

Belowground competition from overstory trees influences Douglas-fir sapling morphology in thinned stands

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Received: 25 April 2008 / Accepted: 25 September 2008 / Published online: 11 October 2008
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Abstract We evaluated effects of belowground competition on morphology of naturally established coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) saplings in 60- to 80-year-old thinned Douglas-fir stands in southwestern Washington. We separately quantified belowground competition from overstory and understory sources using trenching and understory removal. In this light-limited environment of $26 \pm 16\%$ (std. dev.) full sunlight, 2-year exclusion of tree root competition by trenching increased sapling stem biomass by 18%, total aboveground biomass by 21%, number of interwhorl buds by 68%, total foliar biomass by 33%, and foliar biomass on branch components over 4 years old by 143%. Belowground competition did not influence shoot:root ratio or foliar efficiency (i.e., stem growth per unit foliage biomass). Sapling needle size, specific leaf area, and internodal distance also were not affected by belowground competition; these variables were apparently a function of the low-light environment. The principal source of belowground competition was roots of overstory trees; effects of belowground competition from understory vegetation were minor. Thus, under a partial overstory, morphology of Douglas-fir regeneration was influenced by both belowground and aboveground competition from overstory trees. In this environment, understory vegetation control would not likely influence belowground competition to an extent that would affect sapling morphology.

Keywords Douglas-fir · Competition · Morphology · Understory · Regeneration

Introduction

Vegetative competition for light, soil water, and nutrients is a principal management concern in regenerating coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.)

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Franco) in plantations or through natural regeneration, as limitations in these resources may significantly impact the physiology, growth, and morphology of young trees. Because Douglas-fir is traditionally regenerated in the absence of overstory trees, competition for light and soil resources in young, managed stands is a function of the degree to which competing herbaceous and woody vegetation is controlled (Chan and Walstad 1987; Newton and Preest 1988). With recent interest in regenerating Douglas-fir in two-aged or uneven-aged systems (Curtis and Carey 1996; Franklin et al. 2002; Miller and Emmingham 2001), it is important to understand how belowground competition influences Douglas-fir regeneration in conditions of partial sunlight. Under partial overstory removal, the understory response may be complex, as Douglas-fir seedlings compete for belowground resources with both overstory trees and understory vegetation (Brandeis et al. 2001; Devine and Harrington in press; Harrington 2006).

Intermediate in shade tolerance, young Douglas-fir respond to a low-light environment through various morphological adaptations. With decreasing light availability, proportional resource allocation to aboveground components increases (Drew and Ferrell 1977). While low-light conditions are associated with reduced size of individual needles in Douglas-fir, specific leaf area has been shown to increase in shade, producing a greater ratio of foliar surface area to mass (Brand 1986; Del Rio and Berg 1979; Maily and Kimmins 1997). Low light availability also results in fewer needles per stem length, which reduces mutual shading among needles (Brix 1967; Drew and Ferrell 1977). While young Douglas-fir survives at approximately 20% of full sunlight, morphological development is affected where less than 40% of full sunlight is available (Maily and Kimmins 1997).

The morphology of young Douglas-fir may be influenced by availability of belowground resources. Root competition from hardwood sprouts and shrubs reduced foliar and woody growth as well as the number of buds on terminal and lateral shoots of young Douglas-fir (Harrington and Tappeiner 1991; Tappeiner et al. 1987). Soil water stress significantly reduced terminal bud size and number of needle primordia in Douglas-fir seedlings (Khan et al. 1996). For Douglas-fir and other species with determinate growth, both bud size and the number of needle primordia within the bud are correlated with shoot elongation in the following year (Graham and Hobbs 1994; Kozłowski et al. 1973; Pollard and Logan 1977), as the number of needle primordia represents the number of linear shoot segments, or internodes (Critchfield 1985), which determines the fixed growth potential of the shoot (*sensu* Harrington and Tappeiner 1991). Douglas-fir morphology also is affected by nutrient availability. Number of shoots per branch, number of needles per shoot, individual-tree leaf area index, and needle length were positively related to N availability (Brix 1981; Gower et al. 1992).

The influences of aboveground competition on growth and morphology of young Douglas-fir have been studied under a variety of conditions (e.g., Brand 1986; Drever and Lertzman 2001; Maily and Kimmins 1997; Williams et al. 1999), but the effects of belowground competition under a partial overstory canopy on sapling morphology are not well understood. Due to increased interest in regenerating Douglas-fir in multi-aged stands, it is important to identify the relative influences of belowground competition from overstory and understory vegetation on young Douglas-fir. We hypothesized that, under a moderate level of aboveground competition (i.e., a thinned overstory), belowground competition imposes further limitations on morphological development of Douglas-fir saplings. The objective of this study was to separately quantify the effects of belowground competition from overstory and understory vegetation on the morphology of natural Douglas-fir regeneration in stands of thinned mature Douglas-fir.

Methods

Study site

The study was located in western Washington, U.S.A., in the Puget Trough physiographic province on Fort Lewis Military Reservation (47.05° N; 122.55° W; 100–150 m above mean sea level). The study took place in three Douglas-fir stands (10–15 km apart) that originated in 1920–1930 when Douglas-fir naturally regenerated on lowland prairies that had been maintained by frequent anthropogenic fire prior to European settlement (Foster and Shaff 2003). At study establishment in 2005, stand basal area at the study sites averaged 40.3 m² ha⁻¹ (Churchill 2005). Prior to the study, each stand received two or three thinning treatments (Table 1), with 15–20% of basal area removed each time. The last thinning conducted in these stands was a variable-density thinning (Roberts and Harrington 2008), intended to create spatial variability in overstory density and the amount of light reaching the understory. Most of the Douglas-fir saplings in this study probably established in areas where understory light levels were increased by this variable-density thinning treatment. In the first year of this study, photosynthetically active radiation (PAR) in the understory averaged 26 ± 16% of full sunlight. In all stands, the plant association was Douglas-fir/snowberry (*Symphoricarpos albus* (L.) S. F. Blake)—serviceberry (*Amelanchier alnifolia* Nutt.) (Chappell and Crawford 1997). The most prevalent understory species on the study plots were snowberry, California blackberry (*Rubus ursinus* Cham. & Schldl.), orange honeysuckle (*Lonicera ciliosa* (Pursh) Poir. ex DC.), western swordfern (*Polystichum munitum* (Kaulf.) C. Presl), colonial bentgrass (*Agrostis capillaris* L.), and common velvetgrass (*Holcus lanatus* L.). The 50-year site index for Douglas-fir in these stands was between 34 and 38 m (King 1966).

Table 1 Stand and sapling conditions prior to treatment (mean ± standard deviation)

Variable	Stand		
	Kalipso	Shaver	West Weir
Stand conditions			
Stand basal area (m ² ha ⁻¹) ^a	41.6	38.1	41.1
Basal area at study plots (m ² ha ⁻¹) ^b	23.1 ± 14.3	39.8 ± 7.8	34.1 ± 6.6
PAR at study plots (% of full sunlight)	34 ± 19	22 ± 7	24 ± 15
Thinned (year)	1980, 1990, 2001	1985, 1997	1968, 1983, 1997
Study saplings			
Sapling height (cm)	141 ± 41	122 ± 26	189 ± 47
Sapling diameter (mm)	19.3 ± 7.0	12.6 ± 4.1	20.9 ± 6.2
Height:diameter	75.8 ± 14.2	100.8 ± 15.6	92.4 ± 16.6
Crown diameter (cm)	89 ± 34	72 ± 24	115 ± 40
Live crown ratio ^c	0.55 ± 0.19	0.66 ± 0.08	0.65 ± 0.07
Pre-study height growth (cm year ⁻¹)	17.8 ± 6.5	18.2 ± 5.0	15.1 ± 6.9
Age (year)	9.7 ± 3.1	7.6 ± 1.8	12.8 ± 3.4

^a Data reported at the stand level by Churchill (2005)

^b Values differ from stand basal area because study plots were located around natural regeneration which was often located where overstory density was below the stand average

^c The ratio of the length of live crown to total sapling height

Soil in all three stands was a gravelly sandy loam of the Spanaway series (Typic Melanoxerand), formed in glacial outwash. The coarse fragment contents of the A (0–38 cm), Bw (38–48 cm), and C (48+ cm) horizons are 35, 60, and 70%, respectively, and the soil is somewhat excessively drained (Soil Survey Staff 2006). Mean annual temperature is 12°C, with mean temperatures in January and July of 5 and 19°C, respectively (Western Regional Climate Center 2007). Long-term mean annual precipitation at Fort Lewis is 1,026 mm. Precipitation from 1 June through 30 September averages only 150 mm, and during years 1 and 2 of this study it was 124 and 73 mm, respectively.

Study design

The 2-year study followed a randomized block design, with a 2-by-2 factorial treatment arrangement and 12 complete blocks. The study employed a nested blocking design, with four blocks nested within each stand. This replication of blocks within stands permitted analysis of potential interactions between the random stand effect and fixed treatment effects. The experimental unit ($n = 48$) consisted of a 3.0-by-3.0-m plot established around one to three (usually two or three) naturally regenerated Douglas-fir saplings (study saplings), between 0.75 and 3.0 m in height, with little or no evidence of past browse damage (Table 1). Within each plot, study saplings were of the same cohort. The four plots per block were 5–20 m apart and were randomly selected from six potential locations. The four blocks were 50–500 m apart within each stand. The perimeter of each sapling crown was ≥ 0.5 m within the plot boundary, and there was no crown contact among saplings during the study. Post-study root excavation showed little to no overlap of rooting area between saplings. No tree species other than the study saplings occurred on the study plots. Occasionally, understory shrubs partially shaded or directly contacted study saplings. These shrubs were pruned annually during the study so that they would not shade or interfere with sapling growth. This pruning involved removing only one or two branches from shrubs immediately adjacent to saplings; such minimal crown damage to shrubs was not expected to influence their consumption of belowground resources. Mesh bud protectors (Terra Tech, LLC, Eugene, OR) were used to reduce the likelihood of damage from deer browse; protectors were maintained regularly to prevent mechanical damage or deformity.

Treatments, applied between 29 March and 12 April 2005, were presence or absence of belowground competition from overstory trees (+OV or -OV, respectively) and presence or absence of belowground competition from understory vegetation (+UN or -UN, respectively). In the +UN + OV treatment combination (i.e., the control), there was no manipulation of belowground competition. On plots assigned the -OV treatment ($n = 24$), plot perimeters were trenched to a depth of 0.50–0.55 m using a walk-along, gasoline-powered trencher (Ditch Witch 1330, The Charles Machine Works, Inc., Perry, OK). Roots too large to cut with the trencher were cut using a hand saw or chainsaw. Trenches were lined with 0.152-mm flexible plastic sheeting and backfilled. Trenching depth corresponded with the depth to the upper boundary of the soil C horizon. Although some roots of overstory trees occurred within the C horizon, their frequency on similar glacially derived soils was substantially less in the C horizon than in the A and B horizons (Devine and Harrington 2005; Eis 1974). Thus, the -OV treatment probably excluded the majority of tree roots, including those that would have occupied the same rooting zone as the saplings (i.e., A and B horizons) and would thus have provided the most competition.

On the plots receiving the -UN treatment ($n = 24$), all woody and herbaceous understory vegetation was cut back to ground level at study installation and at 2- to 3-week

intervals, depending on growth rate, during the growing seasons using hand tools and an electric trimmer (GH600, Black & Decker, Hunt Valley, MD). The –UN treatment (i.e., elimination of belowground competition from the understory) was based on the assumption that, by removing the leaf area of all understory plants, photosynthesis, and therefore water uptake and most nutrient uptake, would be eliminated. To minimize soil disturbance, roots of understory vegetation were not removed in the –UN treatment. Herbicide application was not permitted in the study area, but manual control in this treatment provided near-total elimination of the aboveground portion of understory vegetation. On plots receiving the +UN treatment, understory coverage of forbs, grasses, and woody shrubs plus vines averaged 30, 18, and 85%, respectively, during the two growing seasons (Devine and Harrington in press). Therefore, including overlap among growth forms, total understory coverage averaged 133% in that treatment.

Data collection

Immediately prior to treatment implementation in 2005, sapling total height, height to live crown, live crown diameter in two perpendicular directions, and inter-whorl distance for the uppermost four branch whorls were measured to the nearest centimeter for all study saplings. Stem diameter was measured (nearest mm) at a marked location 15 cm above ground. Using a hand-held prism (basal area factor $5 \text{ m}^2 \text{ ha}^{-1}$), basal area of overstory trees was measured from the center of each plot. After years one and two of this study, stem diameter was remeasured; diameter measurements were used to calculate stem basal area growth.

In December of study year two (2006), one randomly selected sapling per plot ($n = 48$) was carefully excavated by shovel and separated into stem, branch, and root components in the field. At the laboratory, saplings were further divided into the following categories: (1) 1- and 2-year-old foliage (formed post-treatment), (2) 1- and 2-year-old twigs (formed post-treatment), (3) 3- and 4-year-old foliage (formed pre-treatment), (4) foliage older than 4 years, (5) woody branch components older than 2 years, (6) stem, and (7) roots. Age of foliage was determined by the age of the twig from which it originated. To remove soil from roots, roots were first soaked and then sprayed with water. All biomass samples were oven-dried at 65°C to a constant weight and weighed to the nearest 0.01 g. Foliar fraction was calculated for each sapling by dividing the dry weight of all foliage by the total dry weight of above- and belowground components. Foliar efficiency was calculated by dividing year-two sapling basal area growth (mm^2) by the dry weight of all foliage (g).

For the 48 randomly selected saplings, the number of interwhorl and whorl buds on the year-two terminal shoot was counted. The length and diameter of the terminal bud were measured (nearest 0.1 mm) and a volume index was calculated by multiplying length by diameter-squared. The number of needles on each terminal shoot was counted to determine the number of internodes (i.e., the stem segment between two needles), and this number was divided by shoot length to determine mean internodal distance. For 50 randomly selected needles from the central portion of this shoot, projected needle area (one-sided; LI-3100 area meter, Li-Cor, Lincoln, NE) and dry weight were measured. Length (nearest 0.1 mm) was measured on a randomly selected subset of 25 of these needles. Specific leaf area was determined for each sample by dividing needle area (mm^2) by dry weight (mg). Morphological variables measured on the terminal shoot were from the first flush (fixed growth); only two study saplings produced small second flushes. The saplings on the study plots ($n = 77$) that were not divided into biomass components were severed at groundline, returned to the laboratory, dried to constant weight, and weighed to determine total

aboveground biomass (nearest 0.01 g). Annual rings were counted on all saplings to determine age at groundline.

Photosynthetically active radiation at each study plot was measured on three summer days (20 June, 13 July, and 15 August 2005) using an AccuPAR[®] sensor (Decagon Devices, Inc., Pullman, WA). Conditions on these dates ranged from overcast to clear. The PAR values were expressed as percentages of potential (i.e., unshaded) PAR, measured simultaneously in a nearby clearing, and were averaged across the three dates. Dormant-season foliage samples were collected for both study years in early January following the growing season. Samples were taken from the past year's growth on the highest two branch whorls of each study sapling and composited by plot. Samples were collected to assess N availability during the previous growing season; foliar N levels were assumed to have stabilized during the dormant season (Smith et al. 1981). Total N concentration was determined by dry combustion analysis using a LECO CNS-2000 analyzer (LECO Corporation, St. Joseph, MI). Throughout the study, volumetric soil water content was measured at 4-h intervals on each study plot between 10 and 30 cm beneath the mineral soil surface (soil A horizon) using one Ech₂O[®] EC-20 soil water probe (Decagon Devices, Inc.) per plot. Details of environmental sampling, as well as treatment effects on foliar N and soil water content, are presented in Devine and Harrington (in press).

Data analysis

Treatment effects were analyzed using analysis of covariance models (ANCOVA; PROC MIXED; SAS Institute 2005). The OV and UN treatments were arranged in a 2-by-2 factorial, with stand and block-within-stand factors treated as random effects. The saplings in this study varied among plots in pre-study size and pre-study growth rate; furthermore, due to variation in age and microenvironment, these two variables were not correlated. Analyses of treatment effects were adjusted for the influences of pre-study sapling size and height growth rate by including pre-study individual-sapling basal area and height growth rate (during 2 years prior to the study) as covariates. In analyses of sapling biomass variables, total pre-study height also was included as a covariate. Additional potential covariates including pre-treatment height, age, and 4-year pre-treatment height growth rate were tested but not used, as they explained less variation. Photosynthetically active radiation was used as a covariate to remove the effect of differences in light availability resulting from variation in overstory density among plots. Assumptions of homoscedasticity of treatment groups, normality of residuals, and no interaction between the covariates and fixed effects were tested and found to be valid in all models. Relationships between each of the dependent variables and the variables indicating resources availability (i.e., PAR, soil water content, foliar N) were examined using correlation and regression analyses (PROC CORR, PROC REG, and PROC MIXED; SAS Institute 2005). Potential interactions between these relationships and stand also were tested. Pearson correlation coefficients and adjusted R^2 values are reported for significant relationships. Stepwise variable selection was used to compare slope and intercept values among treatments in linear and quadratic regression analyses (PROC REG; SAS Institute 2005). An alpha level of 0.05 was used in all tests.

Results

Sapling height, height growth, basal area, crown diameter, and height:diameter ratio did not differ significantly among OV or UN treatment groups prior to treatment application.

Post-treatment results are summarized in Table 2. Throughout the study, the UN treatment main effect was never significant, although there were several significant interactions between the UN treatment and other effects. Two years post-treatment, total aboveground dry weight of saplings was 21% greater in the –OV treatment than in the +OV treatment ($P < 0.01$; Table 3). Stem weight was 18% greater in the –OV treatment than in the +OV treatment ($P < 0.01$), although there were significant stand-by-OV and stand-by-UN interactions. In the stand-by-OV interaction ($P = 0.04$), stem weight averaged 28% greater in the –OV treatment than in the +OV treatment at Kalipso and West Weir, while at Shaver, stem weight was 3% less in the –OV treatment than in the +OV treatment. In the stand-by-UN interaction ($P = 0.04$), stem weight was 27% greater in the –UN treatment than in the +UN treatment at West Weir, while at Kalipso and Shaver, stem weight averaged 8% less in the –UN treatment than in the +UN treatment. Branch weight was influenced by a stand-by-OV-by-UN interaction ($P = 0.02$) resulting from a trend toward greater branch weight in the –OV – UN treatment than in the –OV + UN treatment at West Weir. Root weight, the ratio of shoot:root biomass, and foliar efficiency were not influenced by the OV or the UN treatment. The lack of an OV treatment effect on shoot:root ratio was due to the combination of increased shoot biomass and a non-significant increase in root biomass in the –OV treatment. Regression analyses did not detect any significant relationships between the dependent variables listed in Table 3 and PAR, soil water content, or foliar N concentration.

Total foliar dry weight was 33% greater in the –OV treatment compared to the +OV treatment ($P < 0.01$; Table 4). Dry weight of foliage on shoots that formed during the 2-year study (i.e., 1-to-2-year-old foliage) was 24% greater in the –OV treatment than in the +OV treatment ($P < 0.01$); however, a stand-by-OV interaction ($P < 0.01$) indicated that, at Kalipso, foliar dry weight was 69% greater in the –OV treatment than in the +OV treatment, while the differences between the same treatments were 19% at Shaver and –7% at West Weir. Dry weight of twigs that formed during the two study years was not affected

Table 2 Summary of major results for fixed treatment effects (i.e., belowground competition exclusion) and relationships with other independent variables (PAR, foliar N concentration), including references to analysis of covariance results tables

Variable	Treatment effects	Other relationships
Sapling total aboveground weight and stem weight (Table 3)	Reduced by overstory root competition; minor stand \times treatment interactions involving understory root competition	None
Foliar weight (Table 4)	Reduced by overstory root competition; no effect of understory root competition	None
Number of interwhorl buds, terminal bud volume, number of internodes (Tables 5, 6)	Reduced by overstory root competition; no effect of understory root competition	All three variables positively related to foliar N concentration; terminal bud volume positively related to PAR
Needle length, needle area, needle weight, specific leaf area, internodal distance, foliar efficiency (Tables 3, 6)	No overall effect of root competition treatments; only minor stand \times treatment interactions	None

Table 3 Analysis of covariance results for dry weight of biomass components, ratio of shoot:root biomass, and foliar efficiency of Douglas-fir saplings in the presence or absence of belowground competition from overstory (OV) and understory (UN) sources

	Aboveground weight (g)	Stem weight (g)	Branch weight (g)	Root weight (g)	Shoot:root ratio	Foliar efficiency
<i>F value</i>						
OV	9.5**	9.9**	0.9	2.8	1.3	0.0
UN	1.8	0.4	3.2	2.7	0.6	0.0
OV × UN	0.0	0.9	3.9	0.0	0.7	0.9
Stand × OV	1.9	3.7*	0.2	1.0	1.6	1.0
Stand × UN	2.1	3.7*	3.3	1.1	0.3	0.4
Stand × OV × UN	3.2	1.2	4.7*	3.2	2.5	0.6
PAR	0.4	0.3	0.7	0.3	0.9	0.0
Pre-study BA	143.7**	65.8**	97.0**	143.1**	0.8	1.5
Pre-study height	0.3	9.9*	3.8	1.7	4.3*	0.0
Pre-study growth	8.8**	4.1	14.9**	3.9	0.2	0.0
<i>Mean and standard error</i>						
+OV	475.3 (24.7)	220.1 (12.7)	119.4 (7.6)	99.7 (4.9)	4.7 (0.2)	1.45 (0.16)
−OV	574.8 (24.7)	259.1 (12.7)	130.0 (7.9)	111.1 (4.9)	5.0 (0.2)	1.46 (0.16)
+UN	502.1 (24.9)	235.8 (12.7)	114.7 (7.9)	99.6 (4.9)	4.9 (0.2)	1.46 (0.16)
−UN	547.0 (24.9)	243.4 (12.7)	134.6 (7.6)	111.1 (4.9)	4.7 (0.2)	1.45 (0.16)

Photosynthetically active radiation (PAR), pre-study basal area (BA), pre-study height, and pre-study height growth rate are covariates

*, ** Denote significance at $P = 0.05$ and $P = 0.01$ levels, respectively

by the OV treatment, nor was the dry weight of 3-to-4-year-old foliage that was formed during the 2 years prior to the study ($P = 0.07$). On branch components that were more than 4 years old, dry weight of foliage was 143% greater in the −OV treatment than in the +OV treatment ($P = 0.02$). The fraction of total biomass allocated to foliage was significantly greater in the −OV treatment (0.22) than in the +OV treatment (0.18; $P < 0.01$).

Among the covariates used in the dry weight analyses, pre-study sapling basal area generally accounted for the greatest amount of variation not explained by OV and UN treatments, stand, or block effects. The significant covariates were consistently positive in all models. Subsequent regression analysis confirmed that the slope of the linear relationships between 2-year foliar biomass and pre-study sapling basal area did not differ between OV treatments, indicating a constant additive effect of overstory root exclusion regardless of sapling size (Fig. 1). There also was no significant difference between OV treatments in the slope of the regression lines relating all other dependent variables to sapling pre-study basal area, pre-study height, and pre-study height growth rate. These relationships did not differ significantly by stand.

The number of interwhorl buds on the terminal shoot in year two of the study was significantly greater in the −OV treatment than in the +OV treatment ($P < 0.01$; Table 5). The number of interwhorl buds had a quadratic relationship with foliar N concentration in the prior dormant season (Fig. 2); this relationship did not differ significantly between the −OV and +OV treatments. The number of interwhorl buds was not significantly related to foliar N concentration in the following dormant season ($P = 0.18$) or to soil water content in either growing season ($P = 0.32$ for year 1; $P = 0.11$ for year 2). There was a very

Table 4 Analysis of covariance results for foliar biomass components and foliage fraction of Douglas-fir saplings that developed in the presence or absence of belowground competition from overstory (OV) and understory (UN) sources

Effect	Total foliar weight (g)	Foliar weight, 1–2 year-old (g)	Twig weight, 1–2 year-old (g)	Foliar weight, 3–4 year-old (g)	Foliar weight, >4 year-old (g)	Foliar fraction
<i>F value</i>						
OV	10.8**	8.6**	1.6	3.6	7.0*	14.3**
UN	3.8	1.7	0.0	2.2	3.1	0.8
OV × UN	0.7	0.3	4.1	4.2	0.9	2.5
Stand × OV	2.3	6.9**	0.8	0.1	2.1	2.4
Stand × UN	0.8	2.0	3.3	0.1	2.5	0.1
Stand × OV × UN	2.1	2.0	1.2	0.8	1.7	1.0
PAR	2.8	0.0	2.1	4.1	0.8	0.0
Pre-study BA	128.3**	81.9**	24.7**	58.9**	20.4**	2.0
Pre-study height	6.7*	4.7*	1.7	2.8	0.0	2.9
Pre-study growth	5.7*	23.3**	25.0**	0.9	0.0	2.5
<i>Mean and standard error</i>						
+OV	109.4 (7.7)	82.6 (6.4)	32.5 (3.0)	19.9 (3.6)	4.4 (1.6)	0.18 (0.01)
-OV	145.6 (7.7)	102.3 (6.4)	37.1 (3.0)	27.5 (3.7)	10.7 (1.6)	0.22 (0.01)
+UN	116.7 (7.7)	88.0 (6.4)	34.6 (3.1)	19.9 (3.6)	5.4 (1.7)	0.20 (0.01)
-UN	138.4 (7.7)	96.9 (6.4)	35.0 (3.1)	27.5 (3.5)	9.7 (1.7)	0.21 (0.01)

Photosynthetically active radiation (PAR), pre-study basal area (BA), pre-study height, and pre-study height growth rate are covariates
 *, ** Denote significance at $P = 0.05$ and $P = 0.01$ levels, respectively

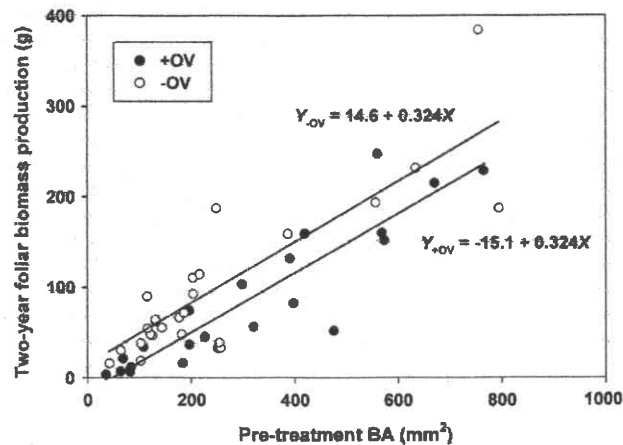


Fig. 1 Foliar biomass produced by Douglas-fir saplings in the presence (+OV) and absence (-OV) of belowground competition from the overstory, as a function of pre-treatment sapling basal area. Regression slopes do not differ ($P > 0.05$). Model $R^2 = 0.76$ ($P < 0.01$)

Table 5 Analysis of covariance results for frequency and size of buds on the terminal shoot of Douglas-fir saplings 2 years after subjecting saplings to the presence or absence of belowground competition from overstory (OV) and understory (UN) sources

Effect	Interwhorl buds (no.)	Terminal cluster (no.)	Term. bud volume index
<i>F value</i>			
OV	10.4**	0.4	6.7*
UN	3.1	2.1	0.3
OV × UN	1.0	0.1	2.8
Stand × OV	1.1	0.5	0.9
Stand × UN	1.4	1.8	0.0
Stand × OV × UN	0.2	1.2	0.6
PAR	0.8	0.0	3.1
Pre-study BA	0.1*	1.9	3.2
Pre-study growth	5.3*	1.2	1.8
<i>Mean and standard error</i>			
+OV	5.3 (1.0)	2.8 (0.3)	82.6 (8.1)
-OV	8.9 (1.0)	3.0 (0.3)	110.5 (8.1)
+UN	8.1 (1.0)	3.1 (0.3)	93.5 (8.1)
-UN	6.1 (1.0)	2.7 (0.3)	99.6 (8.1)

Photosynthetically active radiation (PAR), pre-study basal area (BA), and pre-study height growth rate are covariates

*, ** Denote significance at $P = 0.05$ and $P = 0.01$ levels, respectively

weak, positive relationship between number of interwhorl buds and PAR ($R^2 = 0.07$; $P = 0.04$). The number of buds in the terminal cluster did not differ between OV or UN treatments, although the total number of buds (interwhorl plus terminal cluster buds) in the -OV treatment (11.9 ± 1.0 (std. err.)) was significantly greater ($P < 0.01$) than in the +OV treatment (8.1 ± 1.0). Terminal bud volume index was 34% greater in the -OV treatment than in the +OV treatment ($P = 0.02$). Regression analyses showed a positive linear relationship between terminal bud volume index and foliar N concentration in the prior dormant season ($R^2 = 0.20$; $P < 0.01$) and between terminal bud volume index and PAR ($R^2 = 0.21$; $P < 0.01$); relationships did not differ by stand.

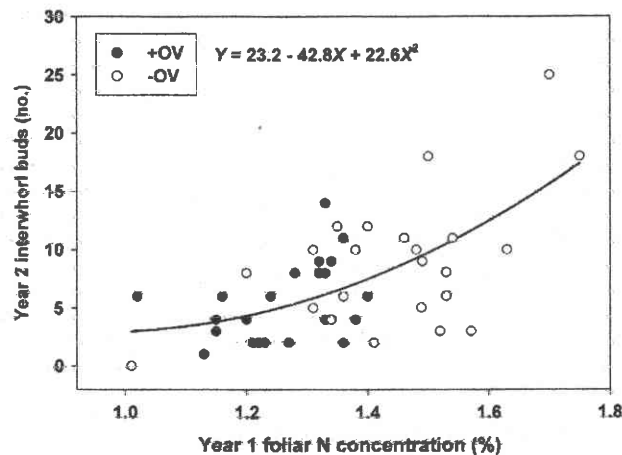


Fig. 2 Number of interwhorl buds produced by Douglas-fir saplings in the presence (+OV) and absence (-OV) of belowground competition from the overstory, as a function of foliar N concentration in the previous dormant season. Treatments were combined for the regression model shown, as slopes and intercepts did not differ between +OV and -OV treatments ($P > 0.05$). Model $R^2 = 0.41$ ($P < 0.01$)

The number of internodes on the year-two terminal shoot was 38% greater in the -OV treatment than in the +OV treatment ($P < 0.01$; Table 6). The number of internodes on the year-two shoot was positively and linearly related to foliar N concentration in the preceding dormant season ($R^2 = 0.30$; $P < 0.01$) but was not related to PAR or soil water content. Year-two internodal distance on the terminal shoot was affected by stand-by-OV and stand-by-UN interactions. In the stand-by-OV interaction ($P < 0.01$), internodal distance was significantly greater (54%) in the -OV treatment than in the +OV treatment at Kalipso but not in the other stands. In the stand-by-UN interaction ($P = 0.03$), internodal distance was 3% less in the -UN treatment than in the +UN treatment at Kalipso, similar at Shaver, and 4% greater in the -UN treatment than in the +UN treatment at West Weir. Although internodal distance was correlated with height growth in the same year ($r = 0.65$; $P < 0.01$), there was no correlation between internodal distance and number of internodes ($r = -0.05$; $P = 0.73$). Needle length, needle weight, needle area, and specific leaf area were not influenced by either OV or UN treatment effects, nor were they significantly related to foliar N, PAR, or soil water content in regression analysis. Specific leaf area was affected by a stand-by-UN interaction ($P = 0.04$), as it was 13% higher in the -UN treatment than in the +UN treatment at Kalipso and Shaver and 6% lower at West Weir.

Discussion

Where belowground competition from overstory trees was excluded, production and retention of foliage by Douglas-fir saplings increased significantly. In manipulative studies, increases in foliar mass have been reported for Douglas-fir in response to greater soil water availability or greater nutrient availability (Brix 1983; Chan et al. 2003; Gower et al. 1992). In response to greater nutrient availability, an increase in foliage production, and, to a lesser extent, an increase in foliar efficiency, have been linked to subsequent increases in stemwood production (Brix 1983). It is more likely that the increased stem growth in the present study was a result of increased foliage production than increased foliar efficiency,

Table 6 Analysis of covariance results for needle morphology of the terminal shoot of Douglas-fir saplings, formed during the second year of a study in which saplings were subjected to the presence or absence of belowground competition from overstory (OV) and understory (UN) sources

Effect	Internodes (no.)	Internodal distance (mm)	Needle length (mm)	Needle area (mm ²)	Needle weight (mg)	Specific leaf area (mm ² mg ⁻¹)
<i>F value</i>						
OV	15.9**	0.1	0.1	1.6	0.1	4.1
UN	0.0	4.1	0.2	0.4	0.1	4.2
OV × UN	2.2	0.8	0.1	0.3	0.0	1.5
Stand × OV	0.5	13.7**	2.7	2.9	2.2	0.8
Stand × UN	0.4	4.4*	0.7	0.9	0.3	3.5*
Stand × OV × UN	1.0	2.6	0.2	0.3	0.2	0.1
PAR	0.9	0.4	1.8	0.1	0.1	0.0
Pre-study BA	0.0	0.3	0.0	0.1	0.2	0.6
Pre-study growth	16.8**	0.2	2.1	1.7	0.1	2.8
<i>Mean and standard error</i>						
+OV	200.0 (16.0)	1.0 (0.1)	23.7 (0.9)	21.4 (1.3)	2.95 (0.20)	7.3 (0.2)
-OV	276.7 (16.0)	1.0 (0.1)	24.0 (0.9)	23.3 (1.3)	3.01 (0.20)	7.8 (0.2)
+UN	236.7 (16.0)	1.0 (0.1)	24.1 (0.9)	22.8 (1.3)	2.95 (0.20)	7.8 (0.2)
-UN	240.0 (16.0)	0.9 (0.1)	23.6 (0.9)	21.9 (1.3)	3.01 (0.20)	7.3 (0.2)

Photosynthetically active radiation (PAR), pre-study basal area (BA), and pre-study height growth rate are covariates

*, ** Denote significance at $P = 0.05$ and $P = 0.01$ levels, respectively

as we detected no response in foliar efficiency to the OV or UN treatments (Table 3). Mean weight of needles on branch components more than 4 years old was significantly higher in the absence of root competition from the overstory. This was apparently due to increased needle retention which may have been a result of increased availability of soil water or nutrients in the absence of belowground competition (Devine and Harrington in press). Other studies have reported greater needle retention when belowground resource availability increased. In 30- to 40-year-old Douglas-fir stands, N fertilization increased the duration of needle retention by an estimated 1–2 years (Gessel and Turner 1976). Similarly, in an N-deficient, 42-year-old Douglas-fir stand, fertilization with N increased needle retention time by at least 1 year (Turner and Olson 1976). De Visser et al. (1994) found that irrigation treatments improved needle retention of 40-year-old Douglas-fir relative to those in a non-irrigated treatment.

The relatively high mean shoot:root ratio of 4.8 for the saplings in this study (cf. Eis 1974; Newton and Cole 1991) suggests that light was more growth-limiting than belowground resources. According to the functional equilibrium model, plants alter biomass allocation in response to resource limitation, increasing foliar allocation when aboveground resources are most limiting and increasing root growth when belowground resources are most limiting (Brouwer 1962; Wilson 1988). Total sapling aboveground weight, stem weight, and foliar fraction were significantly increased by exclusion of belowground competition from overstory trees, while root weight and shoot:root ratio were not significantly affected by this treatment (Tables 3, 4). This suggests that greater belowground resource availability due to competition exclusion facilitated an increase in

aboveground growth rather than an increase in belowground growth, as would be expected if belowground resources were most growth-limiting. Thus, light remained the most limiting resource overall because aboveground components were the primary sink for photosynthates. This aboveground response of understory saplings to increased belowground resources contrasts with the response of understory saplings to an abrupt increase in light (Claveau et al. 2006; Kneeshaw et al. 2002). In the latter scenario, trees generally responded by allocating a high portion of their growth belowground for one or more years in response to a shift of their most limiting resource from aboveground to belowground. The relative influences of above- and belowground resources on Douglas-fir biomass allocation also has been demonstrated under controlled conditions: N availability treatments did not affect the shoot:root ratios of shaded seedlings, while in full sunlight, belowground allocation increased under low N availability (Reed et al. 1983).

The stand-by-treatment interactions may be explained by differences among stands in pre-study sapling condition and resources. The stand-by-OV interaction affecting stem weight may be attributed to the same phenomenon that affected sapling height growth (Devine and Harrington in press). For both stem weight and height growth, the stand-by-OV interaction was due to the lack of an OV treatment difference at Shaver. We attribute this lack of response to two patterns: (1) saplings at Shaver had, on average, a greater pre-study height:diameter ratio than those in the other stands, and (2) in all three stands, sapling height:diameter ratio was negatively correlated with post-treatment stem basal area growth ($r = -0.40$ to -0.65 ; $P < 0.01$). Thus, in the stand with the most slender saplings, the stem-weight growth response to belowground competition exclusion was smallest. This is not surprising because there is a negative correlation between height:diameter ratio and sapling vigor in Douglas-fir (Cole and Newton 1987). It is possible that, due to less vigorous saplings or to the relatively high stand BA around the study plots at Shaver (Table 1), the treatment response at that site was more gradual and thus not detected in the 2-year study. The stand-by-OV interaction, indicating that the OV treatment had no effect on 2-year foliage production at West Weir, may be explained by the fact that foliar N concentration was relatively high across all treatments at West Weir compared to the other stands, and thus, at West Weir, N may not have limited foliage production. While the -OV treatment significantly increased foliar N concentration at all three stands, at West Weir, foliar N was 1.35% in the +OV treatment, a value similar to that of the -OV treatment at the other stands.

The understory exclusion treatment had a minimal effect on the variables measured in this study. Although there were several interactions between the understory treatment and stand, none of these interactions resulted in a significant treatment difference (i.e., the UN treatment effect differed among stands but +UN never differed significantly from -UN within a given stand). Probably because the differences in the UN treatment effect among stands were relatively small, we were unable to relate these differences to any of the measured stand characteristics or to resource differences among stands. The general lack of UN treatment effect is not surprising, as the influence of understory exclusion on soil water content and foliar N was much less than that resulting from the OV treatment (Devine and Harrington in press). Under conditions of reduced overstory density, understory competition would likely be more influential (Harrington 2006).

The number of interwhorl buds and the size of the terminal bud were significantly increased by excluding belowground competition from overstory trees. Bud production of young Douglas-fir has been shown to respond more rapidly than stem growth to manipulated levels of competition, and the number of interwhorl buds may serve as an indicator of vigor, as it is positively related to stem growth in subsequent years (Tappeiner et al.

1987). The effect of competition exclusion on bud production and the relationships between foliar N concentration and interwhorl bud number (Fig. 2) indicate that competition for belowground resources was a major factor influencing sapling bud formation, and hence, the potential for formation of interwhorl branches. In a greenhouse environment, terminal bud size was significantly reduced for Douglas-fir seedlings exposed to controlled water stress treatments (Khan et al. 1996). In the relatively low-light environment of our study sites, PAR and foliar N concentration were positively and linearly related to terminal bud volume. In contrast, the number of interwhorl buds was clearly related to foliar N concentration (Fig. 2) but only weakly to PAR. This suggests that, under these conditions, both light and belowground resource availability influenced potential growth of the terminal shoot (Harrington and Tappeiner 1991), while belowground resources had a greater effect than PAR on potential formation of lateral shoots between whorls. It is uncertain whether this increased number of buds will actually result in a greater number of interwhorl shoots, as some of these lateral buds may abort.

The number of internodes on the terminal shoot in year two was significantly greater where belowground competition from overstory vegetation was eliminated. This increase in internode number indicates greater potential growth, likely a result of greater availability of belowground resources during formation of leaf primordia, which occurred late in the growing season of study year one (Allen and Owens 1972). Internode number in Douglas-fir seedlings and saplings has been shown to decrease in the presence of woody competition (Brand 1986), a pattern likely due at least in part to soil water limitation (Harrington and Tappeiner 1991). Additionally, both light (Drew and Ferrell 1977) and nutrient availability (Carlson and Preisig 1981) have been positively related to the number of internodes formed. In our study, internode number, and thus potential growth, was positively related to foliar N concentration in the previous dormant season and soil water content in the previous growing season, although we found no relationship between internode number and PAR.

Belowground competition had little effect on needle morphology or internodal distance, possibly due to the relatively low level of light availability in the understory environment. Under low-light conditions, specific leaf area of Douglas-fir increases, while individual leaf area decreases (Brand 1986; Del Rio and Berg 1979; Mailly and Kimmins 1997). Our specific and individual leaf area values were comparable to those reported previously under a similar light environment (Mailly and Kimmins 1997). It appears that the low level of light in our study produced a shade-adapted foliar morphology that was not significantly influenced by the different levels of belowground resource availability associated with the OV and UN competition exclusion treatments. A similar phenomenon was reported for Douglas-fir seedlings grown for 3 years under low light ($12 \pm 2\%$ of full sun) in western Oregon: soil water availability had no effect on seedling leaf area or specific leaf area (Chan et al. 2003). In contrast, where light is not growth-limiting, soil water or N availability may significantly affect needle morphology. In southwestern Oregon, competition for soil water reduced needle length of Douglas-fir saplings (Harrington and Tappeiner 1991), and, in western Washington, needle length and weight were positively related to N availability in a 42-year-old Douglas-fir plantation (Turner and Olson 1976).

Conclusions and implications

Morphology and biomass of Douglas-fir regeneration in multi-aged stands is significantly affected by both above- and belowground competition. Previous studies have identified the

light levels necessary for survival and growth of Douglas-fir regeneration under these conditions; however, we found that belowground competition played an important role in determining morphology and biomass of saplings. Variables associated with photosynthesis and sapling growth, including needle and bud production, needle retention, and stem biomass, all were negatively affected by the presence of tree root competition. Thus, sapling morphological traits often associated with light availability also may be influenced by belowground competition from the same overstory trees that are providing the competition for light. Regeneration of Douglas-fir in multi-aged stands therefore requires consideration of overstory competition for belowground resources in addition to overstory competition for light.

While low-intensity thinning of mature Douglas-fir may cause short-term increases in understory light, it will not create a sustained increase in availability of belowground resources. The variable-density thinning treatment applied prior to this study resulted in establishment of Douglas-fir seedlings, but long-term survival of this cohort is unlikely without greater reductions in overstory density. Formation of root gaps of sufficient size and duration to stimulate increases in soil water availability requires substantial reductions in stand basal area (66%; Brix and Mitchell 1986) or creation of relatively large canopy gaps ($>2,000 \text{ m}^2$; Vogt et al. 1995). Greater reductions in overstory density than those studied here, perhaps combined with creation of large canopy gaps and understory vegetation control, may be needed to sustain vigorous growth of understory Douglas-fir in multi-aged stands.

Beneath a partial Douglas-fir canopy, control of understory vegetation is likely to increase belowground resources to some extent (Harrington 2006; Devine and Harrington in press); however, for saplings growing beneath a relatively dense Douglas-fir overstory, we found that roots of overstory trees had a much greater effect on the morphology and biomass of saplings than did understory competition. Thus, management of understory vegetative competition under similar overstory conditions would be expected to produce little change in saplings.

Acknowledgements We thank the Fort Lewis Forestry Program for providing financial and logistical support for this project, particularly Jeffrey Foster and Allan Derickson. We thank members of the Silviculture and Forest Models Team for their assistance with field and office work, and we thank Jeffrey Foster, John Tappinciner, and J.P. (Hamish) Kimmins for providing manuscript reviews.

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