973), therefore attaining greater importance at higher altitudes and towards the south, as well as on south-facing slopes and close to water courses (Donoso 1996; Veblen *et al*. 1996). In contrast to the evergreen *N. dombeyi*, both of the deciduous *Nothofagus* spp. are capable of sprouting after cutting or fire (Donoso 1981; Veblen *et al*. 1996). Our data set included many deciduous stands that appeared to be predominantly of sprout origin, but the high level of uncertainty in distinguishing stems of vegetative and seedling origin precluded our carrying out separate analysis for these two categories.

The associated species that contributed most basal area were *Gevuina avellana*, *Lomatia dentata*, *Lomatia hirsuta* (all Proteaceae), *Persea lingue* (Lauraceae),
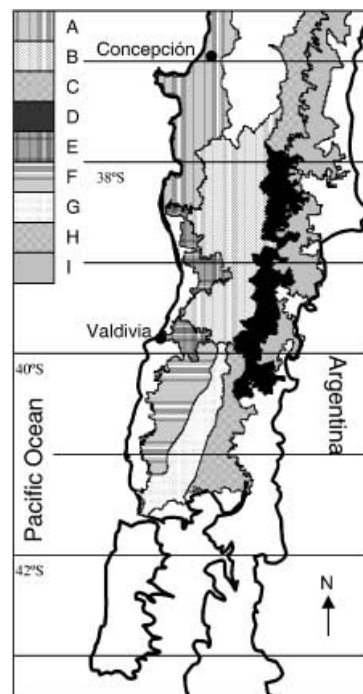
Fig. 1. Map of south-central Chile showing nine zones defined by Ortega & Gezan (1999a) on the basis of climate and vegetation. Distribution of 83 *Nothofagus* stands among zones is shown in Table 1.

Dasyphyllum diacanthoides (Asteraceae) and *Eucryphia cordifolia* (Cunoniaceae). Despite the considerable functional diversity encompassed by this collection of associated species, all are slower-growing, more shade-tolerant and of lesser maximum height than *Nothofagus* spp. (Donoso 1981; Veblen *et al*. 1996; C.H. Lusk & G. Hofmann, unpublished data). Nomenclature follows Marticorena & Quezada (1985) and Marticorena & Rodriguez (in press).

STANDS

Data were obtained from an extensive permanent study plot of second-growth stands in south-central Chile (Ortega & Gezan 1999a,b). This survey used data from the recent Chilean national forest survey (CONAF/CONAMA 1999) to locate plots in a stratified random design. Ortega & Gezan (1999a) divided the study area into nine zones (A–I) of homogeneous climate and vegetation (Fig. 1) and then randomly located plots within each zone, the number of plots varying in proportion to the total area of second-growth forest present in that zone.

Plots of 250 or 500 m² area were sampled, depending on stem density. Species and diameter at breast height (d.b.h) were recorded for all stems ≥ 5·0 cm d.b.h. Heights of 15 trees were measured in each stand, using a stratified random system to ensure inclusion of individuals from across the full range of diameters. Ages of at least 10 randomly selected trees per stand were esti-

mated from increment cores, and the highest ring count was used to approximate stand age.

Here we report data only for stands with a marked vertical segregation between *Nothofagus* spp. and its associates, i.e. stands in which the average height of associates was at least 40% less than that of *Nothofagus*. However, secondary successions can also give rise to stands in which some of these associates form part of the overstorey. As *Nothofagus* spp. are relatively poorly dispersed, this latter type of vertical structure could result from partial site pre-emption by other taxa. Although the data set available to us included such mixed stands lacking clear vertical segregation of *Nothofagus* from its associates, the maximum height attained by *Nothofagus* spp. in these stands was significantly lower on average than that of pure and vertically segregated stands (Tukey–Kramer HSD test, $P < 0·05$). As this finding prevented us from ruling out the possibility that mixed non-segregated stands tend to occur on less productive sites than the other stand structure types, we excluded the former from our analysis.

Three categories of stand vertical structure were recognized. Plots on which species other than *Nothofagus* contributed $< 1·0$ m² ha⁻¹ in basal area were classified as pure stands (Fig. 2a). Understorey development was categorized as 'light' if understorey associates contributed $≥ 1·0$ but $< 6·0$ m² ha⁻¹ (Fig. 2b). Finally, understorey development was described as 'heavy' if associates contributed $≥ 6·0$ m² ha⁻¹ (Fig. 2c). These figures can be seen in the context of total stand basal areas ranging generally between 30 and 70 m² ha⁻¹. Our analysis assumes that at least part of this variation in stand vertical structure reflects differences in propagule availability and disturbance history. Stands containing large residual trees were excluded from the analysis, because of the errors they would introduce in basal area yield estimates.

Stands were further classified by leaf habit of the dominant *Nothofagus* species. We distinguished between plots with an overstorey dominated (in terms of basal area) by the evergreen *N. dombeyi* and those dominated by the deciduous *N. nervosa* and/or *N. obliqua*. Preliminary analyses showed that stands dominated by the two deciduous species (*N. nervosa* and *N. obliqua*) did not differ significantly in total basal area or in canopy height. All deciduous-dominated stands were therefore pooled for all analysis. A contingency table showed that relative representation of deciduous and evergreen stands did not differ greatly among zones (likelihood ratio $\chi^2 = 7·4$, $P = 0·60$, d.f. = 9).

Although the pool of available stands ranged in age from 10 to 90 years, we restricted our analysis to the most abundant age classes (40–70 years), yielding 83 stands (Table 1).

ANALYSES

We used analysis of covariance (ANCOVA) to evaluate the relationship of stand vertical structure with basal
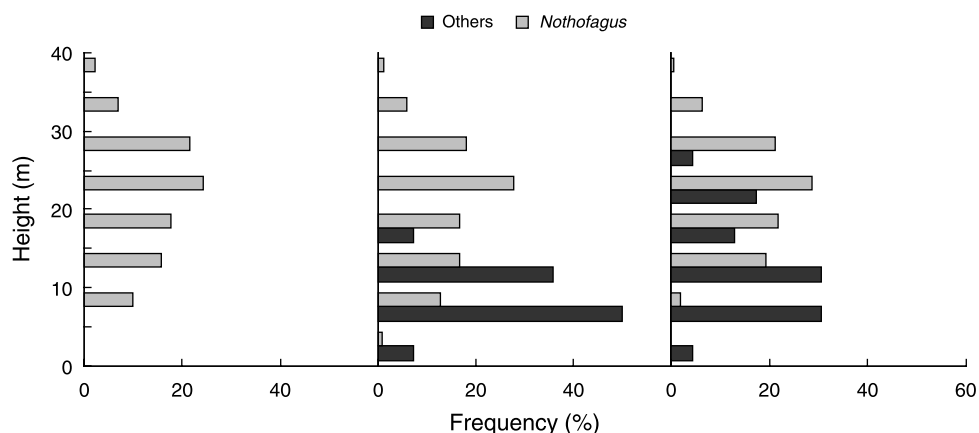
Fig. 2. Tree height distribution of *Nothofagus* and associates in stands with (a) negligible understorey (< 1·0 m² ha⁻¹), (b) light understorey (≥ 1·0 but < 6·0 m² ha⁻¹) and (c) heavy understorey (≥ 6·0 m² ha⁻¹).

Table 1. Breakdown of 83 *Nothofagus* second-growth stands by geographical zone (Fig. 1) and by stand structure

	Understorey development			
Zone	None	Light	Heavy	Total
A	0	3	2	5
B	2	1	4	7
C	1	2	4	7
D	14	5	2	21
E	2	0	0	2
F	1	1	0	2
G	4	5	4	13
H	1	1	0	2
I	11	6	7	24
Total	36	24	23	83

Table 2. Summary of ANCOVA to evaluate relationships of stand structure, overstorey leaf habit, age and geographical zone with canopy height of second-growth *Nothofagus* stands

Source of variation	d.f.	*F*-ratio	*P* > *F*
Stand structure	2	0·35	0·71
Leaf habit	1	1·34	0·26
(Log) stand age	1	1·34	0·25
Zone	9	1·18	0·34

Table 3. Summary of ANCOVA to evaluate relationships of stand structure, overstorey leaf habit, age and geographical zone with basal area development of second-growth *Nothofagus* stands

Source of variation	d.f.	*F*-ratio	*P* > *F*
(a) Total stand basal area			
Stand structure	2	5·14	0·01
Leaf habit	1	18·47	< 0·0001
(Log) stand age	1	11·84	0·0013
Zone	9	1·66	0·13
(b) *Nothofagus* spp. basal area			
Stand structure	2	0·71	0·50
Leaf habit	1	18·66	< 0·0001
(Log) stand age	1	13·92	0·0005
Zone	9	1·49	0·18

area accumulation in our 83 stands. In order to control for probable influences of stand age, overstorey leaf habit and geographical location (zone) on basal area, we included these factors in our model. This permitted comparison of least-squares mean basal area for the three stand structure categories, with the covariables set to neutral values. We also tested for average canopy height differences between stand structure categories as a way of indexing possible differences in site quality. All analyses were carried out using JMP Statistical Discovery Software (SAS Institute, Cary, MA).

Results

Average canopy heights of the three stand structure categories were very similar (Table 2). There were no significant effects of zone, age or overstorey leaf habit on canopy height (Table 2), although evergreen stands were on average slightly taller than those with deciduous-dominated overstoreys (28·3 vs. 25·6 m).

Basal area accumulation was significantly influenced by stand structure (Table 3a), stands with a heavy understorey developing over 25% more on average

than those with little or no understorey, when influences of other factors were filtered out (Fig. 3). Total basal area was also significantly influenced by stand age and overstorey leaf habit, evergreen-dominated stands having > 45% more basal area on average than deciduous-dominated stands (least-squares means 66·3 vs. 44·9 m² h⁻¹). On the other hand, there was no evidence of significant variation in productivity among geographical zones (Table 3a).

In contrast to the situation observed for total stand basal area, basal area of the *Nothofagus* component was very similar in stands of differing structure
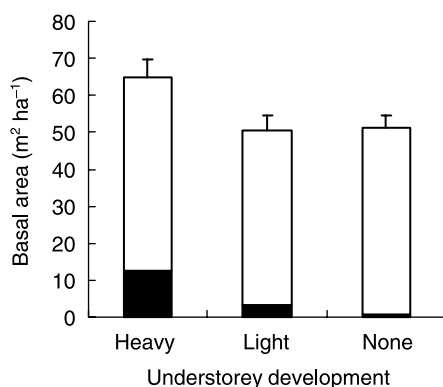
Fig. 3. Least-squares mean basal area (± SE) of 40–70-year-old *Nothofagus* stands with (a) negligible understorey (< 1·0 m² ha⁻¹), (b) light understorey (≥ 1·0 but < 6·0 m² ha⁻¹) and (c) heavy understorey (≥ 6·0 m² ha⁻¹). Basal area of *Nothofagus* in white, understorey associates in black. Stand age, overstorey leaf habit and geographical origin set at neutral values.

Table 4. Summary of ANCOVA to evaluate relationships of overstorey leaf habit, stand age and geographical zone with basal area development of understorey species in second-growth *Nothofagus* stands ($n = 47$)

| Source of variation	d.f.	*F*-ratio	$P > F$
Leaf habit	1	0·01	0·93
Zone	8	1·74	0·16
(Log) stand age	1	0·47	0·50

(Table 3b and Fig. 3). As found for total stand basal area, there were strong effects of stand age and leaf habit, but not of zone (Table 3b).

Mean basal area of understorey species in mixed stands was statistically indistinguishable for plots with deciduous- and evergreen-dominated *Nothofagus* overstoreys (Table 4 and Fig. 4). There were no significant effects of zone or stand age on understorey development.

Discussion

DECIDUOUS VS. EVERGREEN STANDS

Stands dominated by the evergreen *N. dombeyi* developed much higher total basal area at a given age than stands dominated by deciduous *Nothofagus*. This pattern probably stems largely from allometric differences between *N. dombeyi* and its deciduous congeners. *Nothofagus dombeyi* trees tend to have narrower crowns than *N. obliqua* or *N. nervosa* of similar diameter, giving rise to higher stockings in stands of the former (Lara *et al.* 1999; Donoso *et al.* 1999). Inventory data from our stands support this explanation, showing that densities of *Nothofagus* stems were about 45% higher on average in *N. dombeyi*-dominant stands than in deciduous stands of similar age (A. Ortega, unpublished data). On the other hand, there was very little difference in mean stem diameter, suggesting that site quality
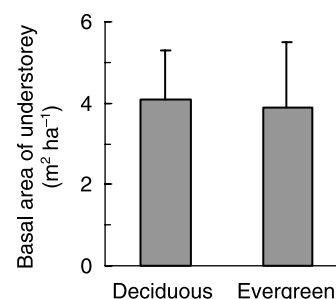
Fig. 4. Basal area (mean ± SE) of woody understorey associates in 40–70-year-old-stands with deciduous ($n = 35$) and evergreen ($n = 12$) *Nothofagus* overstoreys in south-central Chile.

variation contributed little to productivity differences between evergreen and deciduous stands.

There was no evidence that overstorey leaf habit influenced woody understorey development. Although the lesser productivity of the overstorey in deciduous-dominant stands made the understorey contribution proportionally larger, average understorey basal area was very similar in deciduous and evergreen *Nothofagus* stands (Fig. 4 and Table 4). This finding is at variance with the hypothesis that deciduous overstoreys should permit greater understorey development than evergreen-dominated canopies (Kelty 1989), possibly indicating that low temperatures greatly restrict understorey carbon gain during winter when *N. obliqua*– *N. nervosa* overstoreys are leafless.

STAND COMPOSITION, VERTICAL STRUCTURE AND PRODUCTIVITY

Understorey production appeared to be additive to that of the *Nothofagus* overstorey. When age, overstorey leaf habit and geographical zone were held constant by ANCOVA, the *Nothofagus* basal area of stands with a heavy understorey was in fact slightly (although not statistically significantly) higher on average than that of the other stand structure categories (Fig. 3), which might be construed as evidence that the stands with a heavy understorey tend to occur on the most productive sites. However, the similarity of average canopy heights across stand structure categories (Fig. 2 and Table 2) suggests that any such effect is minimal, and that the greater total basal area accumulation of stands with a heavy understorey is at least partly an additive effect, similar to that reported by Kelty (1989) in a previous study of second-growth stands. Our evidence therefore suggests that no significant advantage, in terms of overstorey wood production, will be gained by eliminating a woody understorey in *Nothofagus* second-growth stands, and any benefits derived from this stratum are additive to those produced by the overstorey. However, the observational nature of our data implies a higher level of uncertainty than that associated with well-controlled experiments and it is clear that experimental removal or thinning of understoreys

(Kelty, Gould & Twery 1987) would provide a more conclusive test of this idea.

The presence of a well-developed understorey may bring other benefits besides a minor increase in wood production. Although understorey species contributed about 25% of total basal area in some stands (Fig. 3), their contribution to merchantable timber volume will be considerably less than this. However, ecosystem services and other benefits associated with subcanopy species in these stands can be regarded as additive to benefits obtained from the *Nothofagus* overstorey. Understorey vegetation is often an important wildlife habitat (Diaz 1999; McPherson 1999) and marketable non-timber products are obtained from several sub-canopy species in Chilean *Nothofagus* stands, such as *Gevuina avellana* and *Podocarpus saligna* (Smith-Ramírez 1995).

Although explanations of additive effects have centred on complementary light use (Kelty 1989; Enright & Ogden 1995), nutritional factors might also warrant attention. Whereas the *Nothofagus* spp. of the over-storey are ectomycorrhizal, all of their woody associates have either arbuscular mycorrhizae or (in the case of the Proteaceae) no mycorrhizae (Godoy, Romero & Carrillo 1994). Some recent studies have produced evidence that ectomycorrhizal plants have greater direct access to organic soil nitrogen pools than arbuscular- and non-mycorrhizal plants, which are generally dependent on inorganic sources (Read 1991; Michelsen *et al.* 1996; but see Persson & Näsholm 2001 for evidence to the contrary). Thus the *Nothofagus* overstorey could theoretically enjoy a certain degree of nutritional independence from its associates, which might contribute to its apparent insensitivity to the degree of understorey development (Fig. 3). However, while possible influences of nitrogen pool partitioning have yet to be explored in these ecosystems, additive effects in our stands can be readily explained on the basis of well-documented light-use differences (Veblen 1985; Veblen *et al.* 1996) and, as discussed below, the likelihood of size-asymmetric above-ground competition (Schwinning & Weiner 1998).

This study broadens the evidence for additive effects in mixed stands. Previous work has demonstrated that vertical structure influences productivity of stands varying in taxonomy and leaf habit, including stands with deciduous hardwoods in both strata (*Quercus petraea*/ *Fagus sylvatica*), evergreen conifers in both strata (*Pinus sylvestris*/*Picea abies*), evergreen conifers over deciduous hardwoods (*Pinus sylvestris*/*Fagus sylvatica*) and deciduous hardwoods over evergreen conifers (*Quercus* spp./*Tsuga canadensis*; Assmann 1961, 1970; Kelty 1989). This study reports the first example of additive effects for second-growth forests dominated by broad-leaved evergreen trees in both the overstorey and understorey. The evidence to hand therefore suggests that additive effects are likely whenever propagule availability, succession and/or forest management practices on mesic sites give rise to clear vertical segregation associated with differences in maximum growth rates and shade-tolerance level.

The additive basal area effects reported from some old-growth forests (Enright 1982) are not necessarily comparable with the patterns described here. In some old-growth forests with complex vertical structure, the maximum basal area attained by the species that form the main canopy appears to be independent of that developed by emergent species (Enright 1982; Ogden 1985; Lusk 2002). However, in view of the numerous imponderables in relation to stand and tree ages and biomass losses due to mortality, such cases in old-growth forests cannot be construed as evidence of additive productivity.

SITE QUALITY AND COMPETITION IN FORESTS

Our evidence for additive effects in the maritime temperate climate of south-central Chile lends support to the proposal that size-symmetric below-ground competition between overstorey and understorey trees has little influence on stand development on mesic sites (Kelty 1989). Whereas size differences between plants cause strong asymmetries in competition for light, there is considerable evidence that competition for below-ground resources is much less size-dependent (Schwinning & Weiner 1998), implying that understorey plants could significantly impair growth of larger neighbours by reducing water or nutrient availability. However, Tilman (1988) predicted that below-ground competition should decrease in importance, relative to competition for light, along gradients of increasing soil resource availability. Although the observational origin of our data requires cautious interpretation, our results concur with a body of experimental and observational evidence from other mesic temperate forests (Kelty, Gould & Twery 1987; Kelty 1989) in suggesting that competition for below-ground resources on such sites plays a minor role in stand development after canopy closure.

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