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Effects of density and ontogeny on size and growth ranks of three competing tree species

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Summary

1. Rank reversals in species performance are theoretically important for structuring communities, maintaining diversity and determining the course of forest succession. Species growth ranks can change with ontogeny or in different microenvironments, but interactions between ontogeny and the environment are not well-understood because of the lack of long-term forest competition studies. While early differences in growth among species may reflect intrinsic differences in shade-tolerance and physiology, ontogenetic trends in growth and variation in neighbourhood density and composition may change or even reverse early patterns of growth rankings.

2. We experimentally studied spatial and temporal patterns of species interactions and growth for three northern tree species: *Larix laricina*, *Picea mariana* and *Pinus strobus*. We compared species size and growth rankings over an 11-year period, for different species mixtures planted at four density levels in north-eastern Minnesota, USA.

3. The benefits of different growth strategies changed with ontogeny and density leading to reversals in the size rank of competing species over time and space. High-density stands promoted dominance and resource pre-emption by *L. laricina*, whereas lower-density stands favoured gradual accumulation of biomass and eventual dominance by *P. strobus*. In the absence of strong neighbour competition, ontogenetic trends in growth had greater influence on growth patterns.

4. Species interactions affected the productivity of mixed stands vs. monocultures. Species generally grew more in monoculture than when planted with *P. strobus* at low density, or with *L. laricina* at high density. Only *L. laricina* and *P. mariana* showed potential for greater overall productivity, or over-yielding, when planted together than alone, probably because of improved resource uptake by the highly stratified canopy.

5. *Synthesis*. Density predictably determined whether size-asymmetric growth or ontogenetic growth trends would drive early establishment and growth patterns. Variation in vertical and horizontal structure that results from early competitive dynamics can influence the successional trajectory or character of the mature forest. This study extends previous efforts to identify the causes of rank reversals in communities and understand the importance of temporal changes beyond the early years of seedling establishment.

Key-words: competition, density, ontogeny, over-yielding, rank reversals, sapling growth, shade-tolerance, succession

Introduction

How plant interactions influence community structure and function over space and time remains an enduring question in ecology (Grime 1979; Tilman 1982, 1988; Baraloto *et al.* 2005; Potvin & Gotelli 2008). Competition during early stages of forest establishment can critically influence individual tree growth (Baraloto *et al.* 2005) and determine future stand development patterns (Harper 1977; Kobe 1996; Garber & Maguire 2004). Complex stand structures and diverse community assemblages can develop from the legacies of small differences in initial size and growth rates between individuals and species. Where competition for light is important, initial height differences can build over time as larger individuals

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Table 1. Study species traits, seed mass (mg), shade tolerance category, shade tolerance rank (most tolerant = 1, least tolerant = 8), life form, leaf life span (months), and high light relative growth rate (RGR, mg g^{-1} day^{-1})

	Seed mass (mg)	Shade-tolerance category	Shade-tolerance rank	Life-form	Leaf life span (months)	High light RGR
Larix laricina	1.0	Very intolerant/intolerant	7	Deciduous conifer	5–6	87.5
Pinus strobus	17.2	Intermediate/tolerant	3	Evergreen conifer	20–40	47
Picea mariana	0.7	Tolerant	2	Evergreen conifer	50–60	72

Data are compiled from Walters and Reich (2000) and Reich *et al.* (1998a). Mean seed mass was determined from the mass of 20, 1–2-day-old germinants. Shade-tolerance categories are a composite of published reports and were used to assign numerical shade tolerance rankings (see Walters and Reich (2000) for methods). High light RGR are for first-year seedlings from Reich *et al.* (1998).

pre-empt available light and suppress the growth of smaller individuals (Weiner & Thomas 1986; Weiner 1990; Schwinning 1996; Schwinning & Weiner 1998). Conversely, size differences and competitive advantages may actually decrease over time as smaller individuals catch up to their larger neighbours due to age- and size-related changes in growth potential (Connolly *et al.* 1990; Schwinning 1996; Lusk 2004). These long-term community dynamics are fundamentally related to the nature and strength of interactions between individuals or species. Changes in size or growth hierarchies of competing species across space or over time affect successional trajectories in forests and are theoretically important for maintaining species coexistence (Grime 1979; Tilman 1982; Chesson 1985), yet we do not fully understand the complex controls over community dynamics in mixed-species stands because long-term experimental studies of forest establishment are extremely rare.

Competitive interactions in young plants are positively related to photosynthetic capacity and relative growth rates (RGR; Goldberg & Landa 1991) that have strong positive correlations with plant traits such as specific leaf area and leaf area ratio (Lambers & Poorter 1992; Walters *et al.* 1993a,b; Reich *et al.* 1998a). As trees grow larger, species differences in photosynthetic capacity and RGR often diminish, decreasing the initial competitive advantage of small-seeded, high-light demanding species (Reich 1998; Lusk 2004; Niinemets 2006; but see Thomas & Winner 2002). These changes in growth with increasing size and age, or ontogeny, can lead to reversals in the growth or size rank of competing species over time (Lusk 2004; Niinemets 2006). Most experimental forest studies of growth traits and competitive interactions are limited to short-term investigations of early seedling or sapling growth in the first few months or years following emergence. How might ontogeny influence patterns of growth and competition over the course of stand development? A few recent studies (Bell *et al.* 2000; Lusk 2004; Baraloto *et al.* 2005) have shown that rank reversals in growth rates among species can occur as species increase in size or age over periods up to 5 years. Spatial variation in resource availability should in theory affect these growth trends (Sack & Grubb 2001; Baraloto *et al.* 2005), but we have a poor understanding of how ontogenetic rank reversals are modified by tree density.

Forest structure has important direct and indirect effects on tree interactions, growth and survival. Tree density affects growth directly by altering resource availability, and indirectly by influencing competitive interactions for resources (Firbank & Watkinson 1985). The intensity of competitive interactions increases as the distance between neighbours decreases (Bella 1971; Stoll *et al.* 1994; Canham *et al.* 2004), leading to reduced growth and tree size, but potentially greater size variation as larger individuals pre-empt resources (Ford 1975; Hara & Wyszomirski 1994; Schwinning & Weiner 1998). Changing resource supplies (light, but also soil resources) along a density gradient can also indirectly alter the competitive balance between species (Tilman 1990; Wagner & Radosevich 1998; Kaelke *et al.* 2001; Lusk 2004; Baraloto *et al.* 2005) as different resource environments may favour different competitive strategies or plant traits (Tilman 1988; Suding & Goldberg 2001; Baraloto *et al.* 2005). Examples include the hypothesized trade-offs between above-ground and below-ground competitive ability across fertility gradients (Tilman 1988) or trade-offs between growth rates and survival across light gradients (Walters & Reich 2000; Kaelke *et al.* 2001; Sack & Grubb 2001; Lusk 2004; Poorter & Bongers 2006). Density effects on resources and competition influence the rate of development of forest stands (Ford 1975; Oliver & Larson 1996; Garber & Maguire 2004), and should therefore influence ontogenetic growth processes.

We examined variation in tree size and growth of *Larix laricina* (Duroi) K. Koch (tamarack), *Pinus strobus* L. (white pine) and *Picea mariana* (Miller) BSP (black spruce) in pure and mixed stands at a range of densities for 11 years following planting. These three conifers were selected to represent a wide range of shade-tolerance, growth rates, net photosynthetic capacity, leaf morphologies, leaf life span, leaf respiration rates and other plant traits (Table 1; Reich *et al.* 1998a,b). Even though all three species are conifers, these trait differences should lead to different competitive strategies and therefore diverse species interactions (Kelty 2006). We expected that 2 years after planting, more shade-tolerant species would have higher growth rates in monoculture (because of the strong correlation between shade-tolerance and early RGR in seedlings). We further hypothesized that planting density and ontogenetic growth patterns should have predictable effects on species interactions and potentially lead to reversals in this basic size ranking (as described below).

GROWTH PATTERNS OVER TIME

We hypothesized that species size differences in mixed stands could change over time in one of two ways. Based on theories of size-asymmetric growth and competition (Weiner & Thomas 1986; Weiner 1990; Schwinning & Weiner 1998), we hypothesized that the fast-growing species (*L. laricina*) could achieve early size dominance and therefore pre-empt light resources and increase its size advantage over time (D'Amato & Puettmann 2004). Alternatively, size differences of competing species could diminish or even reverse over time due to ontogenetic changes in RGR and related ecophysiological traits that reduce growth differences of trees with contrasting shade-tolerance (Reich 1998; Lusk 2004) and ultimately favour later-successional species. Changes in density should influence which of these developmental trajectories is followed, as described below.

GROWTH PATTERNS OVER SPACE

Variation in light and soil resource availability along a density gradient should differentially influence the growth rates and interactions of fast-growing, shade-tolerant vs. slower-growing, shade-intolerant trees. Declining light availability and increasing above-ground competition should encourage resource pre-emption by the shade-intolerant species, leading to increasing size variation and stratification in more crowded plant populations (Weiner & Thomas 1986; Schwinning 1996; Schwinning & Weiner 1998). In low-density plots, trees of all species should have more equitable access to light resources, which should reduce the competitive advantage of shade-intolerant trees and increase the potential for size convergence or rank reversals with ontogeny (Garber & Maguire 2004).

INTERACTIONS IN MIXTURES VS. MONOCULTURES

Changes in the nature of inter-specific vs. intra-specific interactions along density gradients or at different ontogenetic stages will influence the overall productivity of species monocultures and mixtures. It is theorized that mixed stands can sometimes achieve greater overall productivity than monocultures if one species reduces competitive effects on the second, or if the two species more completely use the system resources due to niche partitioning (Tilman 1982; Kelty 1992; Pretzsch 2005). Although data for grasslands suggests a strong positive link between productivity and diversity (e.g. Tilman *et al.* 2001), we lack generalizable insights about species diversity and ecosystem productivity in tree-dominated stands because controlled experimental studies in forests are rare. There is, however, renewed focus on this issue (Bristow *et al.* 2006). Such studies suggest that over-yielding may be common (e.g. Bergqvist 1999; Erskine *et al.* 2006; Kelty 2006; Potvin & Gotelli 2008), especially when mixed stands contain species that vary functionally, such as fast-growing shade-intolerants and slower-growing shade-tolerants. Herein we ignore mixed stands that include a nitrogen-fixing species, the presence of which logically might lead to strong facilitation of co-occurring species and thus a greater and/or more consistent stimulation of total stand productivity than might occur due to niche partitioning alone (Kelty 2006). We ask whether there is enough functional variation within a group of conifers to lead to complementary resource use and over-yielding in mixed stands.

The magnitude of the study is novel, both by comparing mixed stands and monocultures of three conifers of differing shade-tolerance across a range of densities and by having growth data for individuals at multiple time points over an 11-year period. This design allows us to explore how ontogenetic growth patterns and density influence inter-specific vs. intra-specific interactions and lead to possible rank reversals among competing species. Furthermore, we can test the 'competitive production principle' in which species have reduced competition and higher growth in mixed stands than in monocultures (Vandermeer 1989).

Methods

STUDY SITE

Two sites were selected at the Cloquet Forestry Center (CFC) of the University of Minnesota in Cloquet, approximately 30 km south-west of Duluth, Minnesota, USA. The climate is cold-temperate, continental with a mean January temperature of –14 °C and a mean July temperature of 19 °C. The soils on the study sites are Omega and Cloquet series (loamy sands) and the sites receive an average of 760 mm of precipitation annually (R. Severs, unpublished data). Before harvest, the East site was occupied by an aspen stand with 18–23 m^2 basal area ha^{-1} while the West site was a sparse old-growth *P. strobus* stand with paper birch (*Betula papyrifera*), aspen (*Populus* spp.) and a mixed conifer understorey (14–18 m^2 basal area/ha). Both field sites were clear-cut in the winter of 1991–92. Slash was piled and burned.

EXPERIMENTAL DESIGN

Trees were planted as seedlings in spring of 1992 and replanted in spring of 1993 as necessary to replace dead individuals. Seedlings of each species (*L. laricina*, *P. strobus* and *P. mariana*) were planted in monoculture and in two-species mixtures with the other species at four densities (1, 4, 16 and 64 trees m^{-2}). Seedlings were planted in a 12 by 12 grid, with 144 trees per plot, and variable plot size depending on the initial tree spacing. Mixtures were planted by alternating rows of each species so that each individual had two immediate neighbours of each species. Three replicates of each plot mixture (three monocultures and three pair-wise mixtures) were established at each of the four densities for a total of 72 plots or 10 368 trees. Two of the three replicates were established at the East site, and one at the West site. In the 2 years following planting, grasses and herbaceous or other woody vegetation were controlled primarily by hand removal, or with directed herbicide use for specific weed problems.

Varying tree spacing allows us to explicitly test density effects on species interactions. A replacement series design, which traditionally uses a constant total plot density, cannot separate these factors (Firbank & Watkinson 1985; Connolly 1986). Keeping the proportion of each species in mixture constant (50%) means we are testing changes in the spacing but not the composition of the competitive neighbourhood across densities. Patterns would likely change in mixtures with very different species proportions.

VARIABLES MEASURED

Survival, height and stem diameter at 5 cm above soil surface were recorded for all trees in the fall of 1993, 1994, 1995, 1997 and 2002, or 2, 3, 4, 6 and 11 years (growing seasons) after planting. The outside two rows of trees in each plot were excluded to control for edge effects. Stem volume index (SVI), a measure of tree biomass (Wagner *et al.* 1999) was calculated as height × diameter^2. We calculated SVI for individual trees at each measurement. RGR for height and diameter growth were calculated for time intervals between all measurements after Hunt (1982) as:

$$\mathrm{RGR} = \frac{(\ln W_2 - \ln W_1)}{(t_2 - t_1)}$$

where W_2 and W_1 are measurements of either tree height or diameter at different ages (t_2 and t_1). For each measurement period, plot mean survival and RGR were calculated separately for each species within a plot because we did not track the growth or survival of individuals over consecutive measurement periods.

STATISTICAL ANALYSES

Patterns in growth rates were analysed by examining the relationships of RGR to tree size over time for each species in monoculture, using plot mean RGR and initial tree size from every measurement interval. RGR is often strongly correlated with tree size, which means RGR needs to be compared among species over time on an equivalent size basis (Walters *et al.* 1993b). We analysed height and diameter RGR relationships separately using an analysis of covariance design (ANCOVA) in SAS. The covariates of initial tree height or diameter were log-transformed to meet assumptions of normality and homogeneity of variances, and *species* and *density* were included as categorical predictor variables.

Individual tree heights, diameters, and volumes (SVI) were analysed across all measurement years using repeated measures ANCOVA. Plot was the repeated measure and we used an unstructured covariance structure. Categorical predictor variables were species, plot composition (mixture), and density. The response variables were log-transformed. The repeated measures analysis revealed that density and mixture only had significant effects on tree size in 2002, so we did a *post hoc* ANCOVA analysis of height and diameter in 2002, using the natural log of density (seedlings m^{-2}) as the continuous predictor variable, and including a random effect of plot.

We used standard regression techniques to look at relationships of interest from the ANCOVA models. Plot mean SVI over time was compared for the three monocultures and three mixed stands in order to test for over-yielding effects. Intra-specific vs. inter-specific effects on tree performance were assessed by comparing 2002 heights and diameters of species in monoculture vs. the two mixed stands at different density levels. This comparison estimates the competitive effect of different species or their ability to suppress the growth of neighbouring trees (*sensu* Goldberg & Landa; 1991). We used absolute rather than relative height and diameter growth as our response variables because we were interested in comparisons within rather than between species, and therefore did not need to adjust for initial size differences across species.

We plotted species heights and diameters for each of the three pair-wise mixed stands as a function of either time (years since planting) or density. Both the predictor and response variables were log-transformed, as in the original ANCOVA analysis, which adequately linearized the species response curves. Residuals did not significantly violate assumptions of normality or homogeneity of variances, and lack-of-fit tests were used to confirm the appropriateness of linear regression techniques. For species pairs that had heterogeneous slopes, we additionally calculated the crossover point (CP), or the value of the *x*-axis where the response curves of the two species intersected, using a method advocated by Sack and Grubb (2001) to look at rank reversals in seedling growth across light gradients:

$$\mathrm{CP} = e^{-(b_A - b_B)/(m_A - m_B)} - 1$$

b and *m* are intercept and slope parameters for the response curves of groups *A* and *B*. The advantage of this technique over traditional correlation analyses is that it provides an estimate of the age or density-level at which the crossover is expected to occur, and this value can be compared across treatments (Sack & Grubb 2001; Kitajima & Bolker 2003). We calculated confidence intervals for the CP using the Johnson-Neyman technique (Johnson & Neyman 1936; White 2003; program was written and provided by Craig White). This is a simple extension of an ANCOVA analysis that compares two groups once the assumption of homogeneity of slopes has been violated. It has been successfully applied to the analysis of crossovers (Huitema 1980; White 2003). The 95% confidence interval on the CP represents the range of values of the independent variable for which there is no statistically significant difference in the two groups being compared (see White 2003 for statistical details).

Table 2. *Larix laricina* seedlings had the most height and diameter growth 1 year after planting. *Pinus strobus* had a distinctly different morphology than the other two species. Means and standard errors were calculated from 1993 measurements, using all density and mixture treatments combined

	Height (cm)		Diameter (cm)		SVI (cm^3)	
Species	Mean	SE	Mean	SE	Mean	SE
Larix laricina	46.44	1.39	0.61	0.01	22.87	1.96
Pinus strobus	24.48	1.02	0.56	0.02	12.82	1.45
Picea mariana	35.84	0.99	0.45	0.01	9.64	0.88

Results

GROWTH PATTERNS IN MONOCULTURE

Larix laricina had higher growth rates and much larger seedling sizes 2 years after planting than the two evergreen conifers (Table 2). Given its greater demand for light, smaller seed mass and high light RGR (Table 1), this was expected. *Pinus strobus* and *P. mariana* had similar volumes, but very different morphologies: *P. strobus* seedlings had larger diameters, but were shorter than *P. mariana*. Species RGRs declined at different rates as seedlings grew larger (Fig. 1). *Larix laricina*'s height and diameter RGR declined more rapidly than the other species at all but the highest density (Fig. 1 & Table 3). As a consequence, species height RGRs converged as they grew larger (Fig. 1b). *Pinus strobus* and *L. laricina* actually reversed their diameter RGR rankings over time: *L. laricina* had a higher diameter RGR as seedlings, whereas *P. strobus* had a higher diameter RGR as larger saplings

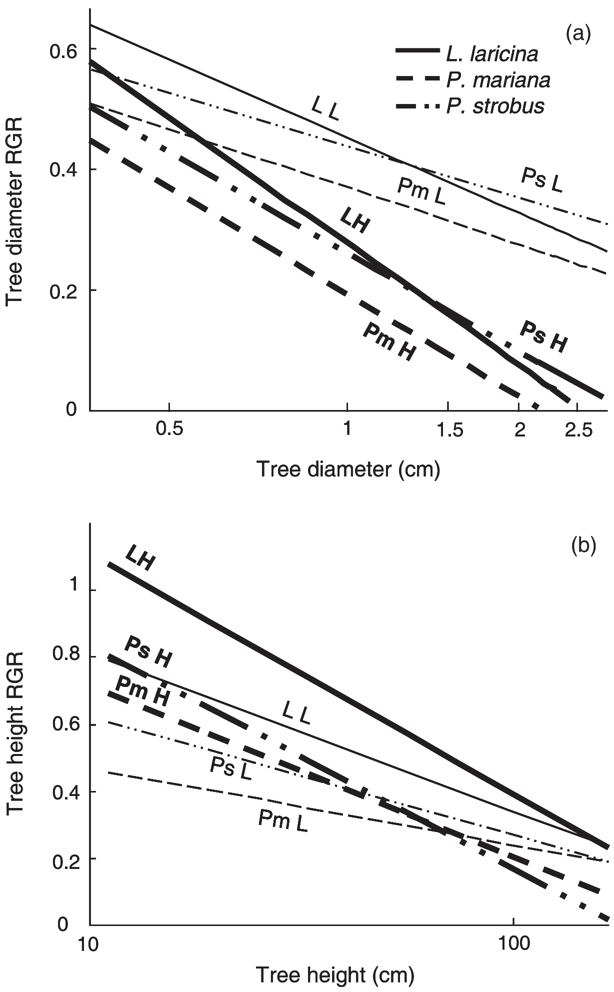

Fig. 1. The relationship of relative growth rates (RGR) of diameter (a) or height (b) to tree size for *Larix laricina*, *Pinus strobus*, and *Picea mariana* grown for 10 years at two densities. Lines are the best-fit relationships of RGRs measured in 1993, 1994, 1995, 1997 and 2002 for trees grown in monoculture. Relationships are shown separately for trees in high density (H, **bold** lines; 64 seedlings m^{-2}) or low density (L, normal lines; 1 seedling m^{-2}) plots. Intermediate densities of 4 and 16 trees m^{-2} (not shown) had intermediate responses. The x-axis is plotted in a log scale for ease of translation. Statistical significance of treatment effects are shown in Table 3.

(Fig. 1a). Higher tree densities accelerated ontogenetic declines in growth rates, leading to several reversals in density effects over time (Fig. 1). Crowding generally stimulated height growth of seedlings and suppressed height growth of saplings (Fig. 1b). All trees had faster diameter growth at low density, and difference in growth rates between high and low density increased significantly as trees grew larger (Fig. 1a).

GROWTH PATTERNS IN MIXTURE OVER TIME

Coexisting species often had very different size distributions and ranks as 11-year-old saplings than as 2-year-old seedlings (Fig. 2 and Table 4), reflecting the changes in growth rates with ontogeny and density. *Larix laricina* maintained or increased its diameter and height advantage over time when competing with *P. mariana* or *P. strobus* in dense plots. In less dense plots, the evergreen conifers caught up to or maintained their sizes relative to *L. laricina* (Fig. 2 and Table 4). *Pinus strobus* swapped height rank with *P. mariana* over time, and it occurred nearly 6 years sooner in low-density plots than in high-density plots (species had converged by the end of the study at high density but the CPI is estimated to be outside the 11-year range of observations (Fig. 2f)).

Table 3. Comparison of species growth and size differences (from regressions in Figs 1,2). Intercepts test the species effect and slopes test the size × species interaction (see Fig. 1), or the time × species interaction (see Fig. 2); *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Species are *Larix laricina*, *Picea mariana* and *Pinus strobus*

	High density		Low density	
	Intercept	Slope	Intercept	Slope
Monoculture (Fig. 1) Diameter RGR vs. Log Diameter				
L. laricina/*P. mariana*	**	**	Ns	Ns
L. laricina/*P. strobus*	**	**	Ns	Ns
P. mariana/*P. strobus*	Ns	**	Ns	Ns
Height RGR vs. Log Height				
L. laricina/*P. mariana*	**	*	**	**
L. laricina/*P. strobus*	Ns	**	*	**
P. mariana/*P. strobus*	Ns	Ns	Ns	Ns
Mixture (Fig. 2) Ln Diameter vs. Ln Time				
L. laricina/*P. mariana*	**	***	Ns	Ns
L. laricina/*P. strobus*	***	Ns	Ns	Ns
P. mariana/*P. strobus*	Ns	Ns	**	Ns
Ln Height vs. Ln Time				
L. laricina/*P. mariana*	***	***	Ns	**
L. laricina/*P. strobus*	***	Ns	***	Ns
P. mariana/*P. strobus*	***	***	***	***

Observed changes in average tree sizes over time were not caused by differences in mortality or changes in plot density across treatments. Although mortality rates over the entire study period were lower in plots with 1 and 4 trees m^{-2} (38 ± 14%) than in plots with 16 and 64 trees m^{-2} (64 ± 17%), mortality was similar across species and for different plot mixtures (species and mixture were insignificant at all density levels in an ANOVA ($P > 0.3$)). In 2002, the average density of live trees across the four planting treatments was 0.6, 2.6, 6.0 and 22.5 trees m^{-2}, so despite considerable mortality, the density gradient was preserved throughout the study and results did not depend on whether initial or final tree density was used in analyses.

GROWTH PATTERNS IN MIXTURE OVER SPACE

After 11 years, strong effects of density on stand development and growth were evident (Fig. 3 and Table 4). *Pinus strobus* showed the greatest sensitivity to crowding, rapidly decreasing in size with increasing density. It had larger diameters and heights than *P. mariana* at low but not high density (Fig. 3e,f andTable 4), and actually reversed diameter rank with *L. laricina* across the density gradient (at a density of 4.4 trees m^{-2};

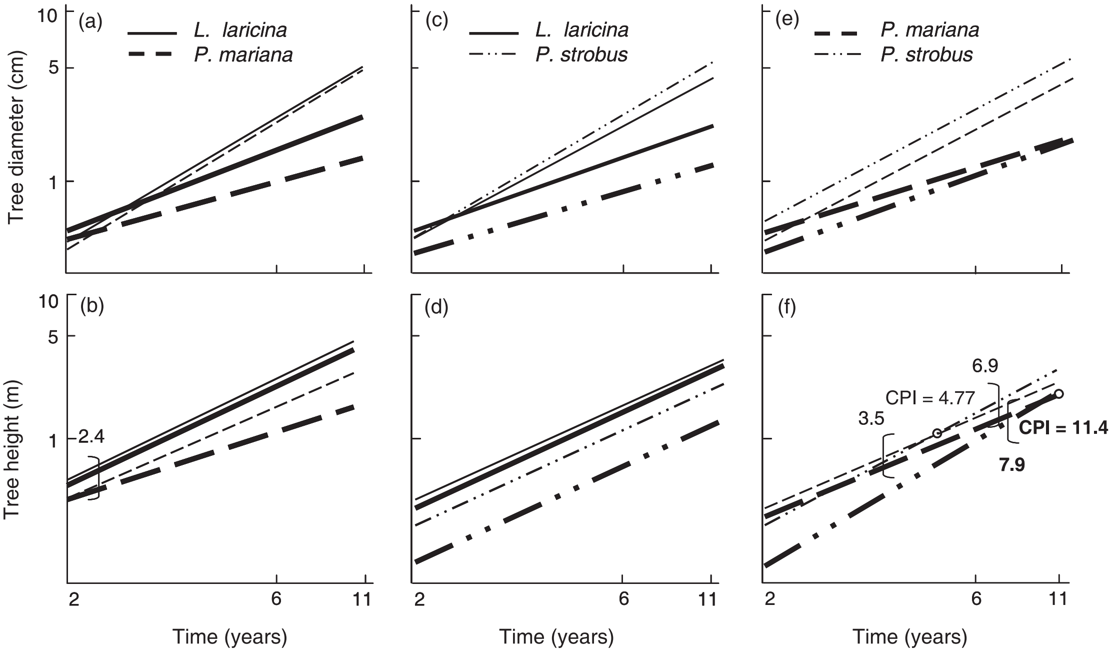

Fig. 2. Change in tree diameters (upper figures) and heights (lower figures) over time for tree seedlings planted in mixtures of *Larix laricina*/*P. mariana* (a, b), *L. laricina*/*P. strobus* (c, d), and *P. mariana*/*P. strobus* (e, f). Species performance diverged and converged (leading to rank reversal) over time. Lines are best-fit relationships from a mixed model analysis plotted on a log scale. Relationships are shown within each mixture for trees in high density (**bold** lines; 64 seedlings m^{-2}) or low density (normal lines; 1 seedling m^{-2}) plots. Statistical significance of treatment effects are given in Table 3 and regression fits are given in Table 4. Crossover point estimates (CPIs) are marked (°) and associated values for the independent variable are shown. 95% upper and/or lower confidence intervals on the crossover point (CPI) are denoted with brackets. There is no evidence of a crossover if both confidence intervals do not fall within the range of our observations (2–11 years).

Table 4. Goodness of fit for regressions comparing species sizes in mixed stands over time (Fig. 2) and across density levels (Fig. 3). Statistics from Fig. 2 are shown first for high density plots (**bold**) and then for low density plots. Large *P*-values in a lack of fit test support the use of a linear regression (*$P < 0.05$, **$P < 0.01$). Species are *Larix laricina*, *Picea mariana* and *Pinus strobus*

	Model fit			Lack of fit	
Model description	R^2	*F*	*P*	*F* ratio	*P*
Ln Diameter vs. Ln Time (Fig. 2)					
L. laricina/*P. mariana*	**0.72**/0.71	**289.9**/268.4	**	**0.74**/1.02	**0.62**/0.44
L. laricina/*P. strobus*	**0.70**/0.70	**261.1**/273.0	**	**0.18**/1.35	**0.97**/0.27
P. mariana/*P. strobus*	**0.71**/0.75	**251.8**/354.6	**	**0.24**/0.77	**0.95**/0.93
Ln Height vs. Ln Time (Fig. 2)					
L. laricina/*P. mariana*	**0.82**/0.70	**527.1**/264.0	**	**0.65**/3.16	**0.68**/0.07
L. laricina/*P. strobus*	**0.83**/0.73	**515.6**/319.7	**	**0.53**/2.49	**0.77**/0.06
P. mariana/*P. strobus*	**0.87**/0.76	**678.5**/375.5	**	**0.49**/2.73	**0.81**/0.09
Ln Diameter vs. Ln Density (Fig. 3)					
L. laricina/*P. mariana*	0.52	91.9	**	0.896	0.48
L. laricina/*P. strobes*	0.47	73.4	**	2.56	0.07
P. mariana/*P. strobes*	0.50	79.5	**	0.198	0.93
Ln Height vs. Ln Density (Fig. 3)					
L. laricina/*P. mariana*	0.52	92.3	**	0.26	0.89
L. laricina/*P. strobes*	0.43	61.8	**	2.46	0.08
P. mariana/*P. strobes*	0.46	72.1	*	0.43	0.78

[Fig. 3c]). Conversely, crowded conditions favoured *L. laricina*: it had increasing size dominance over the other trees with increased density (Fig. 3a–d). These growth differences led to highly stratified canopies in high-density mixed stands of shade-intolerant and more tolerant trees (Fig. 4). We define stratification to mean the significant differentiation of tree heights among two species (*sensu* Oliver & Larson 1996). The mode of species height distributions diverged and height variation increased with density as *L. laricina* dominated the upper canopy and *P. mariana* or *P. strobus* were restricted to intermediate or suppressed positions. Mixed stands of *L. laricina* and *P. mariana* were highly stratified (had significantly higher

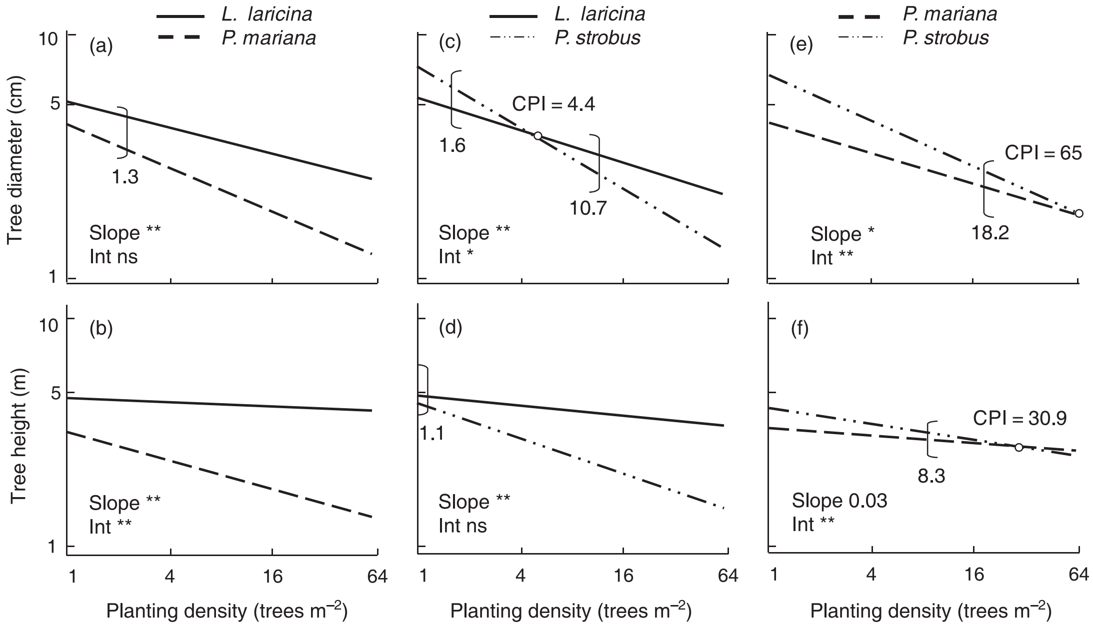

Fig. 3. Response of diameters (upper figures) and heights (lower figures) to planting density for 11-year-old mixtures of *Larix laricina*/*P. mariana* (a, b), *L. laricina*/*P. strobus* (c, d), and *P. mariana*/*P. strobus* (e, f). Species performance showed patterns of divergence and convergence (leading to rank reversal) across a density gradient. Lines are the best-fit relationships from a regression analysis plotted on a log scale. Statistical significance of treatment effects are shown (intercept differences test the species effect, slope differences test the time × species interaction; $^{*}P < 0.01$, $^{**}P < 0.001$). Regression fits are in shown in Table 4. Crossover point estimates (CPIs) are marked (°) and associated values for the independent variable are shown. 95% upper and/or lower confidence intervals on the crossover point (CPI) are denoted with brackets. There is no evidence of a crossover if the confidence intervals do not fall within the range of our observations (1–64 trees m^{-2}).

variance) at high density, but their individual size distributions varied little across the density gradient (height variation within species stayed the same (Fig. 4a,b)). *Larix laricina* and *P. strobus* also had increasing height differentiation at high density and variation within *P. strobus* also increased significantly (Fig. 4c,d). Mixed stands of *P. strobus* and *P. mariana* had slightly more stratification at low density than high density, which is consistent with our observation that *P. strobus* grew taller when less crowded (Fig. 4e,f). Although the percent coefficient of variation for the stand remained constant with increased crowding, the population variance (compared with an *F*-test of variances) for all trees and for *P. mariana* declined at high density.

SPECIES INTERACTIONS IN MIXTURES VS. MONOCULTURES

The different species responses to density influenced the strength of inter-specific vs. intra-specific interactions, or competitive effects, and the overall growth of mixed stands vs. monocultures. Crowded conditions favoured *L. laricina* and open stands favoured *P. strobus*, so *P. strobus* usually had a larger competitive effect than conspecifics at low density, while *L. laricina* had larger competitive effects than conspecifics at high density (Fig. 5).

Pinus strobus trees grew slightly faster with intra-specific than with inter-specific neighbours at all density levels (Fig. 5c,d). As a result, mixed stands containing *P. strobus* showed no evidence of over-yielding; they had intermediate performance compared to monocultures (in terms of average tree volume; [Fig. 6b,c]).

Picea mariana was unaffected by neighbour identity at low densities, but actually grew less in monoculture than in stands with larger, heterospecific neighbours at intermediate densities (Fig. 5a,b). *Larix laricina* had greater heights in monoculture than in mixed stands at the lowest density, but was otherwise suppressed more by intra-specific than inter-specific competition (Fig. 5e,f). The underperformance of *L. laricina* monoculture at high density may in part explain the slightly higher productivity (in terms of total stand volume growth) of *L. laricina* and *P. mariana* in mixture relative to either species in monoculture by year 10 (Fig. 6a). We observed no other instances of over-yielding; at all densities and time periods, mixed stands had lower average tree volumes than monocultures of the most productive species (only one density level shown (Fig. 6)).

Discussion

Variation in shade-tolerance among juvenile trees influences early growth and species interactions and a number of models of forest succession are based on simple concepts of shade-tolerance (see review in McCook 1994). There is growing recognition that the seedling traits controlling light capture and photosynthetic capacity change with ontogeny, contributing to reversals over time in the size and growth ranks of coexisting species of contrasting shade-tolerance (Walters *et al.* 1993a;

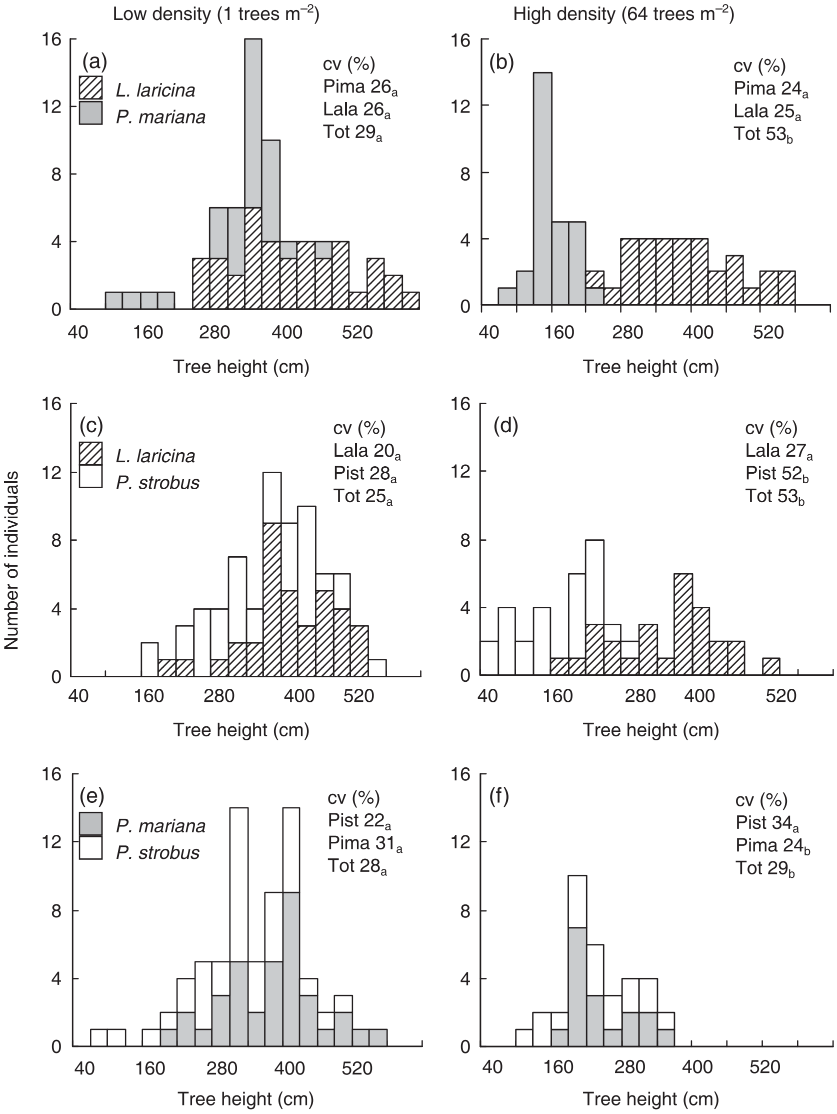

Fig. 4. Height distributions for trees grown for 10 years in mixtures of *Larix laricina*/*P. mariana* (a, b), *L. laricina*/*P. strobus* (c, d), and *P. mariana*/*P. strobus* (e, f). Size distributions are plotted separately for trees planted at low density (1 seedling m^{-2}; left-hand panels), and high density (64 seedlings m^{-2}; right-hand panels). The coefficient of variation is shown for each species separately and for the entire plot. Significant differences in population variance between low and high density plots are shown with different letters (compared with an *F*-test at the $P < 0.05$ level).

Lusk 2004; Niinemets 2006). Additionally, spatial heterogeneity in resource availability can drive rank reversals in growth rates across environmental gradients (Givnish 1988; Sack & Grubb 2001; Baraloto *et al*. 2005). Ontogenetic variation in carbon gain across environmental gradients is not well-understood because long-term experimental studies of tree establishment are rare. By evaluating growth pattern of species mixtures at multiple densities over 10 years, we show that differences in rates of development (as measured by RGR) between light-demanding and shade-tolerant species do affect growth hierarchies and species establishment over time. Furthermore, changes in density amplified or minimized these ontogenetic trends by altering the competitive balance between species and the likelihood of resource pre-emption.

GROWTH RATES IN MONOCULTURE

Early on, shade-intolerant trees have a higher leaf area ratio than shade-tolerant trees, lower leaf mass per unit leaf area and higher rates of carbon assimilation per unit leaf area, all leading to higher seedling RGRs (Lambers & Poorter 1992; Walters *et al*. 1993a,b, Reich *et al*. 1998a; Walters & Reich 1999; Lusk 2004; Niinemets 2006). These established relationships were largely supported by early size and RGR patterns in the current study. *Larix laricina* had higher growth rates and much larger second-year seedling sizes than the two evergreen conifers, as expected. *Larix* is relatively shade intolerant and has a small seed mass and short leaf life span which correlate with higher photosynthetic rates, specific leaf area and relative canopy size per plant mass (Table 1; Reich *et al*. 1998a). *Larix laricina*'s strategy of rapid over-topping through greater allocation to height growth is typical of early successional species adapted to high-resource environments (Cannell *et al*. 1984; Wagner *et al*. 1999). *Pinus strobus* had markedly different allocation patterns, putting proportionately more energy into early diameter growth. *Pinus strobus* is a larger-seeded tree with much lower high-light RGR than the other two species (Table 1). It has also been shown to have slow height growth

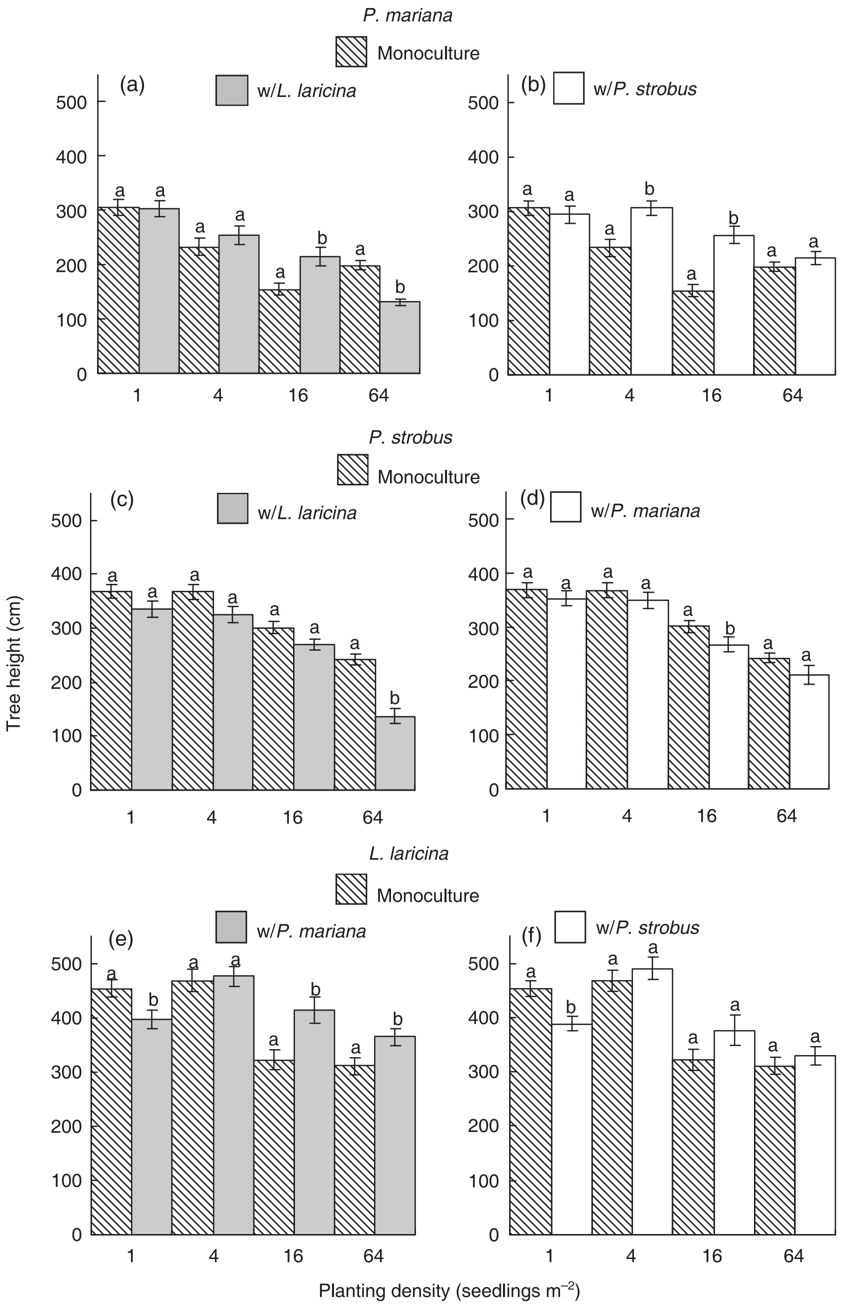

Fig. 5. Average tree height for *Picea mariana* (a, b), *Pinus strobus* (c, d), and *Larix laricina* (e, f) grown for 11 years in monoculture and mixtures at planting densities of 1, 4, 16, and 64 trees m^{-2}. Data show evidence of both inter-specific and intra-specific competition. Within each density level, plot means that are significantly different from one another at the $P < 0.05$ level are shown with different letters. Significant effects from the overall ANCOVA model of 2002 tree height are as follows: (species (SPP): $F_{2,1147} = 178^{**}$; density (DEN): $F_{3,1147} = 105^{**}$; mixture (MIX): $F_{5,1147} = 14.6^{**}$; SPP × DEN: $F_{6,1147} = 13.6^{**}$; MIX × DEN: $F_{15,1147} = 6.5^{**}$; SPP × MIX: $F_{1,1147} = 4.3^{*}$; $^{*}P < 0.01$, $^{**}P < 0.0001$).

relative to other boreal species in the first 8–10 years of establishment (Wagner *et al.* 1999), but is capable of eventually achieving greater volumes and heights than other species in the absence of strong resource competition (Firbank & Watkinson 1985; Küppers 1989; Garber & Maguire 2004). *Picea mariana* has a mix of traits associated with both early- and late-successional species such as high early height growth (associated with high-light RGR and small seed mass; Table 1) but smaller volume growth overall. These early species differences in growth and morphology across density gradients largely fit our expectations based on shade-tolerance rankings, but they changed considerably as seedlings grew larger.

GROWTH PATTERNS OVER TIME

The relationship of shade-tolerance to growth needs to be studied in the context of ontogenetic patterns, because tree morphology and growth depend on tree age and size (Reich 1998; Sack & Grubb 2001; Lusk 2004; Baraloto *et al.* 2005; Niinemets 2006). Declining leaf area ratios and increasing leaf mass per unit of leaf area contribute to reductions in RGR with increasing tree size. These ontogenetic changes in photosynthetic capacity and growth seem to progress more rapidly in shade-intolerant species over the weeks (Walters *et al.* 1993a; Tjoelker *et al.* 1998), months (Lusk 2004) and years (Garber & Maguire 2004; Niinemets 2006) following

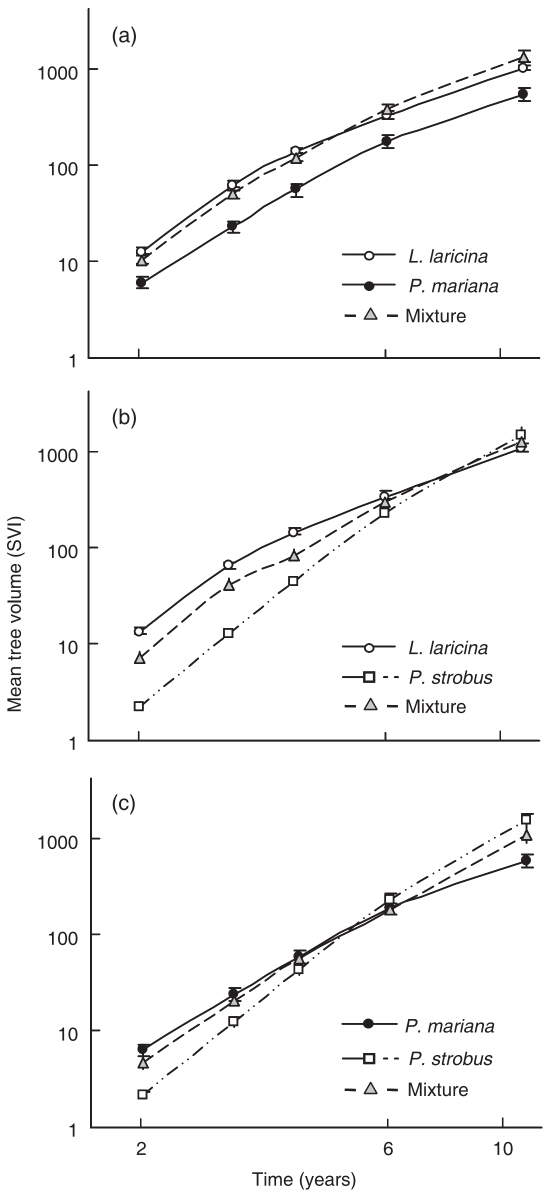

Fig. 6. Tests of over-yielding in species mixtures vs. monocultures over time, based on tree volumes. Average tree volumes are plotted for high density plots (64 seedlings m^{-2}), with standard error bars. Only stands of *L. laricina* and *P. mariana* had slightly, but insignificantly, larger tree volumes in mixtures that pure stands after 10 years of growth.

emergence. Explanations for this trend include the smaller seed size (Table 1) and lower initial plant mass of shade-intolerants (Sack & Grubb 2001; Niinemets 2006), and the longer leaf life spans of shade-tolerant species, which lead to lower rates of carbon loss due to leaf turnover and more gradual accumulation of a full canopy with multiple leaf cohorts (Reich 1998; Lusk 2002). These changes should be even more pronounced when comparing deciduous and evergreen species with large differences in needle retention, as we have done in this study (Table 1). The consequence is that shade-tolerant trees can gradually achieve higher leaf area ratios and thereby presumed higher photosynthetic capacity than their light-demanding neighbours (Sack & Grubb 2001; Lusk 2002; Niinemets 2006). Although we did not directly measure ecophysiological processes, our data support these trends. *Larix laricina* had more rapid reductions in RGR, leading to convergence or even reversals in species growth and size ranks between the seedling and sapling life stages, but only at higher planting densities.

DENSITY EFFECTS ON GROWTH PATTERNS AND SPECIES RANKS

Rank reversals in species performance across spatially or temporal heterogeneous landscapes are theoretically important for structuring communities, maintaining diversity and determining the course of succession (Grime 1979; Tilman 1982; Chesson 1985; Givnish 1988; Suding & Goldberg 2001). Species growth ranks can change with ontogeny (Lusk 2004; Baraloto *et al.* 2005) or in different microenvironments (Sack & Grubb 2001; Baraloto *et al.* 2005; Niinemets 2006), but interactions between ontogeny and the environment are not well-understood. We observed strong interactive effects of neighbour density and ontogeny on species growth patterns over time, particularly in mixed stands that included *L. laricina*. When neighbour competition was less intense and resources were more abundant, ontogenetic trends in growth seemed to have greater influence on growth patterns (Welden & Slauson 1986), allowing shade-tolerant conifers to maintain their relative canopy position or even reverse rank with *L. laricina* over time (due to higher RGR) in low density plots. In more competitive, dense environments early size and height RGR differences between *L. laricina* and the more shade-tolerant species were either maintained or increased over time. Greater size variation in these dense plots indicated that size-asymmetric competition and growth drove these temporal trends; larger *L. laricina* individuals used a disproportionate share of light resources, further suppressing the growth of smaller neighbours (Weiner & Thomas 1986; Weiner 1990; Hara & Wyszomirski 1994; Schwinning & Weiner 1998). Rapid overtopping of slower-growing species and light pre-emption is typical of early successional, shade-intolerant species like *L. laricina* and is particularly advantageous in high-density stands (Cannell *et al.* 1984; Wagner *et al.* 1999). Our uniform planting design and large density gradient minimized the chance that size variation at high density was due to aggregated spatial patterns or other factors (Miller & Weiner 1989; Bonan 1991; Weiner *et al.* 2001).

SPECIES INTERACTIONS IN MIXTURES VS. MONOCULTURES

Mixed species stands have a number of potential advantages over single species stands, including diversity of structure and associated flora and fauna and resistance to disturbance, insects and disease (Kelty 1992, 2006). Whether diverse stands also have greater overall productivity than monocultures is a long debated question, but one which is central to explaining patterns of species coexistence (Tilman 1982; Chesson 1985).

The 'competitive production principle' suggests that reduced competition due to niche partitioning can lead to higher productivity in mixed stands relative to monocultures (Vandermeer 1989), which is consistent with evidence for positive productivity-diversity relations in grasslands (Tilman *et al.* 2001) and in mixed tree stands (Bergqvist 1999; Kelty 2006; Potvin & Gotelli 2008). However, *P. strobus* is neither highly shade-tolerant nor a fast-growing pioneer, which makes competitive reduction or niche separation unlikely in mixed stands containing *P. strobus.* Indeed, inter-specific competition suppressed the height growth of *P. strobus* more than intra-specific competition. As a result, mixed stands containing *P. strobus* always had growth that was intermediate compared to pure stands, although the identity of the highest yielding species changed over time as *P. strobus* reversed rank with both *P. mariana* and *L. laricina* by year 10.

The only indication of over-yielding in this study was in mixed stands of *L. laricina* and *P. mariana*, which is consistent with the notion of positive species interactions for species differing markedly in shade tolerance (allowing for example, separation of canopy layers; Kelty 2006). *Larix laricina* grew poorly in monoculture, most likely due to intensified light competition, yet *P. mariana* showed little response or even benefited from the presence of *L. laricina*. This supports the idea that competition may be reduced in species mixtures, and is consistent with other studies which suggest that stratified forests with a shade-intolerant species overtopping a shade-tolerant species are most likely to show over-yielding due to niche partitioning. The shade-tolerant species in the understorey may be able to exploit light resources that would not otherwise support growth of a less tolerant tree, resulting in improved stand level resource uptake and resource use in mixed stands (Vandermeer 1989; Kelty 1992; Lusk & Ortega 2003; Garber & Maguire 2004; *review in* Pretzsch 2005). It is also possible that the taller species facilitated early growth of *P. mariana* seedlings, since shading from canopy vegetation or shrubs can ameliorate growing conditions for shade-tolerant regeneration (Berkowitz *et al.* 1995). Experimental work is needed to understand the mechanisms that could possibly be driving these interactions. Higher growth of *L. laricina* and *P. mariana* in mixed stands was insignificant and only became apparent 10 years after planting; we don't know if greater over-yielding might occur in the future with continued stand development and canopy stratification.

Summary

Tree growth during early stages of forest development is the result of complex interactions between inherent plant traits and environmental controls. Traditional models of asymmetric competition, resource pre-emption or shade-tolerance, which are largely based on short-term studies of juvenile tree growth or experiments in plant monocultures, may fail to predict the range of potential trajectories for mixed-species stands. This study extends previous efforts to identify the causes of rank reversals in communities and highlights the importance of temporal changes beyond the early years of seedling establishment. Our data suggest that mixtures of juvenile trees with contrasting shade-tolerance appear to have two opposing developmental patterns: size asymmetric growth and competition which generally increase the size advantages of shade-intolerants over time, and ontogenetic growth trends, which generally decrease the size advantages of shade-intolerants over time and can lead to rank reversals. Spatial variation in density, or the degree of resource competition between neighbouring trees, predictably determined which of these opposing processes shaped early establishment and growth patterns. Variation in vertical and horizontal structure that results from early competitive dynamics will impact future growth, mortality and regeneration, potentially changing the successional trajectory or character of the mature forest. Even longer experimental studies on a range of tree species are needed to separate interactive effects of shade-tolerance, density and ontogeny throughout the full span of forest development.

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