Belowground competition influences growth of natural regeneration in thinned Douglas-fir stands

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Abstract: Using a factorial combination of understory removal and trenching treatments, we examined the influences of belowground competition from understory and overstory vegetation on growth of naturally established Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) saplings in thinned stands of Douglas-fir on moderately productive, glacially derived soils near Tacoma, Washington. Under limited light (26% ± 16% of full sun), sapling height and diameter growth were significantly reduced by belowground competition from overstory trees. Regardless of presence or absence of belowground competition from trees, understory vegetation did not have a detectable effect on sapling growth. Nitrogen deficiency in saplings was not detected in the presence of belowground competition: where tree roots were excluded, foliar nitrogen concentration and content increased without an increase in foliar mass. Belowground competition from overstory trees had a greater negative effect on growing season soil water content than did understory vegetation. Under the conditions of restricted light availability in this study, limitations in soil water content from competition had a strong growth-limiting effect on Douglas-fir regeneration. As potential canopy trees in a future uneven-aged stand, this sapling cohort would benefit from root gaps created during harvests.

Résumé : À l'aide d'une combinaison factorielle de traitements qui consistaient à éliminer le sous-bois ou à creuser des tranchées, nous avons étudié l'influence de la compétition de la végétation du sous-bois et de l'étage dominant sur la croissance des gaules de douglas de Menzies typique (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) d'origine naturelle. L'étude a été réalisée dans des peuplements de douglas de Menzies établis sur des sols d'origine glaciaire modérément productifs près de Tacoma, dans l'État de Washington. Dans des conditions de faible luminosité (26 % ± 16 % du plein soleil), la croissance en hauteur et en diamètre des gaules était significativement inhibée par la compétition souterraine des arbres de l'étage dominant. Peu importe la présence ou non de compétition souterraine des arbres, la végétation du sous-bois n'avait pas d'effet détectable sur la croissance des gaules. Aucune déficience en azote n'a été détectée chez les gaules en présence de compétition souterraine. Aux endroits où les racines des arbres ont été exclues, la teneur et la concentration en azote foliaire ont augmenté sans que la masse foliaire augmente. La compétition souterraine des arbres de l'étage dominant avait un effet négatif plus prononcé sur le contenu en eau du sol durant la saison de croissance que la végétation du sous-bois. Dans cette étude où la disponibilité de la lumière était faible, le contenu en eau du sol limité à cause de la compétition a fortement inhibé la croissance de la régénération du douglas de Menzies. En tant qu'arbres potentiels de la canopée dans un futur peuplement inéquienne, cette cohorte de gaules bénéficierait des trouées racinaires créées lors des récoltes.

[Traduit par la Rédaction]

Introduction

The recent emphasis on managing Pacific Northwest Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests for multiple objectives, particularly for wildlife habitat and old-forest aesthetics, has created a renewed interest in uneven-aged management in the region (Emmingham 1998; Franklin et al. 2002, 2007). Some characteristics of uneven-aged stand structure may be achieved through commercial thinning in second-growth Douglas-fir forests, although long-term development of multiple cohorts requires successful establishment and continued growth and survival of conifer regeneration in the understory (Bailey and Tappeiner 1998; Miller and Emmingham 2001). While the growth rate of Douglas-fir regeneration is positively related to light availability, and thus negatively related to overstory density (Carter and Klinka 1992; Drever and Lertzman 2001), the species is moderately tolerant of shade when young and may survive in as little as 20% of full sunlight (Dunlap and Helms 1983; Mailly and Kimmins 1997; Miller and Emmingham 2001). However, continued survival and development of Douglas-fir under such conditions is unlikely without release or subsequent reductions in overstory density (Helms and Standiford 1985; Tesch and Korpela 1993; Bailey and Tappeiner 1998; Brandeis et al. 2001).

Where tree regeneration occurs beneath an overstory canopy, root systems of tree seedlings typically occupy a portion of the soil profile also occupied by roots of overstory trees and understory species. Therefore, soil water and nutrient pools available to seedlings are influenced as a result of uptake by, and interactions between, the overstory and understory vegetation. For example, shading from the overstory influences the amount of soil water consumed by the understory (Aussenac 2000). Where Douglas-fir overstory density is relatively high, the partial influence of the

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understory on soil water content (SWC) is less than where overstory density is low (Harrington 2006; Devine and Harrington 2007). In an old-growth Douglas-fir – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stand, evapotranspiration from the understory was 10% of total stand evapotranspiration (Unsworth et al. 2004), while in a recently thinned, 22-year-old Douglas-fir stand, a salal (*Gaultheria shallon* Pursh) understory accounted for over 45% of total stand evapotranspiration (Tan et al. 1978).

Overstory influences on SWC and soil nutrients have been investigated by root-exclusion (i.e., trenching) studies in numerous ecosystems (Aarssen and Epp 1990; Coomes and Grubb 2000), including Pacific Northwest conifer forests (e.g., Christy 1986; Hart and Sollins 1998; Gray et al. 2002). These studies show that transpiration by overstory trees, combined with insufficient precipitation to recharge the soil profile, causes a cumulative depletion of soil water over the growing season (Hope and Li 1997; Simard et al. 1997; Gray et al. 2002; Lindh et al. 2003). The overstory also influences soil water through canopy interception, which may significantly reduce the amount of precipitation reaching the forest floor (Rothacher 1963; Dunlap and Helms 1983; Devine and Harrington 2007). The level of nutrient competition from the overstory varies by forest type and the native fertility of the soil (Riegel et al. 1992; Coomes and Grubb 1998; Lewis and Tanner 2000). In the coastal Pacific Northwest, the role of nutrient competition is less clear than the role of competition for soil water, as N availability is variable following exclusion of tree roots (Vitousek et al. 1982; Simard et al. 1997; Hart and Sollins 1998). Because the level of tree root competition is negatively related to SWC, and because N mineralization rate is positively related to SWC (Stanford and Epstein 1974; Walters et al. 2006), it seems likely that N availability would be less in the presence of tree root competition regardless of the level of N uptake by trees.

Previous research indicates that the relative influences and interactive effects of root competition from overstory and understory vegetation are poorly understood. In a study located in mature Douglas-fir stands previously subjected to variable-density thinning, our first objective was to separate and quantify the effects of belowground competition from overstory and understory vegetation on growth of naturally established Douglas-fir saplings. Based on previous research (Harrington 2006), we hypothesized that growth of saplings is negatively influenced by belowground competition from both overstory and understory vegetation and that, in combination, these negative effects on growth would be additive. We tested this hypothesis by manipulating belowground competition sources independent of overstory shading. The second objective of the study was to determine how SWC and nutrient status of the Douglas-fir saplings are influenced by these sources of belowground competition and to what extent sapling growth is related to belowground resource and light availability.

Methods

Study site

The study was conducted in the Puget Trough physiographic province on the Fort Lewis Military Reservation (47.05°N, 122.55°W; 100 m above mean sea level) near Tacoma, Washington, USA. Prior to European settlement in the mid-1800s, the study area consisted of lowland prairies maintained by frequent anthropogenic fire (Foster and Shaff 2003). After settlement, the area was used for livestock grazing but was gradually colonized by natural Douglas-fir regeneration. The study was installed in three Douglas-fir stands that resulted from this colonization. The stands, named Kalipso, Shaver, and West Weir, originated about 1920–1930 and are located 10–15 km apart. These stands were thinned two or three times (15%–20% of basal area removed each time) prior to study establishment in 2005 (Table 1). The most recent thinning in each stand was a variable-density thinning, designed to create spatial variability in overstory density and understory light availability. It is likely that much of the natural Douglas-fir regeneration that is the subject of this study established in areas where these thinnings increased the amount of sunlight reaching the forest floor. The 50-year site index for Douglas-fir in the study area is between 34 and 38 m (King 1966). The plant association is *P. menziesii* var. *menziesii* – *Symphoricarpos albus* (L.) Blake – *Amelanchier alnifolia* Nutt. (Chappell and Crawford 1997).

The soil at all three stands is a gravelly sandy loam of the Spanaway series (Typic Melanoxerand), formed in glacial outwash deposited following the Vashon Glaciation approximately 14 000 years BP. The A horizon (0–38 cm) of the Spanaway series is a gravelly sandy loam, strongly acidic, and somewhat excessively drained, with approximately 35% gravel (i.e., pebbles 2–75 mm in diameter) by volume (Soil Survey Staff 2006). The gravel content increases to 60% in the Bw horizon (38–48 cm, very gravelly sandy loam) and to 70% in the C horizon (48+ cm, extremely gravelly sand).

The study area has a maritime climate with dry summers and mild, wet winters. Mean annual temperature is 12 °C; mean temperatures in January and July are 5 and 19 °C, respectively (Western Regional Climate Center 2007). Long-term mean annual precipitation at Fort Lewis is 1026 mm, although precipitation from 1 June through 30 September averages only 150 mm. Precipitation totals for that interval during years 1 and 2 of this study (2005 and 2006) were 124 and 73 mm, respectively.

Study design

The 2-year study followed a randomized-block design with a 2 by 2 factorial treatment arrangement in each of 12 complete blocks. A nested blocking design was used with four blocks nested within each stand. The replication of blocks within stand permitted analysis of potential interactions between the random stand effect and the fixed treatment effects. The experimental unit (n = 48, 4 per block) was a 3.0 by 3.0 m square plot established around naturally regenerated Douglas-fir saplings (so-called "study saplings"). Treatments 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). Plots were 5–20 m apart within each block, and four blocks were located 50–500 m apart in each stand. During study installation, plot locations were randomly chosen within each block by first identifying six potential plots and then

Table 1. Characteristics (mean ± 1 SD) of three thinned Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) stands on Fort Lewis Military Reservation near Tacoma, Washington.

	Stand		
Variable	Kalipso	Shaver	West Weir
Overstory			
Stand BA ($m^2 \cdot ha^{-1}$)[a]	41.6	38.1	41.1
BA at study plots ($m^2 \cdot ha^{-1}$)[b]	23.1±14.3	39.8±7.8	34.1±6.6
Trees (ha^{-1})[a]	217	128	124
Thinned (years)	1980, 1990, 2001	1985, 1997	1968, 1983, 1997
Understory			
PAR (% of full sunlight)	34±19	22±7	24±15
Forbs, year 1 (% cover)	37±30	15±17	30±27
Grasses, year 1 (% cover)	37±33	13±10	4±9
Shrubs and vines, year 1 (% cover)	64±22	94±7	92±9
Forbs, year 2 (% cover)	34±30	27±26	34±25
Grasses, year 2 (% cover)	35±32	13±7	7±12
Shrubs and vines, year 2 (% cover)	71±29	92±15	94±10
Study saplings[c]			
Sapling height (cm)	136±38	121±27	183±49
Sapling diameter (mm)	17.7±6.4	12.2±3.7	20.8±6.3
Height to diameter ratio	90.1±14.5	102.6±17.9	91.4±24.4
Crown diameter (cm)	87±31	72±24	109±33
Pretreatment height growth ($cm \cdot year^{-1}$)[d]	16.8±5.8	18.1±5.2	14.5±6.8
Age (years)	8.4±2.5	7.2±2.1	11.3±3.1

[a]Basal area (BA) and trees per hectare reported at the stand level by Churchill (2005).

[b]Measured with 5 $m^2 \cdot ha^{-1}$ BA factor prism from the center of each plot (n = 48). Values differ from stand BA because study plots were located around natural regeneration, which was often located where overstory density was below the stand average.

[c]Mean values measured prior to the study year 1 (n = 124).

[d]Mean annual growth during the 2 years prior to treatment implementation.

randomly selecting four of these. To quantify the influence of overstory density, which varied both between and within the 12 blocks, photosynthetically active radiation (PAR) (described below) was measured at each plot and treated as a covariate.

Each study plot was established around two or three Douglas-fir saplings of the same cohort with no major stem defects or evidence of severe browsing by deer. These study saplings were 0.75–3.0 m in height, but within each plot, saplings were of similar size (height of the tallest <30% greater than that of the smallest) and age (assessed by counting branch whorls). The perimeter of each sapling's crown was ≥0.5 m within the plot boundary, and there was no crown contact between saplings. Poststudy excavation of the root systems of 48 of the saplings confirmed little or no overlap of root systems between adjacent saplings. On all study plots, tree seedlings or saplings other than the study saplings, including Douglas-fir, were severed at the ground line prior to treatment. To minimize the effect of this removal on the understory competitive environment of the study saplings, plots were selected with little or no presence of additional tree regeneration. To eliminate light competition from the understory, vegetation contacting or shading crowns of study saplings was cut back annually. Where this was necessary, it typically involved pruning one or two branches from an adjacent shrub; it did not cause mortality or substantially alter the foliar biomass of competitors. Mesh bud protectors (Terra Tech, LLC, Eugene, Oregon) were used to reduce the likelihood of damage from deer browse; protectors were maintained regularly to prevent mechanical damage or deformity.

Treatment application

The OV and UN treatments were initiated between 29 March and 12 April 2005. In the +OV+UN treatment combination (i.e., the nontreated control), no treatment was applied beyond the plot establishment procedure described above. In the –OV treatment, plot perimeters (n = 24) were trenched to a depth of 0.50–0.55 m using a walkalong, gasoline-powered trencher (Ditch Witch 1330; The Charles Machine Works, Inc., Perry, Oklahoma). Roots too large to cut with the trencher were cut with a handsaw or chainsaw. Trenches were lined with 0.152 mm flexible plastic sheeting and backfilled with soil. Trenching depth was based on the approximate depth at which the soil C horizon began. Although roots of overstory trees certainly occurred within the C horizon, the frequency of tree root occurrence on similar glacially derived soils was substantially less in the C horizon than in the A and B horizons (Eis 1974; Devine and Harrington 2005). Thus, while the –OV treatment did not exclude all overstory root competition, the treatment probably excluded most of it, including the roots that would have occupied the rooting zone of the saplings.

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

3-week intervals, depending on growth rate, during the growing season using hand tools and an electric trimmer (GH600; Black & Decker, Hunt Valley, Maryland). Herbicide application was not permitted at the study site, but manual control provided near-total removal of the aboveground portion of understory vegetation. To minimize soil disturbance, roots of understory vegetation were not removed in the –UN treatment.

Data collection

At study installation, total sapling height, crown diameter in two perpendicular directions, and interwhorl distance of the uppermost four branch whorls were measured to the nearest centimetre for all study saplings. Stem diameter was measured to the nearest millimetre at a marked location 15 cm above ground. Basal area of overstory trees was measured from the center of each plot using a hand-held prism (basal area factor of 5 $m^2 \cdot ha^{-1}$). After each growing season of this study, stem diameter, length of new terminal growth, and evidence of damage were recorded for study saplings.

Dormant-season foliar samples were collected in early January following study years 1 and 2. Foliar samples were collected from the past year's growth in the upper two branch whorls of each study sapling and composited by plot. These dormant-season samples were collected as an indication of N availability during the previous growing season; foliar N levels were assumed to have stabilized during the dormant season. For each foliar sample, dry needle mass was measured on a subsample of 100 randomly selected needles. Total N concentration was determined by dry combustion analysis using a LECO CNS-2000 analyzer (LECO Corporation, St. Joseph, Michigan). Total P and K concentrations in year 2 were determined by inductively coupled plasma atomic emission spectroscopy using a Perkin Elmer OPTIMA 3000 DV (PerkinElmer, Inc., Waltham, Massachusetts).

Crown cover (percent) of understory vegetation was visually estimated for each plot in the +UN treatments on 2 August of year 1 and 10 August of year 2. Cover for each growth form class (graminoids, forbs, woody vines and shrubs) was recorded to the nearest 5% for covers between 5% and 95% and to the nearest 1% outside this range.

One Ech_2o EC-20 soil water probe (Decagon Devices, Inc., Pullman, Washington) was installed in each plot to measure volumetric SWC for the duration of the study. The 20 cm probes measured SWC between 10 and 30 cm beneath the mineral soil surface in the A horizon. This interval was chosen as representative of the rooting depth of the saplings based on observations of excavated saplings in the study area. Within each plot, the probe location was a random point ≥0.5 m from the plot edge and ≥0.5 m from the crown perimeter of the nearest sapling. Measurements from the four soil water probes in each block were recorded at 4 h intervals using an EM5 datalogger (Decagon Devices, Inc.). Millivolt data recorded by the logger were converted to SWC (cubic metres per cubic metre) through a soil-specific calibration developed in the laboratory using soil samples from the study area. A soil water retention curve for the Spanaway soil series was created from series-specific particle size distribution and soil water retention data (Soil Survey Staff 2007) using the ROSETTA model (Schaap et al. 2001). From this curve, it was determined that water potentials of –10, –100, –200, –400, and –1500 kPa are equivalent to SWCs of 0.29, 0.18, 0.15, 0.12, and 0.08 $m^3 \cdot m^{-3}$, respectively.

PAR in the understory was measured on three summer days in year 1 (20 June, 13 July, and 15 August 2005) using an AccuPAR light sensor (Decagon Devices, Inc.). Conditions on these dates ranged from overcast to clear, and all data were collected within 2 h of solar noon. Measurements were made in 10 locations per plot, at the height of the tallest sapling, while a second datalogger simultaneously measured potential PAR in a nearby clearing. The PAR readings were expressed as a percentage of potential PAR and were averaged by plot across the three dates. The resulting value was used as an index of PAR in our analyses.

Data analysis

Objective 1: Sapling growth

Effects of competition on sapling growth (annual increments in stem cross-sectional area and height) were analyzed using repeated-measures analysis of covariance (ANCOVA) (PROC MIXED; SAS Institute Inc. 2005). The OV and UN treatments were arranged in a 2 by 2 factorial, with stand and block within stand as random effects and year as a within-subject effect. The saplings in this study varied in pretreatment size and pretreatment growth rate; furthermore, owing to variation in cohort age and microenvironment, pretreatment size and growth rate were not correlated. To adjust for the effects of these pretreatment differences, pretreatment sapling cross-sectional (basal) area (BA) and pretreatment height growth rate (during 2 years prior to the study) were included as covariates. Other potential covariates such as pretreatment sapling height, age, and growth rate during 4 years prior to the study explained less variation and therefore were not used. To remove the effect of differences in light availability resulting from variation in overstory density, PAR also was used as a covariate. Analysis of variance (ANOVA) assumptions of normality, equal variance, and absence of an interaction between covariates and fixed effects, including year, were tested and found to be valid in all cases. An alpha level of 0.05 was used in all tests, and multiple comparisons of least-squares adjusted means were performed using the Bonferroni procedure (Rice 1989).

Objective 2: SWC and foliar nutrients

Effects of belowground competition treatments on growing season SWC were analyzed for each year using a repeated-measures ANOVA model with a 2 by 2 factorial treatment arrangement and with stand and block within stand as random effects. Month (n = 5 per year) was the within-subject effect.

Nutrient status of saplings in each year was assessed by vector analysis following the diagnostic procedure described by Timmer and Stone (1978). In this procedure, foliar mass (100-needle sample), foliar nutrient content, and foliar nutrient concentration are simultaneously assessed to determine if treatments resulted in nutrient dilution, nutrient deficiency, luxury consumption (i.e., nutrient uptake in ex-

Table 2. Results of ANCOVA for testing effects of belowground competition from overstory trees (OV) and understory vegetation (UN), and the interactions between these factors and stand, on sapling height and basal area (BA) growth, with photosynthetically active radiation (PAR), pretreatment BA, and pretreatment height growth rate as covariates.

	Height growth		BA growth	
	F	*P* > *F*	*F*	*P* > *F*
OV	10.1	**0.004**	8.6	**0.007**
UN	0.8	0.368	1.0	0.322
OV × UN	0.0	0.900	0.3	0.575
Year	13.6	**<0.001**	13.9	**<0.001**
Year × OV	8.2	**0.005**	0.3	0.591
Year × UN	0.2	0.674	0.0	0.925
Year × OV × UN	1.2	0.268	0.2	0.688
Stand × OV	3.9	**0.034**	0.4	0.650
Stand × UN	1.3	0.286	1.9	0.165
Stand × OV × UN	0.4	0.661	0.6	0.551
Stand × year	0.1	0.931	0.4	0.670
Stand × year × OV	0.2	0.808	2.0	0.136
Stand × year × UN	0.6	0.535	0.1	0.867
Stand × year × OV × UN	0.9	0.394	1.8	0.173
PAR	0.2	0.666	0.9	0.350
Pretreatment BA	16.5	**<0.001**	136.2	**<0.001**
Pretreatment height growth	35.3	**<0.001**	14.3	**<0.001**

Note: Numerator df = 1 for all effects except stand (df = 2). Significant treatment effects ($P < 0.05$) are shown in bold text.

cess of that required for optimum growth), or toxic accumulation. ANOVA models with Bonferroni comparisons of adjusted means (experimentwise alpha level = 0.05) were used to determine whether foliar nutrient concentration, foliar nutrient content, and foliar mass differed significantly between the control (+OV+UN) and each of the other three treatment combinations. A repeated-measures ANOVA model was used for foliar N analysis because it was measured in both study years.

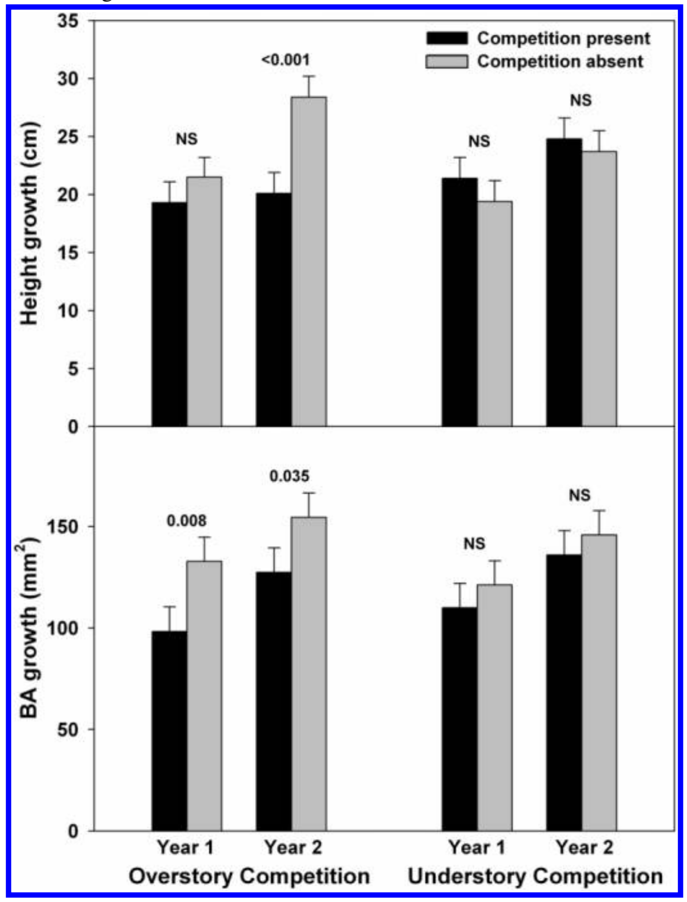
The relative importance of SWC, PAR, and pretreatment sapling size and growth rate on sapling BA and height growth in each study year was assessed by modelling BA and height growth using multiple regression with stepwise variable selection (PROC REG; SAS Institute Inc. 2005). Independent variables were monthly mean SWC in July, August, and September of year 1 (year 1 models) or from both years (year 2 models), PAR measured in year 1 (we assumed that PAR did not change between years), pretreatment sapling BA, and pretreatment sapling height growth rate. Significant variables ($P < 0.05$) were retained in the final models. Relationships between SWC, foliar nutrient concentrations, PAR, vegetation cover, and sapling growth were examined using simple correlation analysis (PROC CORR; SAS Institute Inc. 2005).

Results

Objective 1: Sapling growth

Pretreatment sapling conditions appear in Table 1. Post-treatment sapling height growth was influenced by a significant interaction between the OV treatment and study year

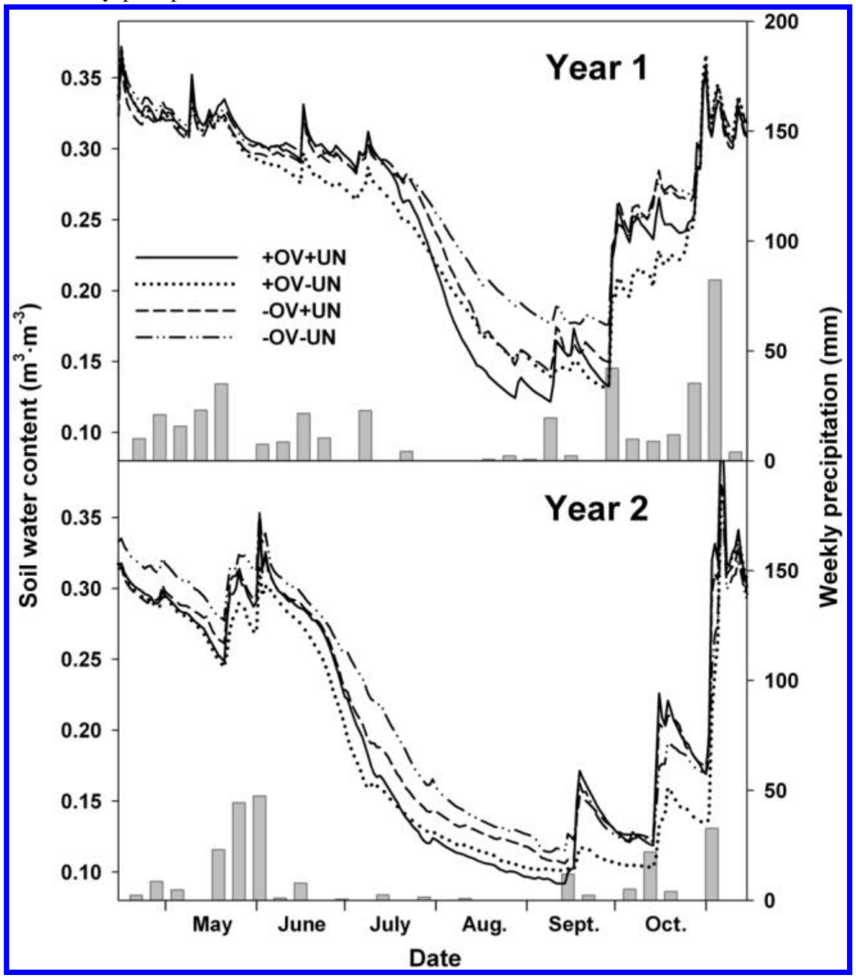
Fig. 1. Height and basal area (BA) growth (with standard error) of naturally regenerated Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) saplings subjected to the presence or absence of belowground competition from overstory and understory vegetation. *P* values indicate significance of differences between paired bars; ns, not significant.



($P = 0.005$) (Table 2). In year 1, height growth did not differ between OV treatments, but in year 2, height growth was 41% greater in the –OV treatment than in the +OV treatment (Fig. 1). Within the +OV treatment, height growth was similar in study years 1 and 2. There was a significant stand by OV interaction affecting height growth: the –OV treatment exhibited differences in height growth of +26%, –2%, and +55%, relative to the +OV treatment, in the Kalipso, Shaver, and West Weir stands, respectively. Height growth did not vary significantly between UN treatments ($P = 0.368$), nor was there a significant interaction between the OV and UN treatments or between the UN treatment and year.

Across years, sapling BA growth was 27% greater in the –OV treatment than in the +OV treatment ($P = 0.007$) (Table 2). The UN treatment did not significantly influence BA growth, nor did the UN treatment interact with the OV treatment or year. Mean annual BA growth in the +OV–UN treatment (121.1 ± 13.0 mm^2) did not differ from that of the control treatment (+OV+UN) (104.6 ± 13.9 mm^2), while the –OV+UN and –OV–UN treatments (141.5 ± 12.9 and 146.0 ± 13.1 mm^2, respectively) were significantly greater than the control ($P < 0.05$). BA growth was less in year 1 than in year 2 (115.6 ± 10.2 versus 141.0 ± 10.2 mm^2, re-

Fig. 2. Soil water content (represented by lines) at a 10–30 cm soil depth in a thinned Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) stand on plots with the presence (+) or absence (–) of belowground competition from overstory (OV) and understory vegetation (UN). Vertical bars represent the sum of weekly precipitation.



spectively). However, when BA growth was expressed as annual percent change, growth was 41% and 42% in the +OV treatment in years 1 and 2, respectively, and 58% and 45% in the –OV treatment in years 1 and 2, respectively. There were no significant treatment by stand interactions influencing BA growth.

The relationships between the significant covariates (i.e., pretreatment BA and pretreatment height growth rate) and sapling growth in the height and BA models were positive in all cases. PAR was not significant in the height or BA models, and PAR did not interact with the fixed effects in the models.

Objective 2: SWC and foliar nutrients

Overall, SWC remained low for a longer period in year 2 than in year 1 (Fig. 2). In year 1, SWC in the control treatment (+OV+UN) never fell below 0.120 m^3·m^{-3}, but in year 2, SWC remained below 0.120 m^3·m^{-3} for 48 days, beginning 3 August. The minimum SWC in the control treatment (0.092 m^3·m^{-3}) occurred in mid-September of year 2.

In both study years, SWC was greater in the –OV treatment than in the +OV treatment (Table 3; Fig. 2). An OV by month interaction occurred in both years, with the OV treatment significant in the months of July, August, and September. During year 1, the magnitude of this treatment effect was greatest in the month of August when SWC was 0.166 m^3·m^{-3} in the +OV treatments and 0.199 m^3·m^{-3} in the –OV treatment. During year 2, the treatment effect was greatest in July when SWC was 0.158 m^3·m^{-3} in the +OV treatment and 0.192 m^3·m^{-3} in the –OV treatment. A month by UN interaction occurred in year 1; in August, SWC was significantly greater in the –UN treatment relative to the +UN treatment (a difference of 0.030 m^3·m^{-3}). In both years, there was a significant stand by OV interaction that peaked in magnitude in June. In June of year 1, SWC in the –OV treatment differed by –0.027, –0.008, and +0.054 m^3·m^{-3} relative to the +OV treatment in the Kalipso, Shaver, and West Weir stands, respectively. No relationships were detected between coverage of understory vegetation and SWC.

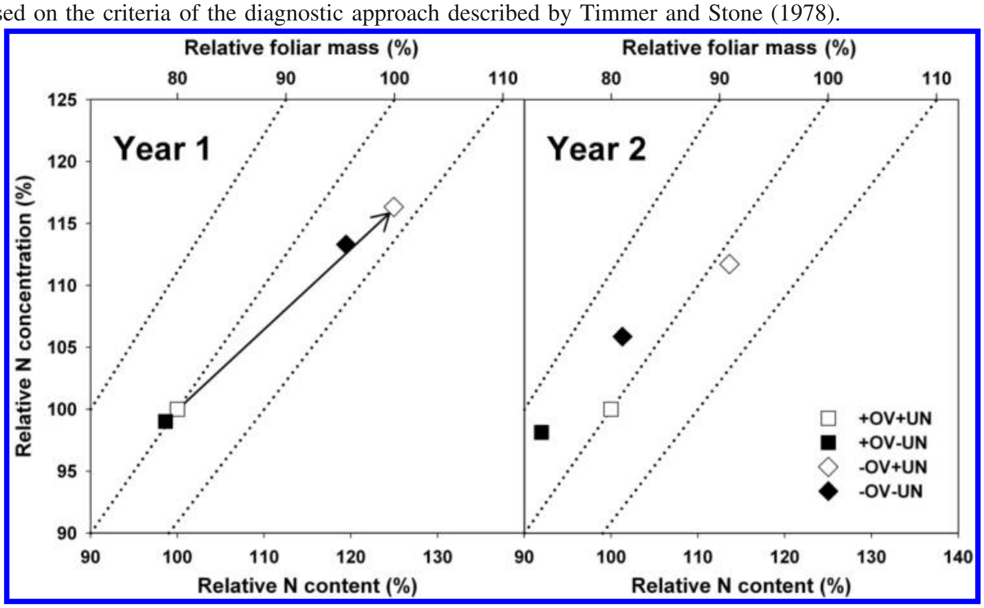
Across all treatments, foliar N concentration averaged 1.35% ± 0.16% and 1.15% ± 0.11% in years 1 and 2, respectively. Concentration of foliar N was significantly lower in the +OV treatment than in the –OV treatment in years 1 and 2, although an OV by year interaction indicated that the OV effect was larger in year 1 (Table 4). The UN treatment did not affect foliar N in either year, nor were there OV by UN interactions. Foliar P concentration in year

Table 3. Results of repeated-measures ANOVA for testing effects of belowground competition from overstory trees (OV) and understory vegetation (UN), and the interactions between these factors and stand, on volumetric soil water content at a soil depth of 10–30 cm during two growing seasons (May–September).

		Year 1		Year 2	
	Numerator df	*F*	*P* > *F*	*F*	*P* > *F*
OV	1	7.2	**0.012**	7.5	**0.011**
UN	1	0.4	0.519	0.2	0.658
OV × UN	1	1.9	0.186	1.9	0.182
Month	4	684.3	**<0.001**	907.9	**<0.001**
Month × OV	4	6.5	**<0.001**	2.5	**0.046**
Month × UN	4	8.9	**<0.001**	1.7	0.159
Month × OV × UN	4	0.3	0.893	0.8	0.529
Stand × OV	2	13.3	**<0.001**	5.5	**0.010**
Stand × UN	2	2.0	0.152	2.3	0.123
Stand × OV × UN	2	1.0	0.366	0.1	0.904
Stand × month	8	7.9	**<0.001**	2.3	**0.025**
Stand × month × OV	8	0.9	0.496	1.6	0.147
Stand × month × UN	8	1.1	0.347	1.6	0.134
Stand × month × OV × UN	8	1.2	0.300	0.5	0.860

Note: Significant values ($P < 0.05$) are shown in bold text.

Fig. 3. Relative N concentration, N content, and foliar mass (100-needle sample) for naturally regenerated Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) saplings subjected to presence (+) or absence (–) of belowground competition from overstory (OV) and understory vegetation (UN) using the +OV+UN treatment combination as the control (i.e., 100%). An arrow indicates significant ($P < 0.05$) deviation from the control based on the criteria of the diagnostic approach described by Timmer and Stone (1978).



2 was affected by an OV by UN interaction: in the –OV treatment, foliar P concentration was higher in the presence versus absence of the understory (0.14% versus 0.12%). Foliar K was not affected by either treatment. Treatment effects on foliar nutrient concentrations did not differ among stands.

Vector analysis of year 1 foliar N indicated that, relative to the control treatment (+OV+UN), the –OV+UN treatment resulted in significantly increased foliar N content and concentration with no significant change in foliar mass (Fig. 3). A similar pattern occurred for the –OV–UN treatment, although the increase in foliar N content was not significant ($P = 0.081$). Foliar N concentration and content in the +OV–UN treatment did not differ from the control treatment. Year 2 vector analysis showed no significant differences between the control treatment and the other treatments in foliar N content, foliar N concentration, or foliar mass. Vector analyses of year 2 foliar P and K showed no significant vectors (data not shown).

Simple correlation between PAR and both height and BA increment revealed several positive relationships (Fig. 4). A significant SWC – height growth correlation occurred in year 2. Correlations between foliar N concentration and growth were stronger in year 1 than in year 2. There was no significant correlation between PAR and foliar N concentration in either year (data not shown). When data from both

Table 4. ANOVA results and treatment means (SE in parentheses) for foliar nutrient concentrations (%) for naturally regenerated Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) saplings subjected to presence (+) or absence (–) of belowground competition from overstory trees (OV) and understory vegetation (UN).

	N		P (year 2)		K (year 2)	
	F	*P* > *F*	*F*	*P* > *F*	*F*	*P* > *F*
OV	43.0	**<0.001**	0.8	0.374	0.4	0.539
UN	2.2	0.148	6.2	**0.020**	3.8	0.060
OV × UN	0.6	0.452	8.6	**0.007**	0.0	0.878
Year	98.4	**<0.001**				
Year × OV	4.6	**0.039**				
Year × UN	0.2	0.662				
Year × OV × UN	0.1	0.819				
Stand × OV	0.1	0.881	2.1	0.145	1.3	0.287
Stand × UN	0.1	0.974	1.7	0.203	0.4	0.665
Stand × OV × UN	1.0	0.393	1.4	0.267	0.2	0.835
Stand × year	0.4	0.672				
Stand × year × OV	1.0	0.392				
Stand × year × UN	0.8	0.441				
Stand × year × OV × UN	0.4	0.699				
+OV+UN, year 1	1.26 (0.04)b					
+OV–UN, year 1	1.25 (0.04)b					
–OV+UN, year 1	1.47 (0.04)a					
–OV–UN, year 1	1.43 (0.04)a					
+OV+UN, year 2	1.11 (0.03)bc		0.13 (0.01)ab		0.53 (0.04)a	
+OV–UN, year 2	1.09 (0.03)c		0.13 (0.01)ab		0.48 (0.04)a	
–OV+UN, year 2	1.24 (0.03)a		0.14 (0.01)a		0.55 (0.04)a	
–OV–UN, year 2	1.18 (0.03)ab		0.12 (0.01)b		0.50 (0.04)a	

Note: Means within a given year followed by the same letter are not significantly different according to the Bonferroni test ($P > 0.05$).

years were pooled, July SWC was significantly correlated with N concentration of the same year's foliage, assessed during the dormant season (Fig. 5). August SWC also was correlated with foliar N concentration, although the relationship was not as strong as for July ($r = 0.56$, $P < 0.001$). There were no significant correlations between sapling growth and cover of understory vegetation.

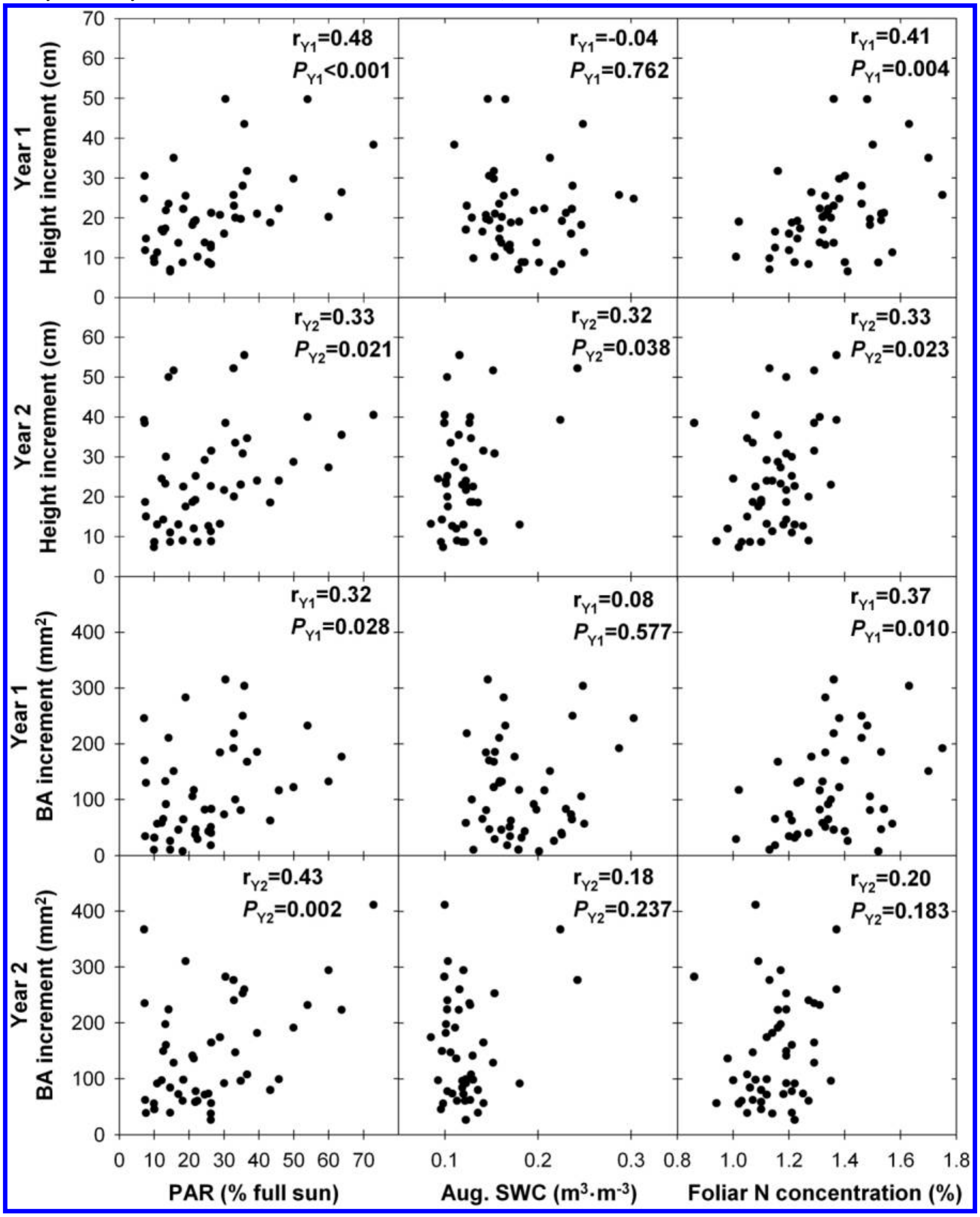
Results of the multiple regression analysis indicated that, in year 2, July SWC was a significant predictor of height growth and August SWC was a significant predictor of BA growth (Table 5). SWC during any of the months in year 1 was not a significant predictor of growth. PAR, pretreatment BA, and pretreatment height growth rate were significant in all models, except the model of second-year BA growth in which pretreatment height growth was not significant (P = 0.084).

Discussion

In the light-limited understory environment of the thinned Douglas-fir stands, growth of naturally regenerated Douglas-fir saplings was significantly reduced by belowground competition from overstory trees but not by belowground competition from the understory. Where both sources of belowground competition were removed, sapling growth was similar to that where only belowground competition from the overstory was removed. These results fail to support our hypothesis of an additive reduction in growth owing to belowground competition from overstory and understory sources. For other conifer species, it has been shown that the negative effect of understory competition on growth of young trees is dependent on overstory density and that this response to overstory density varies according to a species' shade tolerance (Christy 1986; Mitchell et al. 2004; Harrington 2006). For Douglas-fir, the negative impact of understory competition on seedling growth decreases with increasing overstory density, although, regardless of understory competition, seedling growth rates are lower beneath a forest canopy (Harrington 2006). Given the overall level of shading in this study, it is likely that the low-light conditions limited the response of saplings to manipulation of belowground competition. When belowground resources were increased (i.e., the –OV treatment), light availability in this study was too low to elicit the type of response to soil resources that occurs where Douglas-fir saplings grow in conditions at or above approximately 40% of full sunlight (Drever and Lertzman 2001).

SWC was more consistently influenced by overstory competition than by understory competition, with the –OV treatment effect similar in magnitude to that of previous trenching experiments on similar soil types (Hope and Li 1997; Devine and Harrington 2007). Effects of overstory and understory competition sources on SWC were additive, with the greatest soil water depletion occurring in the presence of both. Harrington (2006) found that, in the presence of understory competition, overstory presence had little effect on SWC because understory water uptake was greater in the absence of overstory trees, compensating for the lack

Fig. 4. Correlation between height and basal area (BA) growth of naturally regenerated Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) saplings, photosynthetically active radiation (PAR), soil water content (SWC), and foliar N concentration.



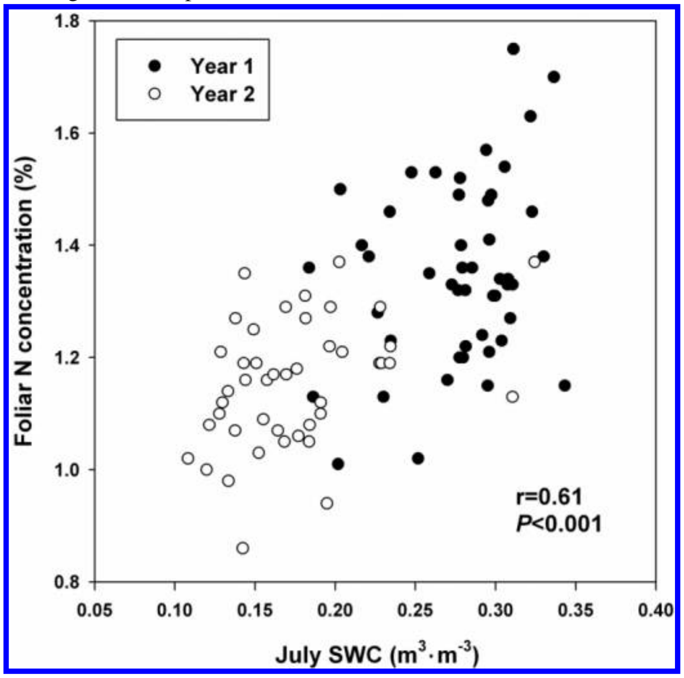
of overstory uptake. In this study, we did not find a significant compensation by the understory when overstory root competition was excluded: understory vegetation depleted mean August SWC by approximately the same amount (0.020 $m^3 \cdot m^{-3}$) with or without root competition from the overstory. The lack of a significant compensation by understory plants was probably due to deficiency of solar radiation in the understory, which limited evapotranspiration (Kramer and Kozlowski 1979). However, in both study years, SWC in the +OV+UN treatment declined relative to that in the +OV–UN treatment during mid- to late summer (Figs. 2). This indicates that, although the overstory was responsible for the majority of soil water depletion, the understory vegetation was capable of further depletion of soil water in the 10–30 cm soil depth interval. As demonstrated in other ecosystems, it is likely that overstory trees were accessing soil water at greater depths than understory vegetation (Scott et al. 2003; Baldocchi et al. 2004). Our data

Table 5. Significant coefficients ($P < 0.05$), with squared partial correlation coefficient in parentheses, for multiple regression models of height and basal area (BA) growth of saplings on plots ($n = 48$) in a thinned Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) forest.

	Height growth (cm)		BA growth (mm^2)	
Variable	Year 1	Year 2	Year 1	Year 2
Intercept	–4.34	–14.53	–93.09	–90.58
SWC, July of year 2 ($m^3 \cdot m^{-3}$)	—	97.21 (0.12)	—	—
SWC, Aug. of year 2 ($m^3 \cdot m^{-3}$)	—	—	—	734.41 (0.10)
PAR (% of potential)	0.12 (0.05)	0.17 (0.04)	1.47 (0.12)	1.84 (0.14)
Pretreatment BA	0.02 (0.28)	0.02 (0.09)	0.38 (0.65)	0.37 (0.53)
Pretreatment height growth	0.94 (0.34)	0.75 (0.10)	4.62 (0.19)	—
Adjusted R^2	0.58	0.37	0.74	0.61

Note: SWC, soil water content; PAR, photosynthetically active radiation. All models were significant at $P < 0.001$.

Fig. 5. Correlation between July soil water content (SWC) and foliar N concentration in the following dormant season in a 2-year study of naturally regenerated Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) saplings subjected to various combinations of belowground competition.



represent the proportional soil water depletion by the overstory and the understory only in the 10–30 cm soil depth interval. Because understory roots were likely more common in this interval than at greater soil depths, the relative effect of the understory on SWC probably appears exaggerated compared with what occurred lower in the soil profile.

Different growing season precipitation in years 1 and 2 affected seasonal soil water patterns and treatment effects. In year 1, when summer SWC across treatments was relatively higher than in year 2, SWC was not a significant predictor of BA growth (Table 5). Conversely, SWC was a significant predictor of BA growth in year 2, the drier year. It is not surprising that, in year 2, height growth was best predicted by July SWC, while BA growth was best predicted by August SWC. Shoot elongation likely began in late spring and ended during July, while radial grow continued through September (Cleary et al. 1978; Olszyk et al. 1998). Foliar N variables were not included in regression models because root uptake of N is reliant upon uptake of soil water and SWC (Nye and Tinker 1977); therefore, sapling N status was not independent of SWC. This was evident in the positive correlation between SWC and foliar N concentration (Fig. 5) and in the decline in overall foliar N concentration from 1.35% in the first year of the study to 1.15% in the drier second year. SWC likely affected the availability of mineral N in this system, as ammonification and total N mineralization are positively correlated with SWC (Barg and Edmonds 1999; Walters et al. 2006).

Based on general guidelines developed for Douglas-fir, foliar P and K concentrations in this study were slightly deficient, while foliar N concentrations were adequate to slightly deficient in the –OV treatment in year 1 and severely deficient for the +OV treatment in year 1 as well as for all treatments in year 2 (Ballard and Carter 1985). However, the results of our vector analysis indicate that saplings were not N deficient. The analysis indicated that exclusion of overstory root competition resulted in increases of foliar N concentration and content without a significant increase in foliar mass. Also, despite the foliar N concentration falling from 1.26% to 1.10%, there was no reduction in sapling growth in the +OV treatment from year 1 to year 2, nor were symptoms of N deficiency visually apparent in the saplings. The lack of an increase in foliar mass with increased foliar N concentration was probably due to the low-light conditions of this study. At low light levels, Douglas-fir needle morphology is altered, as individual leaf area decreases and surface area per unit dry mass increases (Drew and Ferrell 1977; Mailly and Kimmins 1997). The apparently shade-adapted needles in this study did not respond to increased foliar N concentration with an increase in needle mass in any of the treatments. Although available N and foliar N concentration are positively related to chlorophyll content and photosynthetic capacity, the photosynthesis rate of Douglas-fir is still light limited under low-light conditions (Brix 1971). Under controlled conditions, N availability did not influence height or diameter growth of Douglas-fir seedlings at shade levels similar to those of this study, whereas under full sunlight, growth was substantially affected by N availability (Reed et al. 1983). Thus, we attribute the apparent lack of N deficiency to a decreased N requirement owing to the relatively low light conditions.

There were two limitations of the study design that may have influenced the treatment effects to some degree. First, the removal of the aboveground portion of understory vegetation in the –UN treatment was intended to eliminate the effect of the understory on belowground competition, but this removal also likely reduced understory interception of precipitation and thus may have had an unquantified effect on the amount of water reaching the forest floor. And, although the UN treatment did not influence foliar N concentration, it is possible that the potential treatment effect was diminished to some extent by nutrient uptake of the living root systems of understory plants in the –UN treatment. Second, sapling height growth in year 1 was certainly influenced by environmental conditions during bud set in the previous year (Kramer and Kozlowski 1979; Cline and Harrington 2007), prior to treatment implementation. The significant OV by year interaction affecting height growth was due to the positive effect of the –OV treatment occurring only in year 2.

The stand by OV interaction affecting height growth (Table 2) was due to a lack of height growth response to the –OV treatment at Shaver, whereas the other two stands averaged a 41% increase under the –OV treatment compared with the +OV treatment. There was no stand by OV interaction affecting BA growth. We were unable to relate the lack of height growth response at Shaver to overstory BA, PAR, SWC, or foliar nutrients. The only measured difference between Shaver and the other stands was that saplings at Shaver had a smaller mean pretreatment diameter resulting in a somewhat greater mean height to diameter ratio (Table 1). A negative correlation between pretreatment height to diameter ratio and posttreatment height growth ($r = -0.58$, $P < 0.001$) suggests that saplings exhibiting this slender stem morphology had a reduced rate of height response relative to BA response.

The growth rates in this study were typical for Douglas-fir growing in the low-light conditions of an understory (Carter and Klinka 1992; Mailly and Kimmins 1997; Brandeis et al. 2001; Miller and Emmingham 2001; Harrington 2006). Based on previous research conducted on the same study sites (Churchill 2005), the saplings generally exhibited typical characteristics of shade-grown Douglas-fir including high shoot to root ratios (mean = 4.8) and height to diameter ratios (mean = 94.7) and sparse crowns. Likely owing to the limited range in PAR in our study (only seven plots had ≥40% potential PAR), we were not able to detect significant relationships between PAR and sapling growth rate within each treatment. The limited range in PAR as well as the fact that some PAR influences may have been accounted for by blocking effects and pretreatment sapling growth rate were likely reasons that PAR was not a significant variable in the ANOVA models (Table 2). Correlations and regression models assessing PAR–growth relationships across all treatments and stands were positive (Fig. 4), although somewhat weaker than previously reported relationships for understory Douglas-fir, such as a linear relationship (Mailly and Kimmins 1997) or a relationship described by the Michaelis–Menten equation (Drever and Lertzman 2001).

This study was designed to assess the relative importance of belowground competition from overstory and understory vegetation to the growth of saplings in mature Douglas-fir stands that had previously received a variable-density thinning. In the presence or absence of belowground competition from overstory trees, competition from nonovertopping understory vegetation did not have a detectable effect on sapling growth. Given the low-light conditions of the understory, soil water was a relatively important growth-limiting resource. Alternatively, there was no evidence that N was growth limiting. The negative influence of tree root competition on Douglas-fir sapling growth suggests that a thinning treatment must not only achieve the requisite understory light environment (Spies and Franklin 1989; Mailly and Kimmins 1997) but must also create openings large enough so that the density of roots from edge trees is reduced sufficiently to decrease competition for belowground resources (i.e., a root gap effect; Sanford 1989). For example, in mature and old-growth Douglas-fir stands, growing season SWC in gaps 14 m or more in diameter was greater than that in single-tree gaps 7–10 m in diameter (Gray et al. 2002).

The majority of the Douglas-fir saplings in this study probably established in small canopy gaps resulting from previous stand thinnings. These gaps provided sufficient understory light and soil moisture for establishment, but the continued development of this cohort of Douglas-fir depends on subsequent stand manipulation to reduce overstory density and increase understory light. However, after reductions in overstory density, shifts in belowground competition and resource availability are likely to occur.

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