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Aboveground growth interactions of paired conifer seedlings in close proximity

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Abstract Where belowground resources are relatively abundant, naturally established trees sometimes occur in very close proximity to one another. We conducted a two-year study to assess the aboveground interactions between Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*) and noble fir (*Abies procera*) seedlings planted in closely spaced (stems 10 cm apart) conspecific and heterospecific pairs. Paired seedling growth also was compared to seedlings planted with no neighbor. Stem height growth was not affected by the presence of a neighbor seedling, although diameter growth was slightly reduced. Branch diameter growth and weight were reduced where seedling crowns overlapped; branch morphological data suggested that this was caused by shading rather than mechanical interactions. Light measurements showed the potential for significant shading, particularly by the relatively large, dense crowns of Douglas-fir. Heterospecific pairs including Douglas-fir demonstrated the competitive production principle in that their mean growth was greater than the average of conspecific pairs of both species. Neighbor seedling height significantly affected subject seedling growth; neighbor effects were similar whether the neighbor seedling was growing on the north or south side of the subject seedling. Light reflected from Douglas-fir crowns had a lower red: far-red ratio than that of noble fir, although there was no evidence of a phytochrome-mediated growth response to the neighbor seedling. While heterospecific seedling pairs showed reduced competition, we found no evidence of facilitation for seedlings growing in very close proximity.

Keywords Seedling · Competition · Facilitation · Light · *Pseudotsuga menziesii* · *Abies grandis* · *Abies procera*

Introduction

The spacing of naturally established plants may be influenced by below- or aboveground competition. Where a belowground resource limits plant establishment, plants competing

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for that resource cannot survive in close proximity to one another and a regular dispersion pattern may result (Phillips and MacMahon 1981; Casper and Jackson 1997). In most forests, aboveground competition, specifically competition for sunlight, limits the establishment and survival of trees. However, in some forest types, two or more mature trees of the same or different species commonly grow in very close proximity to one another, with stems contacting or nearly so. At maturity, possible advantages of such a close spatial association include increased sway dampening and wind-firmness (Milne 1991; Wilson and Oliver 2000). At the seedling stage, possible advantages of close proximity include protection from herbivory and a temporarily increased rate of height growth resulting from the phytochrome-mediated shade-avoidance response (Holmes and Smith 1975; Ritchie 1997; Smith and Whitelam 1997). A disadvantage of growing in very close proximity is a potentially high level of resource-mediated competition for light and growing space (Stoll and Weiner 2000).

Trees growing in close proximity are known to interact in ways that alter crown morphology. Shading from an adjacent tree may substantially alter lateral crown growth, depending on a species' degree of shade tolerance (Larson and Oliver 1996). The response of a shade-intolerant species to partial crown shading includes both decreased growth of shaded limbs and increased growth of unshaded limbs (Stoll and Schmid 1998). The latter can result from an increase in number of buds on those limbs, or in some species, from indeterminate growth or multiple growth flushes (Sprugel et al. 1991). In herbaceous plants and young trees, a variety of studies have supported the hypothesis that the shade-avoidance response is a reaction to the ratio of red: far-red light reflected from neighboring vegetation (Smith and Whitelam 1997; Aphalo et al. 1999). Therefore, the species composition and proximity of neighboring vegetation may influence the spectrum of light received by a tree seedling and thus affect its morphology (Billings and Morris 1951; Ritchie 1997; Aphalo et al. 1999).

Modified crown morphology also can result from physical interaction between two or more trees, although the mechanism of crown modification differs according to the species of the subject tree and that of the neighboring tree (Franco 1986; Larson and Oliver 1996). In some conifer species (e.g., lodgepole pine (*Pinus contorta*)), branches stop growing or assume a new direction of growth when they contact another tree (Franco 1986). In other species, including Japanese larch (*Larix kaempferi*), branch growth is limited by physical abrasion of branch tips; when the tips die, growth from the branch's lateral buds, rather than the terminal bud, is favored (Franco 1986; Jones and Harper 1987a, b). While light-related effects on crown growth have been reported primarily for seedlings and saplings (Ritchie 1997; Aphalo et al. 1999), physical interactions have rarely been studied in young trees (Franco 1986 is an exception) but are well-known for mature trees (Larson and Oliver 1996).

A number of studies have examined density effects on the mechanisms of competition in young conifer plantations, some with spacings as close as 17 cm (e.g., Cole and Newton 1987; Shainsky and Radosevich 1992; Zutter et al. 1997; Woodruff et al. 2002). However, there is little documentation of the interactions between individual pairs of young trees growing in very close proximity (Jones and Harper 1987a, b studied *Betula pendula* sapling trios) despite the fact that this spatial arrangement often occurs naturally where multiple seeds germinate in the same microsite. It also is unclear how closely paired seedlings of different species interact, given the potential for asymmetric competition where growth rates differ. Competitive interactions between paired seedlings are likely tempered by microenvironment, including soil nutrient and water availability and ambient near-ground carbon dioxide concentration, which changes as the seedlings increase in size.

Our objective was to evaluate the aboveground interactions between seedlings of three native Pacific Northwest conifer species growing in closely planted pairs. In most previous studies of high-density seedling or sapling competition, the competition for belowground resources was key in understanding seedling interactions. Because we were interested in aboveground interactions at the seedling level, we chose to supplement belowground resources so that soil water and nutrients would not be growth-limiting. Given these conditions, we made the following hypotheses:

H_1 Assuming no belowground competition, the facilitative effect of a neighbor's presence increases stem growth rate, owing to the spectrum of light reflected by the neighbor.

H_2 Aboveground resource limitation (i.e., growing space or access to sunlight) results in a crown morphologic response to the presence of a neighbor seedling that differs according to neighbor species.

H_3 Responses of seedlings to neighbor competition vary according to the species and size of the neighbor.

H_4 The influence of a neighbor seedling on growth and morphology is greater when the neighbor is to the south, rather than to the north, owing to a greater influence of the neighbor on the light environment.

Methods

Study site

The two-year study was located in 10 raised beds at the Forestry Sciences Laboratory in Olympia, Washington (46.95° N; 122.96 W). The climate is mild with mean January and July temperatures of 3.3 and 17.4°C, respectively. Annual precipitation averages 1,289 mm. Each raised bed was 4.9 m long by 1.2 m wide and 0.6 m high. Beds were oriented west-east and were located in a row running north–south. All beds received full sunlight during most of the day (approximately 9:00 to 18:00 Pacific Standard Time) in summer months. Beds were filled with commercially produced, screened topsoil amended with compost prior to acquisition. A soil fertility assessment using Plant Root Simulator probes (Western Ag Innovations Inc., Saskatoon, Canada) indicated that the soil had very high available N and sufficient P and K. During the first growing season (2007), weeds were controlled by hand pulling. On 25 April 2008, the following broadcast treatment was applied to the beds with a backpack sprayer equipped with a hooded nozzle to reduce spray drift: 1% solution of Accord® Concentrate (glyphosate; Dow AgroSciences, Indianapolis, IN), 0.5% suspension of Garlon® 4 (triclopyr; Dow AgroSciences), and 0.5% solution of non-ionic surfactant (R11®; Wilbur-Ellis, Fresno, CA). All seedlings were carefully bagged during the application to prevent exposure to the herbicides. On 27 May 2008, organic corn gluten (Preen®; Lebanon Seaboard Corporation, Lebanon, PA) was applied as a broadcast pre-emergent treatment to prevent germination of weed seedlings. Minimal hand weeding was necessary throughout the 2008 growing season.

Because the study design intended belowground resources to be non-limiting (to minimize effects of belowground competition between paired seedlings), irrigation water was supplied by an automated system with one pressure-compensating dripper (3.8 L h^{-1}) at each seedling. Water was applied as necessary throughout the growing-season; soil water content was monitored once or twice per week using 12 ECH_2O EC-20 probes (Decagon

Devices Inc., Pullman, WA). In addition to monitoring overall soil water content, probes were used to compare soil water content near paired seedlings to that near single seedlings; no significant differences were detected at any point during the study. Fertilizer (Technigro 20-18-18 Plus, Sun Gro Horticulture, Bellevue, WA) dissolved in water was applied at the recommended rate around the base of each seedling at a three-week interval during both growing seasons.

Seedlings

Two hundred seedlings each of Douglas-fir (*Pseudotsuga menziesii*; DF), grand fir (*Abies grandis*; GF) and noble fir (*Abies procera*; NF) were obtained from the Washington State Department of Natural Resources Webster Nursery in Olympia, WA. These species were chosen because they occupy some of the same forest types in the coastal Pacific Northwest region. While the seed zones for the DF and GF seedlings (Kitsap and Upper Chehalis, respectively) encompassed the study site, the NF seed zone (Lewis) did not because that species is typically found at elevations above 900 meters. To increase uniformity in initial seedling size among species, the smallest DF stock type (plug + 0) and the largest GF and NF stock types available (2 + 0) were chosen. To further increase species uniformity, seedlings of each species were sorted according to an ocular assessment of stem height and diameter, and the smallest 40% of DF seedlings and the largest 40% of GF and NF seedlings were selected for the study. Seedling pairs were planted 2 April 2007, with stem bases in each pair 10 cm apart. Of the selected seedlings, 30 randomly chosen seedlings per species were destructively sampled to develop equations to estimate initial dry weight of the planted seedlings based on initial fresh weight which was measured for every seedling in the study. Because DF seedlings were a plug stock type, all growing media was carefully washed from the roots before weighing. Equations for predicting total dry weight of individual bareroot seedlings (including roots) were:

$$\text{DF dry weight} = 0.2539\,FW + 0.0542 \left(R^2 = 0.920\right)$$
$$\text{GF dry weight} = 0.3622\,FW - 0.3528 \left(R^2 = 0.995\right)$$
$$\text{NF dry weight} = 0.3536\,FW - 0.2709 \left(R^2 = 0.983\right)$$

where dry weight is measured in grams and *FW* is fresh weight (g).

Experimental design

The study used paired seedlings to investigate the effect of a 'neighbor' seedling on a 'subject' seedling. Subject seedlings ($n = 150$), each an experimental unit, consisted of a single DF, GF, or NF. Neighbor seedlings were either the same species or one of the other two species. A fourth level of neighbor consisted of a vacant neighbor location (i.e., subject seedling without neighbor; $n = 10$ per species). Neighbor seedlings were located either on the north or south side of the subject seedlings. The study had three fixed treatment effects: subject species (3 levels), neighbor species (4 levels), and neighbor direction (2 levels) applied in a randomized complete-block design. Raised beds were blocked in pairs from north to south (5 blocks). Each raised bed was divided into 9 cells (18 per block), and a treatment combination was randomly assigned to each cell. The distance between seedling pairs in adjacent cells was 100 cm.

Data collection and analysis

Immediately after planting, stem diameter (nearest 0.1 mm) at a marked height 1.0 cm above ground and total height (nearest mm) were recorded for each seedling; these measurements were repeated after each of the following two growing seasons. After the first growing season (2007), 4 branches from the current year's whorl were randomly selected for measurement and marked. If fewer than 4 branches existed in the whorl, then all were selected. For each selected branch, and for the terminal shoot, the length of each new growth flush and the numbers of whorl and interwhorl second-order branches on each growth flush were recorded. Diameter 1.0 cm beyond the base of each selected branch, branch azimuth class (N, NE, E, SE, S, SW, W, or NW), and overall crown diameter at the widest point in north–south and west-east directions were recorded. At the end of the second growing season (2008), all measurements were repeated for the same branches, as were crown width measurements. Then, each of the selected branches was severed at its base, dried to constant weight at 65°C, and weighed to the nearest 0.01 g.

Photosynthetic photon flux density (PPFD; mmol s^{-1} m^{-2}) was measured within 2 h of solar noon on a cloudless day, 27 June 2008. A LI-190 Quantum Sensor (LI-COR Biosciences, Lincoln, NE) was mounted in an upright level position in 6 locations near each of the 10 seedlings per species without a neighbor. The 6 measurement locations were heights of 44, 27, and 18 cm above ground (50% of the average heights of DF, GF, and NF, respectively, at the time of measurement), 10 cm north and 10 cm south of each seedling (i.e., where a neighbor seedling would have been located). Light spectra reflected by the foliage of the same 30 seedlings was measured 27 June and 5 September 2008 (both cloudless days) using an Ocean Optics S2000 spectrometer with a CC-3 probe (Ocean Optics, Inc., Dunedin, FL). Measurements of reflected light were taken at a horizontal distance of 10 cm from the seedling, with the probe pointed downward at a 45-degree angle toward the foliage of the seedling's highest branch whorl. Measurements were taken from the north and south sides of each seedling.

Treatment effects were modeled using analysis of variance (ANOVA) (PROC MIXED; SAS Institute 2005), and single-degree-of-freedom contrasts were used to test specific *a priori* hypotheses. For contrasts, Holm's adjustment was used to set the experiment-wise error rate at $\alpha = 0.05$ (Holm 1979). ANOVA fixed effects were subject species, neighbor species, and neighbor direction; block was a random effect. Following the initial ANOVA, we tested the hypothesis that neighbor competition is a function of both neighbor size and neighbor species by adding neighbor height to the model as a covariate (height was the strongest measure of neighbor competition). We re-ran the model with the covariate but without the neighborless seedlings to test whether neighbor species and neighbor height were both significant. ANOVA also was used to test species, height, and direction effects on PPFD and species and direction effects on red:far-red light. All treatment comparisons not made with contrasts were tested using Tukey's HSD test with minimum significance level of $\alpha = 0.05$. In analyses of branch-related variables, branches were classified as 'facing the neighbor' if the neighbor (or empty planting location in the case of no neighbor) was to the N and the branch pointed NW, N, or NE, or if the neighbor was to the S and the branch pointed SE, S, or SW. Conversely, branches were classified as 'opposing the neighbor' if the neighbor was to the N and the branch pointed SE, S, or SW, or if the neighbor was to the S and the branch pointed NW, N, or NE. Regression analysis with stepwise variable selection was used to further explore the relationships between variables, including the effect of subject: neighbor height on subject seedling growth (PROC REG; SAS Institute 2005).

Results

While estimated dry weight at planting did not differ among species, there were differences in initial stem diameter and height (Table 1). One year post-planting, seedling height and diameter growth differed significantly by species (Table 2). Height growth followed the species ranking DF > GF = NF, while diameter growth was ranked DF > GF > NF. The latter species ranking also occurred for height and diameter growth in year 2 and for total seedling diameter and height after year 2. Neighbor species had no significant effect on stem growth in year 1, but in year 2, for all 3 species, subject seedlings with no neighbor had greater diameter growth than those with a DF neighbor (Fig. 1). Year-2 height growth was not affected by neighbor species.

In year 2, branch diameter growth, length growth, weight, and morphology differed among subject species, generally following the ranking DF > GF > NF (Tables 2 and 3; Fig. 1). Total length of facing branches after year 2 followed the same species ranking, with lengths of 51.6 ± 1.6, 26.9 ± 1.6, and 20.7 ± 1.5 cm, respectively. Number of growth flushes on facing branches in year two followed the same ranking with 1.9 ± 0.1, 1.3 ± 0.1, and 1.0 ± 0.1, respectively. Branch growth was more sensitive to the presence of a neighbor seedling than stem height or diameter growth; the variables influenced by neighbor were weight and year-2 diameter growth of facing branches and weight and year-2 diameter growth of facing: opposing branches (Table 2; Fig. 1).

The neighbor direction term (i.e., N or S) was not significant in any of the ANOVA models, nor were there any significant interactions between it and subject or neighbor species.

We tested the hypothesis that neighbor size and neighbor species simultaneously influenced subject seedling growth by re-running each ANOVA model, with and without neighbor height as a covariate. In every model, the addition of this covariate resulted in the neighbor species term becoming non-significant ($P \geq 0.05$), indicating that the variation in the response variable explained by neighbor size and neighbor species were not substantially different (Table 2). As a covariate, neighbor height explained more variation in the subject seedling's growth than other measures of neighbor size. We further explored the effect of neighbor size by regressing the ratio of facing: opposing branch diameter growth against the ratio of subject height: neighbor height (Fig. 2). This relationship differed among the three species. NF had the steepest decline in branch diameter growth, most notably where subject: neighbor height was less than 1.0. By contrast, DF branch diameter growth showed little response to subject: neighbor height above approximately 2.0. The response of GF was intermediate between the other two species.

PPFD increased with measurement height for all three subject species (Fig. 3). PPFD measured near the three species followed the ranking NF > GF > DF, except at a height of 44 cm where NF = GF > DF. At the 27-cm height, PPFD was significantly greater on the south side of DF, compared to that on the north side. The ratio of red: far-red reflected light

Table 1 Size and estimated dry weight at the time of planting for Douglas-fir, grand fir, and noble fir seedlings

Species	Diameter (mm)	Height (cm)	Estimated dry weight (g)
Douglas-fir	3.7 b	31.4 a	5.0 a
Grand fir	3.7 b	23.2 b	5.0 a
Noble fir	4.2 a	15.4 c	5.2 a

Means followed by the same letter within the same column do not differ at the 95% confidence level

Table 2 Significance of ANOVA fixed effects (Pr > F) in models of various dependent variables

Assessment	Dependent variable	Significance of ANOVA source			
		Subject species	Neighbor species	Neighbor species (covariate model[a])	Neighbor height (covariate model)
Seedling size (yr 1)	Height growth	<0.001	–	–	–
	Stem diameter growth	<0.001	–	–	–
	Crown width ratio (N–S: W–E)	–[b]	–	–	–
Seedling size (yr 2)	Height growth	<0.001	–	–	–
	Stem diameter growth	<0.001	0.002	–	–
	Crown width ratio (N–S: W–E)	–	–	–	–
Branches (yr 2)	Diameter growth, facing	<0.001	<0.001	–	0.043
	Diameter growth, opposing	<0.001	–	–	–
	Diameter growth, facing: diameter growth, opposing	0.011	<0.001	–	–
	Diameter growth, all sampled branches	<0.001	–	–	0.001
	Length growth, facing	<0.001	–	–	
	Length growth, opposing	<0.001	–	–	–
	Length growth, facing: length growth opposing	–	–	–	–
	Mean weight, facing	<0.001	0.014	–	–
	Mean weight, opposing	<0.001	–	–	–
	Mean weight, facing: mean weight, opposing	–	0.036	–	–
	Mean weight, all sampled branches	<0.001	–	–	0.023
	2nd-order branches on facing branches (no.)	<0.001	–	–	–
	2nd-order branches on opposing branches (no.)	<0.001	–	–	–
	Growth flushes, facing (no.)	<0.001	–	–	–
	Branch length growth beyond initial flush, facing	<0.001	–	–	–

The neighbor direction effect, and all interactions between subject species, neighbor species, and neighbor direction are not shown because they were never significant

[a] Significance of the neighbor species ANOVA term when neighbor height at the end of year 1 was included in the model as a covariate

[b] – denotes non-significance at $\alpha = 0.05$

was lowest for DF and highest for NF, although red: far-red spectra declined for all three species in early-September compared to late-June (Fig. 4). The ratio of red: far-red light did not differ between readings taken from the north or south sides of the seedlings.

Discussion

H_1 Assuming no belowground competition, the facilitative effect of a neighbor's presence increases stem growth rate, owing to the spectrum of light reflected by the neighbor.

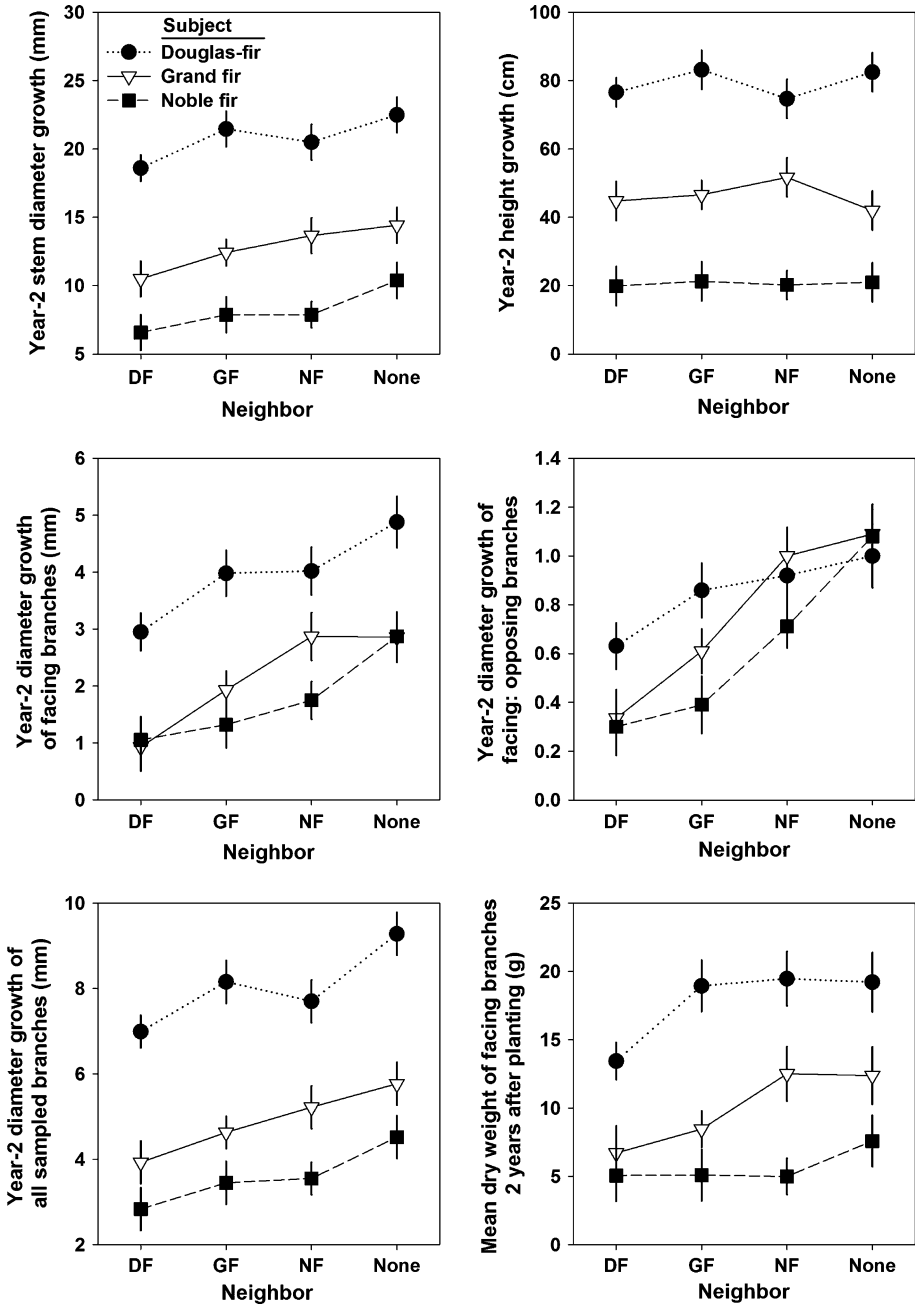

Fig. 1 Second-year growth response, and branch weight after year 2, for seedlings of 3 subject species in response to 4 neighbor treatments consisting of closely planted Douglas-fir (DF), grand fir (GF), noble fir (NF), or no neighbor

Table 3 Significant effects (expressed as positive or negative percentage change) of various neighbor seedling treatments on year-2 stem and branch growth, and on branch weight following year 2, for subject seedlings of three species

Comparison	Subject species	Year-2 stem diameter growth (mm)	Year-2 branch diameter growth, facing (mm)	Branch diameter growth facing: opposing	Branch diameter growth, all sampled (mm)	Mean weight, facing branches (g)	Mean weight, all sampled branches (g)
Presence of a neighbor vs. no neighbor[a]	Douglas-fir	n.s.	−25%**	n.s.	−18%**	n.s.	n.s.
	Grand fir	n.s.	n.s.	−37%***	n.s.	n.s.	n.s.
	Noble fir	n.s.	−52%***	−57%***	n.s.	n.s.	n.s.
Neighbor of same species vs. no neighbor	Douglas-fir	n.s.	−40%***	−38%*	−25%***	n.s.	n.s.
	Grand fir	n.s.	n.s.	−34%*	n.s.	n.s.	n.s.
	Noble fir	n.s.	−39%**	−34%**	n.s.	n.s.	n.s.
Neighbor of same species vs. other two species	Douglas-fir	n.s.	−26%**	−32%*	n.s.	−30%**	n.s.
	Grand fir	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Noble fir	n.s.	n.s.	+51%***	n.s.	n.s.	n.s.

[a] The average effect of all three species as neighbor

*, **, and *** indicate significance at the 0.05, 0.01, and 0.001 alpha levels, respectively; n.s. indicates no significance

The minimum alpha level was calculated using Holm's test (Holm 1979) with an experiment-wise error rate of 0.05. The calculated alpha varied by contrast but was always less than 0.05

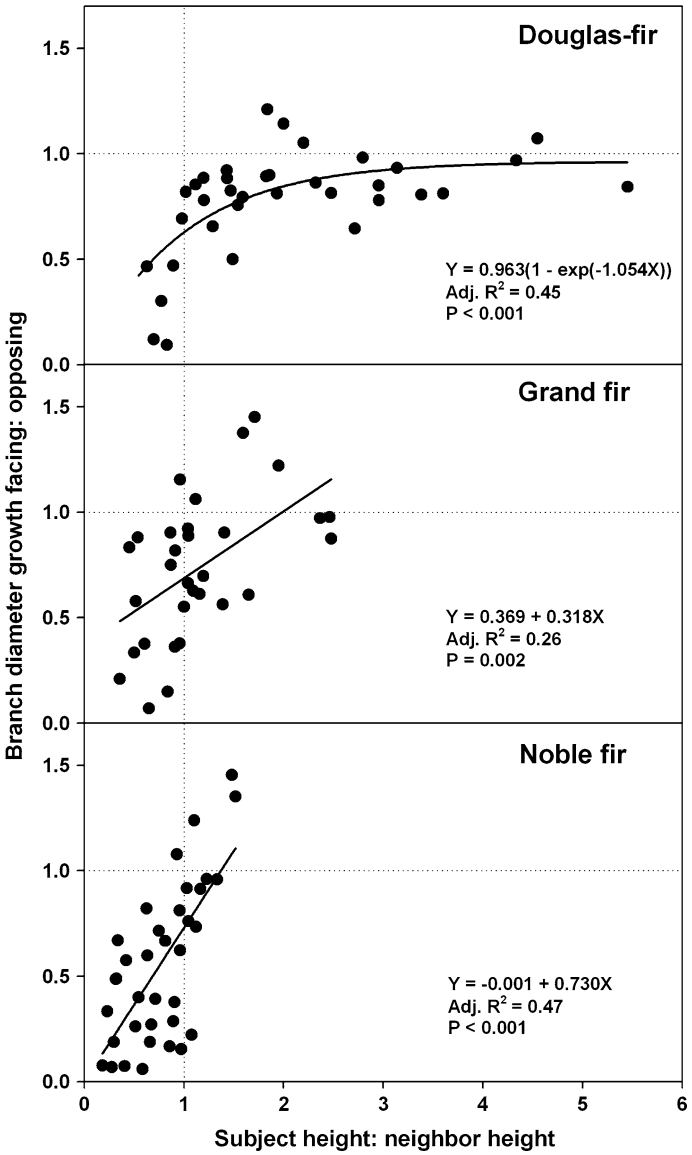

Fig. 2 Ratio of branch diameter growth of facing to opposing branches in year 2 in response to the ratio of the subject seedling's height to the neighbor seedling's height (regardless of neighbor species) for three species of conifer seedlings

The lack of a positive neighbor effect on seedling height or diameter growth in any of the species studied fails to support H_1. Previous studies documented a significant positive effect of intraspecific interference on stem growth in young DF (Ritchie 1997; Woodruff et al. 2002), red alder (Knowe and Hibbs 1996), and eucalyptus (Cameron et al. 1989) that were attributed to phytochrome responses. In those cases, the effect was observed where tree density was very high and belowground resources were not yet limiting. As trees grew

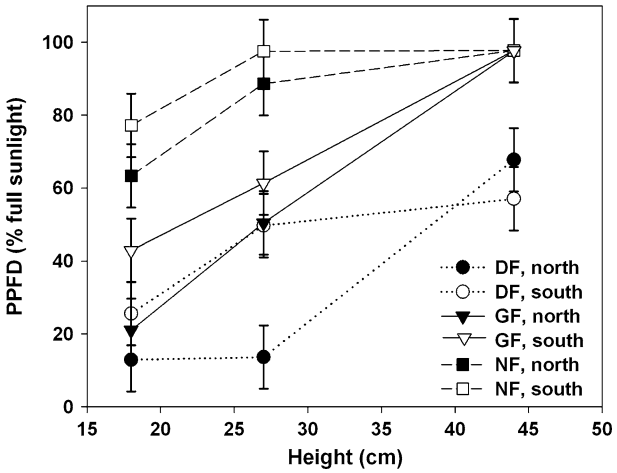

Fig. 3 Photosynthetic photon flux density (PPFD), expressed as a percentage of that in full sunlight, at three measurement heights to the north and south of Douglas-fir (DF), grand fir (GF), and noble fir (NF) seedlings in their second year post-planting. Each data point is the mean of measurements at 10 seedlings

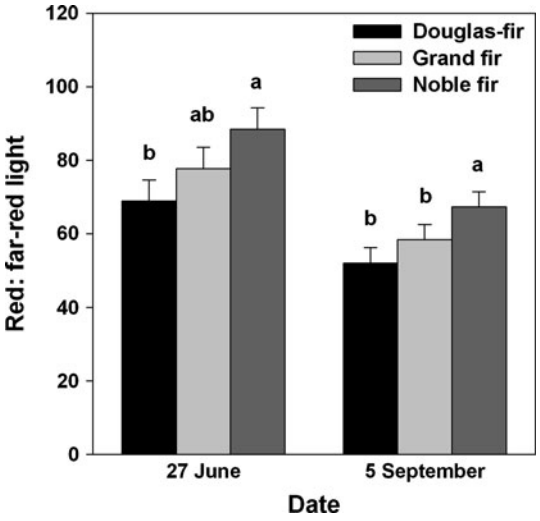

Fig. 4 Ratio of red: far-red light reflected from single seedlings of three species on two dates in year 2. Bars within each date accompanied by the same letter do not differ at $\alpha = 0.05$

larger and began to compete with one another for belowground resources, the positive effect of density diminished. There are at least two possible explanations as to why we did not observe the phytochrome-mediated growth response that is understood to occur in young DF (Ritchie 1997; Woodruff et al. 2002). First, a single neighbor seedling may not have had a sufficient effect on the subject seedling's red: far-red light environment to elicit the phytochrome response. In the previous studies, trees were surrounded by neighbors. Second, because nine seedling pairs or solo seedlings were grown in each test bed, reflected light from these other seedlings may have created background light conditions that diluted the net effect of the neighbor seedling on the subject's light environment, especially with increases in seedling size in year 2. It is unclear to what distance tree

seedlings influence the red: far-red ratio of the light that they reflect. A 2.5-m-tall DF hedge modified red: far-red light to a distance of 3 meters (Ritchie 1997), while herbaceous plants affected light to a distance of only approximately 30 cm (Smith et al. 1990).

Although we detected no evidence that reflected light affected the growth of subject seedlings, we found that the red: far-red ratio of reflected light differed significantly among species, with DF reflecting a lower red: far-red ratio compared to NF. Compared to that of the other species, the lower red: far-red ratio in light reflected by DF suggests that the species is capable of reflecting a relatively strong "shade signal" (Aphalo et al. 1999) that could potentially be received by the phytochrome systems of its neighbors.

H_2 Aboveground resource limitation (i.e., growing space or access to sunlight) results in a crown morphologic response to the presence of a neighbor seedling that differs according to neighbor species.

Significant neighbor species effects on branch diameter growth and branch weight support H_2. By the end of year 2, seedling crowns overlapped substantially, with branches of all three species typically extending into the neighbor's crown, past its stem. While weight and diameter growth of these facing branches was reduced (to an extent dependent upon the species of the neighbor), length growth, number of growth flushes, and number of lateral buds on these facing branches were not affected by the presence of the neighbor, nor was crown width ratio. This pattern suggests that shading, rather than mechanical interaction, was the dominant mechanism leading to the changes in crown morphology. Shaded branches have reduced diameter growth and weight compared to branches on the same tree that are exposed to sunlight (Stoll and Schmid 1998; Sprugel 2002). Because photosynthates are translocated among branches during the growing season (Sprugel and Hinckley 1990), it is possible that reduced growth of a shaded branch may result not only from its reduced photosynthate production but also from translocation of its photosynthates to other, unshaded branches (Stoll and Schmid 1998). In contrast to the effects of light competition, mechanical interactions between tree crowns are likely to produce abrasion (Larson and Oliver 1996), reductions in tip growth (Franco 1986), or changes in the number of lateral buds (Jones and Harper 1987a), none of which were evident in the present study. Thus, competition for sunlight rather than competition for growing space appears to have been responsible for the morphological effects of the neighbor seedling. This is supported by our PPFD measurements that show sharply declining PPFD at the lower measurement heights.

To assess whether there was a benefit of having a heterospecific neighbor, we compared heterospecific seedling pairs to conspecific pairs to test whether seedling growth followed the competitive production principle (*sensu* Vandermeer 1989). Under this principle, also known as reduced competition, greater combined growth of heterospecific pairs would be expected owing to the two species' exploitation of different components of the same limited resource(s). The species most affected by differences in neighbor species was DF. Notably, DF had reduced mean weight of all sampled branches when paired with itself compared to pairings with the other species. Mean weight of branches of GF and NF did not differ when paired with DF, compared to conspecific pairings. Thus, heterospecific pairings that included DF support the competitive production principle: combined growth of these pairs (i.e., DFGF or DFNF) was greater than the mean growth of conspecific pairs of both species [i.e., (DFDF + GFGF)/2 or (DFDF + NFNF)/2]. The advantage of hetero- versus conspecific pairs was 31.3 vs. 26.5 grams for the DFGF combination and 26.5 vs. 21.9 grams for the DFNF combination. The relative yield (*sensu* Harper 1977) of the DFGF and DFNF pairs, compared to the conspecific pairs was 1.17 and 1.16, respectively. This phenomenon is apparently a result of DF encountering greater competition for light or

growing space when paired with itself than with the other species. The competitive production principle has been observed in a variety of other tree species combinations, usually where crown structure or shade tolerance differs between species (Larson and Oliver 1996). In plantations of mixed conifers, the competitive production principle has been reported for Douglas-fir and western hemlock (*Tsuga heterophylla*) at age 24 (Erickson et al. 2009) and grand fir and ponderosa pine (*Pinus ponderosa*) at age 26 (Garber and Maguire 2004); both of these pairs are composed of species differing in shade tolerance. Owing to the high level of shade tolerance of GF and the rapid early growth rate of DF, the DFGF seedling combination seems to hold the most promise for continued demonstration of the competitive production principle.

H_3 Responses of seedlings to neighbor competition vary according to both the species and size of the neighbor.

Larger-than-expected differences in growth rate among species meant that our test of this hypothesis was not meaningful. By the end of year 1, neighbor size was effectively a surrogate for the neighbor species variable. While neighbor size was a significant predictor of subject seedling growth, we were unable to test interactions between neighbor size and neighbor species owing to the lack of independence of these two variables.

Hypothesis 3 was based on the assumption that different crown structures among neighbor species would result in different levels of aboveground competition. Although crown structures differed by species as anticipated, height also differed by species, to a greater extent than expected. It is not surprising that neighbor height was the strongest measured predictor of competition; a study of 7 herbaceous species found that the difference in height between a subject plant and its neighbor explained, across all 7 species, the competitive effect of the neighbor (Keddy and Shipley 1989). If the seedlings in our study had grown to the point where some were completely overtopped by their neighbor's crown, then the species' differences in shade-tolerance might have played a greater role. GF is classified as very shade tolerant, while NF and DF are intermediate in shade tolerance, although DF's shade tolerance is greatest when it is in the seedling stage (Foiles et al. 1990; Franklin 1990; Hermann and Lavender 1990).

Owing to the large size differences among species and the fact that neighbor size was an important factor determining the level of competition, we tested whether asymmetric competition (Keddy and Shipley 1989; Schwinning and Weiner 1998) was occurring between each type of heterospecific seedling pair. Asymmetric competition within a pair would be indicated by increased growth of one species and decreased growth of the second species, relative to each species' growth in a conspecific pair. We tested all dependent variables, and in only one instance was there an asymmetric effect between any of the heterospecific pairs. Within the DFGF pair, diameter growth of facing branches of DF increased relative to conspecific pairing, while that of GF decreased. This effect on facing branches indicates a crown morphological response, but owing to crown plasticity, it does not imply that overall crown growth was affected (Sorrensen-Cothern et al. 1993). In fact, mean growth of all sampled branches did not show asymmetric competition in the DFGF pair. Beyond the fact that seedling size, and therefore the degree of interaction, was limited by the length of the study, we attribute the lack of aboveground competitive asymmetry, at least in part, to the relative abundance of belowground resources (Thomas and Weiner 1989). Assuming soil resources are uniformly distributed, belowground competition is generally size symmetric (Weiner et al. 1997). Thus, the only asymmetric competition in this study was probably that for light, and the degree of this competitive asymmetry was limited by the fact that seedling crowns only partially overlapped during the study.

H_4 The influence of a neighbor seedling on growth and morphology is greater when the neighbor is to the south, rather than to the north, owing to a greater influence of the neighbor on the light environment.

Because the neighbor direction term was not significant in any of the ANOVA models, there was no evidence to support H_4. We already inferred that reductions in growth of branches facing the neighbor seedling were probably a result of shading by the neighbor through crown overlap, and it is now apparent that this effect was not directionally sensitive. A branch's growth and survival are influenced not only by its light environment but also by its light environment relative to the light environment of the other branches on the same tree (Stoll and Schmid 1998; Sprugel 2002). For example, a shade-tolerant tree growing in full sunlight may self-prune its lowest, most-shaded branches even if those branches receive more sunlight than those on trees of the same species receive when growing in an understory position. This explains why growth of the shaded, overlapping branches of shade-tolerant GF was reduced, even when it grew on the south side of its neighbor.

Direct measurements confirmed that PPFD was similar on the north and south sides of seedlings with the exception of the middle (27-cm high) measurement on DF, where PPFD was greater on the south side. We attribute the species difference in PPFD at each measurement height to species' differences in total seedling height at the time of measurement and to crown density differences among species. DF and GF formed more than twice as many whorl and interwhorl branches as NF during the 2 years of this study; after year 2, branches of DF were approximately twice as long as those of the other species. The combination of more and longer branches contributed to an overall greater crown density for DF and apparently contributed to a reduction in PPFD on its north side. The fact that this reduced PPFD did not affect growth of seedlings to the north differently than those to the south may be attributed to the amount of diffuse light that the northern seedling received or to the fact that the sensor measured light at a single point that was not indicative of the full crown's light environment. At northern latitudes, conifer crowns develop asymmetrically in response to competition to maximize their exposure to sunlight (Rouvinen and Kuuluvainen 1997). In the present study, it is likely that 2 years was insufficient time to detect such changes; additional crown development would likely be necessary to evaluate whether the response of these species would have a direction-dependent response at the latitude of the study site.

In summation, the interactions between paired seedlings were a result of shading by the faster-growing (i.e., larger) seedling in the pair. Interactions in the second year post-planting were predominantly morphological: branches overlapped by the neighbor's crown had reduced growth. A small but significant second-year reduction in stem diameter growth in the presence of the largest neighbor species (DF) suggests that this crown overlap will lead to future reductions in stem growth. Although there was little evidence of asymmetric competition between heterospecific pairs, we expect that this competition will become more apparent as trees mature and competition for growing space increases. In years 1 and 2, a relatively small fraction of the pairs' crowns overlapped owing to the initial 10-cm spacing; as crown overlap increases with time, asymmetric competition will become more likely between heterospecific seedlings with different growth rates. Our findings do not support the idea that a pair of trees growing in very close proximity benefits from phytochrome-mediated facilitation as seedlings. Our results indicate that, under controlled conditions, the overall impact of a neighbor on the growth of conifer seedlings is relatively minor in the

early years, given that both species are of intermediate to high shade tolerance. Similarity in early growth rates appears to be essential for sustaining this compatibility.

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