Five-year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition[1]

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Abstract: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don) seedlings were planted in March 2001 within three clearcut-harvested, shelterwood, or thinned stands of mature Douglas-fir near Olympia, Washington. From 2002 to 2005, areas of vegetation control of 0, 4.5, or 9 m^2 were maintained with herbicides around a total 162 seedlings per species. Photosynthetically active radiation (PAR) was 34%, 62%, and 100% of full sunlight in thinned stands, shelterwoods, and clearcuts, respectively. Effects of overstory level and vegetation control on seedling growth and resource availability generally were additive. Seedling stem volume index in clearcuts averaged four to eight times that observed in thinned stands, and with vegetation control, it averaged two to four times that observed without it. In thinned stands, relative growth rate of seedling stem volume index had a positive linear relationship with PAR (R^2 = 0.38). Foliar nitrogen content of Douglas-fir explained 71% of the variation in relative growth rate. Factors explaining the most variation in foliar nitrogen content differed between thinned stands (PAR, R^2 = 0.34) and clearcuts or shelterwoods (midday water potential, R^2 = 0.63), suggesting that light and root competition, respectively, were the primary growth-limiting factors for these overstory levels.

Résumé : Des semis de douglas vert (*Pseudotsuga menziesii* (Mirb.) Franco), de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et de thuya géant (*Thuja plicata* Donn ex D. Don) ont été plantés en mars 2001 près d'Olympia dans l'État de Washington, aux États-Unis, dans trois peuplements matures de douglas vert ayant subi une coupe à blanc, une coupe progressive ou une éclaircie. De 2002 à 2005, des aires de maîtrise de la végétation de 0, 4,5 ou 9 m^2 ont été entretenues à l'aide d'herbicides autour de 162 semis par espèce. Le rayonnement photosynthétiquement actif a atteint respectivement 34 %, 62 % et 100 % des valeurs à découvert dans les coupes d'éclaircie, les coupes progressives et les coupes à blanc. Les effets du degré de couverture de l'étage dominant et de maîtrise de la végétation sur la croissance des semis et sur la disponibilité des ressources étaient généralement additifs. L'indice de volume de la tige des semis dans les coupes à blanc a atteint, en moyenne, des valeurs quatre à huit fois supérieures à celles qui ont été observées dans les peuplements éclaircis. La maîtrise de la végétation a produit des valeurs deux à quatre fois supérieures à ce qui a été observé sans maîtrise de la végétation. Dans les peuplements éclaircis, le taux relatif de croissance de l'indice de volume des tiges était positivement et linéairement relié au rayonnement photosynthétiquement actif (R^2 = 0,38). Le contenu foliaire en azote du douglas vert expliquait 71 % de la variation du taux relatif de croissance. Les facteurs les plus fortement associés au contenu foliaire en azote différaient entre les peuplements éclaircis (rayonnement photosynthétiquement actif, R^2 = 0,34) et les coupes à blanc ou progressives (potentiel hydrique à mi-journée, R^2 = 0,63). Ces résultats suggèrent que la compétition pour la lumière et la compétition entre les racines sont, dans l'ordre, les principaux facteurs qui limitent la croissance pour ces degrés de couverture de l'étage dominant.

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Introduction

Perhaps the greatest challenge to regenerating Pacific Northwestern conifers in multicohort stands is intense competition from overstory trees and understory vegetation for limited availabilities of light, soil water, and nutrients. Such competition can delay a seedling's attainment of a free-to-grow condition (Mitchell et al. 2004), resulting in uncertainty in its crop potential. Without significant reductions in density of mature stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), understory seedlings of most Northwestern conifer species do not have sufficient light to sustain their normal development. However, reductions in overstory density usually are accompanied by increased

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abundance of understory vegetation (Bailey et al. 1998), and associated competition for soil water and nutrients. If multicohort stands are to be managed as sustainable silvicultural systems, forest managers must know the densities of overstory trees and understory vegetation that support vigorous development of conifer seedlings.

The resource requirements of a tree species provide the basis for classifying its tolerances to shade and root competition (Barnes et al. 1998). For example, Douglas-fir seedlings need greater than 20% of full sunlight to survive, at least 40% for continued morphological development (Mailly and Kimmins 1997), and full sunlight for maximum growth rates (Drever and Lertzman 2001). Western redcedar (*Thuja plicata* Donn ex D. Don) seedlings require only 10% of full sunlight to survive (Wang et al. 1994), and their maximum growth rates can occur at only 30% of full sunlight (Drever and Lertzman 2001). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is considered among the most shade tolerant of Northwestern conifers (Packee 1990). However, each of these species can exhibit greater shade tolerance on sites of lower soil water availability (Carter and Klinka 1992). Douglas-fir thrives under a wide variety of climatic conditions (Hermann and Lavender 1990), in part, because of its moderate tolerance to root competition. Although western hemlock does best in a moist, coastal environment (Packee 1990), once established it will grow on many of the same sites as Douglas-fir, where it is usually considered the climax species (Franklin and Dyrness 1973). Western redcedar is regenerated most successfully in mesic environments characterized by the presence of lady fern (*Athyrium filix-femina* (L.) Roth.), queen's cup (*Clintonia uniflora* (Schult.) Kunth.), mountain woodfern (*Dryopteris austriaca* (Jacq.) Woynar), oak-fern (*Gymnocarpium dryopteris* (L.) Newm.), and thimbleberry (*Rubus parviflorus* Nutt.) (Minore 1990).

Understanding how shade and root competition affect seedling development is complicated by the fact that one factor rarely operates alone, but rather its effects are usually modified by another factor (Carter and Klinka 1992). Soil-trenching studies from contrasting regions have shown that root competition from overstory trees can impose equal or greater limitations to development of understory seedlings as the shade they cast (Harrington et al. 2003; Lindh et al. 2003). Yet even when soil resources are readily available in a forest understory, light availability must be sufficient to sustain normal root development of an intolerant species, or else it will die of a subsequent drought (Lutz 1945). Competition studies in stands of western hemlock (Mitchell 2001) and Douglas-fir (Barg and Edmonds 1999) have detected little difference in availability of soil resources between clearcuts and partial overstory retention, supporting the hypothesis that light is the primary factor limiting seedling growth for a wide range of overstory densities. However, roots of residual trees and understory vegetation probably colonized the growing space made available by removal of overstory trees, thus confounding attempts to detect increases in soil resources.

Several recent studies have varied density of overstory trees and understory vegetation independently to avoid this confounding and to enable quantification of their separate competitive effects (Brandeis et al. 2001; Mitchell et al. 2004). This approach can be used to identify critical factors that limit seedling growth for a variety of stand structures. In this study, seedlings of three conifer species were grown for 5 years after manipulating densities of overstory trees and understory vegetation. The objectives of the research were to quantify effects of competition source and intensity on species' performances, to identify relationships of seedling growth versus resource availability that explain the response mechanisms, and to test the following hypotheses.

(1) Species will vary in their tolerances to shade and root competition. Using the relative range in seedling size across levels of shade or root competition as an index of tolerance (i.e., smallest range = greatest tolerance), species will differ in shade tolerance as hemlock > redcedar > Douglas-fir and in tolerance to root competition as Douglas-fir > hemlock > redcedar.
(2) Increases in soil water availability from control of competing vegetation will decrease as overstory density increases.
(3) Shade tolerance will increase with decreasing soil water availability. Limitations in soil water availability will reduce the rate at which seedling growth declines with decreasing light availability.

Methods

Study sites and treatments

The research was conducted in the Overstory Density Study (Brodie et al. 2004) of Capitol State Forest near Olympia, Washington (Table 1). At each of three sites supporting 40- or 70-year-old Douglas-fir, plots at least 1.9 ha in area (137 m × 137 m) were randomly assigned a wide range of overstory densities (ODs) quantified as a percentage of full basal area stocking equal to a relative density (RD) of 9.4 (RD = $BA/d_q^{0.5}$, where BA is stand basal area ($m^2 \cdot ha^{-1}$) at 1.3 m height and d_q is quadratic mean stem diameter (cm); Curtis 1982). Stands were thinned in summer 2000 to leave a uniform spacing of well-formed trees of high growth potential, and advanced conifer regeneration and large hardwoods or shrubs also were cut. In March 2001, an alternating mixture of Douglas-fir, western hemlock, and western redcedar seedlings was planted at 3 m spacing within each plot. In April 2002, three plots at each site were selected to represent overstory levels hereafter designated as clearcuts (0% OD), shelterwoods (16% OD at sites 1 and 3, and 24% OD at site 2), or thinned stands (40% OD). The research was conducted within the outer 30.5 m buffer area of each plot to avoid disturbing ongoing genetic and species-mixture studies underway in the interior of each plot. Although growing conditions probably differed somewhat between the exterior and interior of each plot, the three overstory levels selected per site provided a broad range of stand structures in which to study overstory and understory competition. Eighteen candidate seedlings per species were randomly selected in each plot to be spaced 4 m or more apart and to have moderate to high levels of vigor and minimal damage from deer browse. Six of the 18 seedlings were randomly assigned to receive one of three areas of competing vegetation control (AVC): 0, 4.5, or 9 m^2. Vegetation around seedlings assigned 0 m^2 AVC was left intact. In June 2002–2005, a 3% solution of Accord® (glyphosate) herbicide (Dow Agrosciences, Indianapolis, Indiana) in water

Table 1. Characteristics of the three sites of the overstory density study near Olympia, Washington.

Descriptor	Site 1	Site 2	Site 3
County	Grays Harbor	Grays Harbor	Thurston
Location	46°57′N, 123°13′W	46°53′N, 123°13′W	46°55′N, 123°8′W
Slope (%)	<2	0–5	0–15
Aspect	SE	S	SE
Elevation (m)	520	200	350
Soil series	Bunker silt loam	Olympic clay loam and Raught silt loam	Olympic silt loam
Soil class	Typic Fulvudand	Xeric and Typic Palehumult	Xeric Palehumult
Approximate age at overstory treatment (years)	40	70	70
Average dominant height (m)	29	47	45
Stem density (trees·ha^{-1})	279	277	230
Stand basal area (BA) (m^2·ha^{-1})	49	63	52
Overstory species composition (% of BA)	79% PSME	98% PSME	91% PSME
	18% TSHE	1% TSHE	6% TSHE
	3% ABAM	1% ALRU, THPL	2% THPL
			1% ALRU

Note: PSME, Douglas-fir (*Pseduotsuga menziesii*); TSHE, western hemlock (*Tsuga heterophylla*); ABAM, Pacific silver fir (*Abies amabilis*); ALRU, red alder (*Alnus rubra*); THPL, western redcedar (*Thuja plicata*).

was applied with a two-nozzle, 2 m length boom of a backpack sprayer to create square areas, 2.1 m (4.5 m^2 AVC) or 3 m (9 m^2 AVC) wide, centered at the seedling and parallel to the planting rows. The spray mixture in 2002 included a 1% concentration of Garlon®4 (triclopyr) herbicide (Dow Agrosciences) to control evergreen shrubs. Each conifer seedling was covered in a plastic bag during treatment to minimize herbicide exposure. A 10% solution of Garlon®4 in JLB oil (Brewer International, Vero Beach, Florida) was applied as a directed spray in winter 2004 and 2005 to maintain control of evergreen shrubs. In spring of 2002–2004, Havahart® Deeraway powder (Woodstream Corp., Lititz, Pennsylvania) was applied to the elongating terminal shoot of each seedling to minimize deer browse. Total sample size per conifer species was 162 seedlings (3 sites × 3 overstory levels × 3 levels of AVC × 6 seedlings).

Vegetation and resource measurements

Stand basal area of overstory trees around individual seedlings was measured with a prism having a factor of 3 m^2·ha^{-1}. In August 2004, overtopping (%) from neighboring understory vegetation was assessed by visually projecting an inverted 60° cone from the base of the terminal shoot of each seedling and estimating the percentage of occlusion of open sky in the circle defined above (Howard and Newton 1984). Rainfall was measured daily at a weather station located in the clearcut plot of sites 1 and 3. Photosynthetically active radiation (PAR) was measured in July 2004 with an Accupar® ceptometer (Decagon Devices, Pullman, Washington) at 1.3 m height on the south side of each seedling within shelterwood and thinned stands. PAR readings were taken within 2 h of solar noon on 3 adjacent cloudless days. Readings were not taken in clearcuts, because full sunlight existed during the measurement period. PAR values were expressed as a proportion of open sky readings measured simultaneously within an adjacent clearcut by a LI-190 quantum sensor and recorded every 30 s by a LI-1400 datalogger (LI-COR Biosciences, Lincoln, Nebraska). In April 2002 and July 2002–2004, cover (nearest 5%) of each species of competing understory vegetation (herbaceous species and woody species with a stem diameter at 1.3 m height of 2.5 cm or less) was visually estimated within a 1.5 m radius of each seedling. This sample area provided an accurate representation of vegetation abundance within the full growing space (9 m^2) of seedlings assigned 0 or 9 m^2 AVC. For seedlings assigned 4.5 m^2 AVC, cover values were adjusted as follows to represent the full growing space:

$$[1] \quad COV_{adj} = 100 \times \frac{(COV/100)(SA) + (COV_{0\,m^2AVC}/100)(9 - SA)}{9}$$

where COV_{adj} is adjusted cover, COV is observed cover, SA is the sample area for the cover measurement (1.5 m radius circle = 7.07 m^2), and $COV_{0\,m^2AVC}$ is mean cover around seedlings assigned 0 m^2 AVC located on the same plot. Understory plant species having an average cover of 1% or more were salal (*Gaultheria shallon* Pursh, 10% cover), sword-fern (*Polystichum munitum* (Kaulf.) Presl, 4%), trailing blackberry (*Rubus ursinus* Cham. & Schlecht., 2%), salmonberry (*Rubus spectabilis* Pursh, 2%), bracken fern (*Pteridium aquilinum* (L.) Kuhn., 2%), vine maple (*Acer circinatum* Pursh, 1%), wood-sorrel (*Oxalis oregana* Nutt., 1%), Oregon grape (*Mahonia nervosa* (Pursh), Nutt., 1%), and red huckleberry (*Vaccinium parvifolium* Smith, 1%). In April 2002 and fall 2002–2005, height (cm) and stem diameter (mm) at 15 cm height were measured on each seedling. Seedlings also were coded for presence of injury from herbicides or browsing by black-tailed deer (*Odocoileus hemioniz columbiana*).

Availability of belowground resources was quantified for a subset of 81 Douglas-fir seedlings comprising three seedlings randomly selected for each combination of site, overstory level, and AVC. Beginning in July 2002, volumetric soil water content (%) at 0–12 cm depth was measured with a Hydrosense® TDR probe (Campbell Scientific, Inc., Logan, Utah) at approximate monthly intervals during the growing seasons (April to October) of 2002–2004 and during February 2003–2004. The soil water measurements were taken at a distance of 30–60 cm from the stem of each seedling. The measurements were calibrated by taking Hydrosense® readings and collecting adjacent fixed-volume soil samples from various locations at each site five times between August 2002 and January 2003. The calibration data were used to develop a polynomial regression equation that related actual volumetric water content to values predicted from the Hydrosense®. In October 2004, foliar analyses were conducted on the same 81 Douglas-fir seedlings. Two to four current-year shoots were excised from the first whorl of each seedling. Shoots were dried in a forced-draft oven for 48 h at 65 °C, needles were removed, and the mass (g) of 100 needles was recorded. Nitrogen concentration (%) of each seedling's foliage sample and three samples of known concentration (for verification) were measured with a LECO CNS-2000 Macro Analyzer (LECO Corp., St. Joseph, Michigan) at the Central Analytical Laboratory, Oregon State University, Corvallis, Oregon. Nitrogen content (mg) of each needle sample was calculated as the product of nitrogen concentration and 100-needle mass. Midday water potential (–MPa) was measured with a pressure chamber (PMS Instrument Company, Albany Oregon) on current-year shoots from each of the 81 Douglas-fir seedlings. Water potential measurements were taken between 1000 and 1500 h DST on several cloudless days in early September 2005 at the peak of summer drought.

Statistical analysis

All statistical analyses were performed with SAS (SAS Institute Inc. 1999). The experimental design was a randomized complete block with a split-plot arrangement of three levels of AVC within three overstory levels replicated at three sites (blocks). Parabolic stem volume was calculated to provide an index of cumulative growth for each conifer seedling:

$$[2] \qquad \mathrm{SVI} = \pi(D/20)^2 \times H/2$$

where SVI is stem volume index (cm^3), D is stem diameter (mm), and H is height (cm). Annual values of SVI and competing vegetation cover summed by herbaceous and woody categories were averaged for each combination of site, overstory level, and AVC. Initial values of SVI and vegetation cover measured in April 2002 were designated as 2001 measurements. Mean values were subjected to a repeated-measures analysis of variance (ANOVA) in SAS procedure MIXED to determine the significance ($\alpha = 0.05$) of overstory level, AVC, and their interaction. Analyses were conducted with maximum likelihood estimation assuming an autoregressive covariance structure to account for time series trends. The same approach was used to analyze monthly averages of soil water content. The average value of maximum soil water content observed near each seedling was included as a covariate in the ANOVA to adjust for within-site differences in soil bulk density (Harrington et al. 2003). Cumulative 5th-year seedling survival and average annual frequency of deer browse were expressed as proportions. For single-measurement variables, values were averaged for each combination of site, overstory level, and AVC, and subjected to ANOVA for a split-plot design in SAS procedure MIXED, assuming random effects of sites and fixed effects of overstory level and AVC. Prior to ANOVA, all variables expressed as proportions were normalized with an arc-sine, square-root transformation (Sokal and Rohlf 1981). SVI values were transformed to natural logarithms to linearize their relationship with time and enable testing of treatment effects on seedling relative growth rates (i.e., RGR ($cm^3 \cdot cm^{-3} \cdot year^{-1}$) is the slope of the relationship of $\log_e$(SVI) versus measurement year). For each ANOVA, residuals were plotted against predicted values of the dependent variable to verify that residual variances were relatively homogeneous. The following orthogonal contrasts were performed to partition effects of overstory level (contrasts 1 and 2), vegetation control (contrasts 3 and 4), and their interaction (contrasts 5–8).

(1) Absence versus presence of overstory trees (clearcuts versus the mean of shelterwoods and thinned stands).
(2) Shelterwoods versus thinned stands.
(3) Absence versus presence of competing vegetation control (0 m^2 AVC versus the mean of 4.5 and 9 m^2 AVC).
(4) 4.5 versus 9 m^2 AVC.
(5) Effects of absence versus presence of competing vegetation control differ in the absence versus presence of overstory trees.
(6) Effects of absence versus presence of competing vegetation control differ in shelterwoods versus thinned stands.
(7) Effects of 4.5 versus 9 m^2 AVC differ in the absence versus presence of overstory trees.
(8) Effects of 4.5 versus 9 m^2 AVC differ in shelterwoods versus thinned stands.

Results from each ANOVA are reported in the tables below, except that those for orthogonal contrasts 5–8 are reported in the text only when significant ($P \le 0.05$). All treatment responses are reported as least-squares (adjusted) means. If a significant interaction was detected between measurement interval and overstory level or AVC, multiple comparisons of least-squares means were conducted with Bonferroni adjusted probabilities (Sokal and Rohlf 1981). Vector analysis was used to characterize relative changes in dry mass, nitrogen concentration, and nitrogen content of Douglas-fir foliage attributable to overstory level and AVC (Timmer and Stone 1978). For each foliage variable, least-squares means for the interaction of overstory level and AVC were expressed as a percentage of values for seedlings in clearcuts with 0 m^2 AVC (designated as the reference treatment) and then plotted on a nomogram. Indicator variables were specified for each treatment except the reference. Stepwise linear regression in SAS procedure REG was performed to compare treatment-specific intercepts and slopes (Sokal and Rohlf 1981) and thereby identify the best model describing the relationship of relative nitrogen concentration versus relative nitrogen content. This relationship assumes that nitrogen concentration (c) is a linear function of nitrogen uptake (a) and biomass accumulation (m): $c = a/m$, where a and m are expressed as nitrogen content and foliage dry mass, respectively (Imo and Timmer 1998). Stepwise regression analysis was used similarly to identify the best models describing relationships of RGR versus overstory basal area, PAR, covers of herbaceous and woody vegetation, nitrogen content, and midday water potential.

Results

Vegetation responses

The effects of overstory level and vegetation control on

Table 2. Results of the analysis of variance for overstory basal area, overtopping, and cover of understory herbaceous and woody vegetation in response to overstory level (OL), area of vegetation control (AVC), and measurement year.

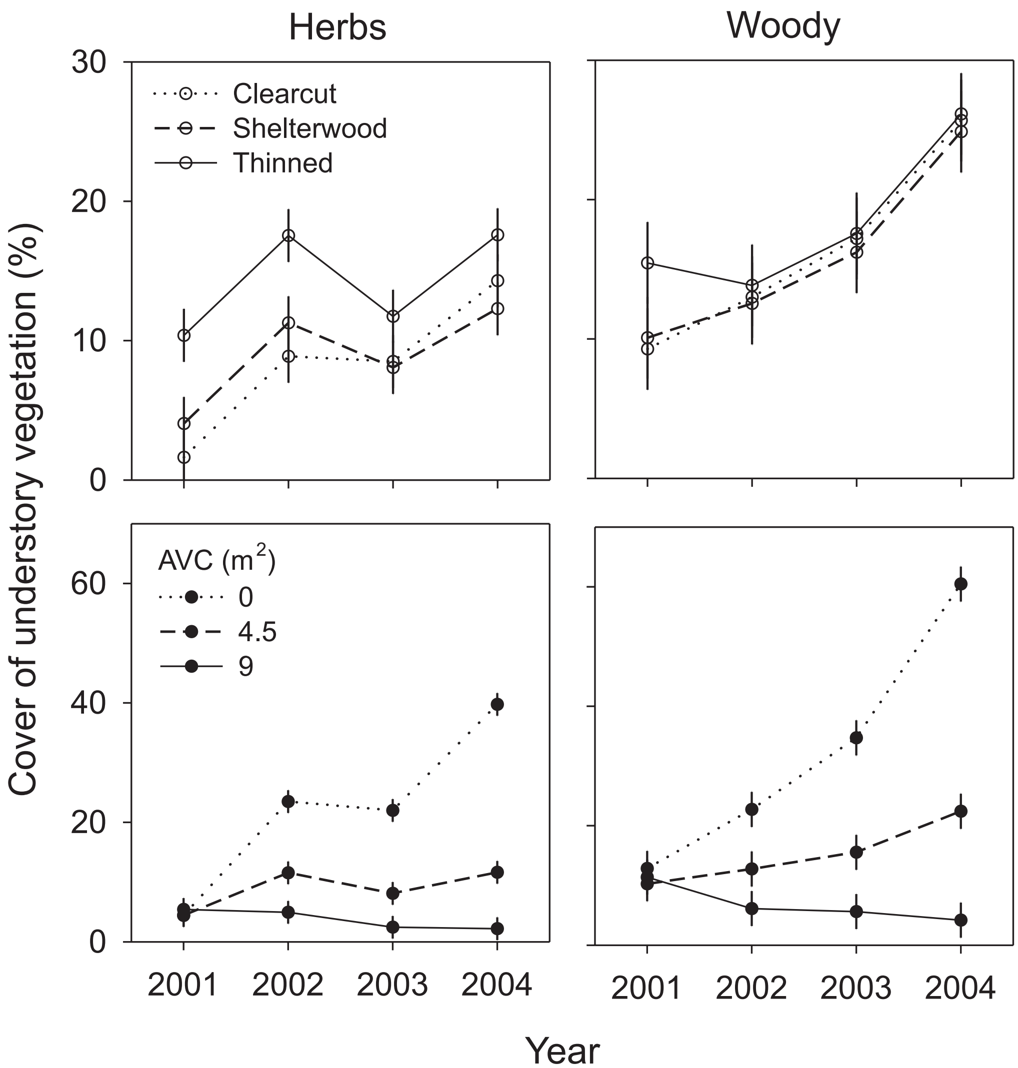
Variable	Source[a]	Numerator df[b]	Denominator df	Prob. > F
Overstory basal area	OL contrasts	(2)	4	
	(1) CC vs. (SH and TH)	1	4	<0.001
	(2) SH vs. TH	1	4	<0.001
	AVC contrasts	(2)	12	
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	12	0.457
	(4) AVC: 4.5 vs. 9 m^2	1	12	0.064
	OL × AVC	4	12	0.441
Overtopping	OL contrasts	(2)	4	
	(1) CC vs. (SH and TH)	1	4	0.163
	(2) SH vs. TH	1	4	0.055
	AVC contrasts	(2)	12	
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	12	<0.001
	(4) AVC: 4.5 vs. 9 m^2	1	12	0.249
	OL × AVC	4	12	0.967
Herb cover	OL	(2)	18	
	(1) CC vs. (SH and TH)	1	18	0.051
	(2) SH vs. TH	1	18	0.022
	Year	3	54	<0.001
	OL × year	6	54	0.154
	AVC	(2)	18	
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	18	<0.001
	(4) AVC: 4.5 vs. 9 m^2	1	18	0.006
	AVC × year	6	54	<0.001
	OL × AVC	4	18	0.741
	OL × AVC × year	12	54	0.994
Woody cover	OL	(2)	18	
	(1) CC vs. (SH and TH)	1	18	0.787
	(2) SH vs. TH	1	18	0.542
	Year	3	54	<0.001
	OL × year	6	54	0.026
	AVC	(2)	18	
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	18	<0.001
	(4) AVC: 4.5 vs. 9 m^2	1	18	0.019
	AVC × year	6	54	<0.001
	OL × AVC	4	18	0.978
	OL × AVC × year	12	54	0.448

[a]Overstory levels: CC, clearcut; SH, shelterwood; TH, thinned.
[b]Parentheses indicate degrees of freedom that were partitioned into orthogonal contrasts.

vegetation responses generally were additive, and interactions of the two factors were not significant. Overstory basal area was less in the absence (1.7 $m^2 \cdot ha^{-1}$) versus presence (19.1 $m^2 \cdot ha^{-1}$) of overstory trees, and it was less in shelterwoods (12.4 $m^2 \cdot ha^{-1}$) than in thinned stands (25.7 $m^2 \cdot ha^{-1}$) (Table 2). The non-zero basal area in clearcuts resulted from edge trees of neighboring plots. Overtopping of seedlings was greater in the absence (8%) versus presence (0.4%) of competing vegetation control. Cover of competing vegetation differed according to the additive effects of overstory level and AVC. Throughout the duration of the study, herb cover was greater in the presence versus absence of overstory trees and in thinned stands versus shelterwoods (Fig. 1). This difference was partially attributable to the greater abundance of swordfern in thinned stands (7% cover) than in clearcuts or shelterwoods (1%–3% cover). Although the interaction of overstory level and measurement year was significant for woody cover (P = 0.026), multiple comparisons of overstory level means failed to reveal any differences within a given year. Initial values of herbaceous and woody covers (designated as 2001 measurements) did not differ by AVC; however, in 2002, 2003 and 2004, values were greater in 0 m^2 AVC than in 4.5 or 9 m^2 AVC. Vegetation cover was greater in 4.5 m^2 AVC than in 9 m^2 AVC in 2003–2004 (woody) and 2002–2004 (herbaceous).

By 2005, a total of 10 Douglas-fir, five western hemlock, and three western redcedar seedlings had died. Symptoms of the dead seedlings suggested that herbicide exposure from contact with treated vegetation or volatility of triclopyr probably killed five Douglas-fir, one hemlock, and one redcedar. Cumulative survival of each species did not vary significantly with overstory level, AVC, or their interaction (Table 3), although Douglas-fir survival was somewhat lower in thinned stands (94%) than in shelterwoods (100%)

Fig. 1. Average cover of understory herbaceous and woody vegetation (with SE bars) in response to the main effects of overstory level and area of vegetation control (AVC).



(P = 0.073). Survival of redcedar in clearcuts decreased slightly as AVC increased from 4.5 to 9 m^2 (100% vs. 98%, respectively), whereas for shelterwoods or thinned stands it increased slightly (99% vs. 100%, respectively) (P = 0.044 for orthogonal contrast 7). Frequency of deer browse on redcedar was greater in the absence (54%) versus presence (34%) of overstory trees, and it was greater in shelterwoods (39%) versus thinned stands (30%). Although not statistically significant (P = 0.088), frequency of deer browse on Douglas-fir was somewhat higher in the absence (25%) versus presence (16%) of overstory trees. Similarly, frequency of deer browse on redcedar was somewhat higher (P = 0.065) in the presence (42%) versus absence (37%) of vegetation control. Very few symptoms of deer browse were observed on hemlock seedlings.

The growth trajectories of SVI were approximately exponential with increasing steepness of the curves, as either overstory level decreased or AVC increased (Fig. 2). In 2005, SVI of hemlock in clearcuts was 2.6 and 17.4 times that of Douglas-fir and redcedar, respectively. For each species, relative SVI responses to overstory level spanned a greater range than responses to vegetation control. In thinned stands, 5th-year SVI of Douglas-fir and hemlock was 13% and 15%, respectively, of the mean values observed in clearcuts, where their growth responses were greatest. SVI of Douglas-fir and hemlock in shelterwoods was intermediate to that in thinned stands and clearcuts. For redcedar, SVI in thinned stands was 24% of its maximum value, which occurred in shelterwoods, whereas SVI in clearcuts was 86% of its maximum value. As AVC increased from 0 to 9 m^2, SVI of Douglas-fir, hemlock, and redcedar ranged from 27% to 52%, from 21% to 76%, and from 32% to 87% of species' maximum values, respectively. Species having the smallest relative range in SVI across levels of a given factor were considered most tolerant, and vice versa. Species were ranked by shade tolerance as redcedar > hemlock > Douglas-fir because average SVI varied among overstory levels by factors of 4.2, 6.6, and 7.6, respectively. Species were ranked by tolerance to root competition as Douglas-fir > redcedar > hemlock, because average SVI varied among levels of AVC by factors of 1.9, 2.8, and 3.6, respectively. Both rankings of species are somewhat different

Table 3. Results of the analysis of variance for cumulative survival in 2005 and average frequency of deer browsing of Douglas-fir, western hemlock, and western redcedar in response to overstory level (OL) and area of vegetation control (AVC).

Species	Source[a]	Numerator df[b]	Denominator df	Prob. > *F*	
				Survival	Browse
Douglas-fir	OL contrasts	(2)	4		
	(1) CC vs. (SH and TH)	1	4	0.892	0.088
	(2) SH vs. TH	1	4	0.073	0.821
	AVC contrasts	(2)	12		
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	12	0.887	0.259
	(4) AVC: 4.5 vs. 9 m^2	1	12	0.207	0.282
	OL × AVC	4	12	0.849	0.544
Western hemlock	OL contrasts	(2)	4		
	(1) CC vs. (SH and TH)	1	4	0.326	1.000
	(2) SH vs. TH	1	4	1.000	0.158
	AVC contrasts	(2)	12		
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	12	0.586	1.000
	(4) AVC: 4.5 vs. 9 m^2	1	12	0.729	1.000
	OL × AVC	4	12	0.263	0.263
Western redcedar	OL contrasts	(2)	4		
	(1) CC vs. (SH and TH)	1	4	1.000	0.002
	(2) SH vs. TH	1	4	0.158	0.032
	AVC contrasts	(2)	12		
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	12	1.000	0.065
	(4) AVC: 4.5 vs. 9 m^2	1	12	1.000	0.915
	OL × AVC	4	12	0.124	0.854

[a]Overstory levels: CC, clearcut; SH, shelterwood; TH, thinned.
[b]Parentheses indicate degrees of freedom that were partitioned into orthogonal contrasts.

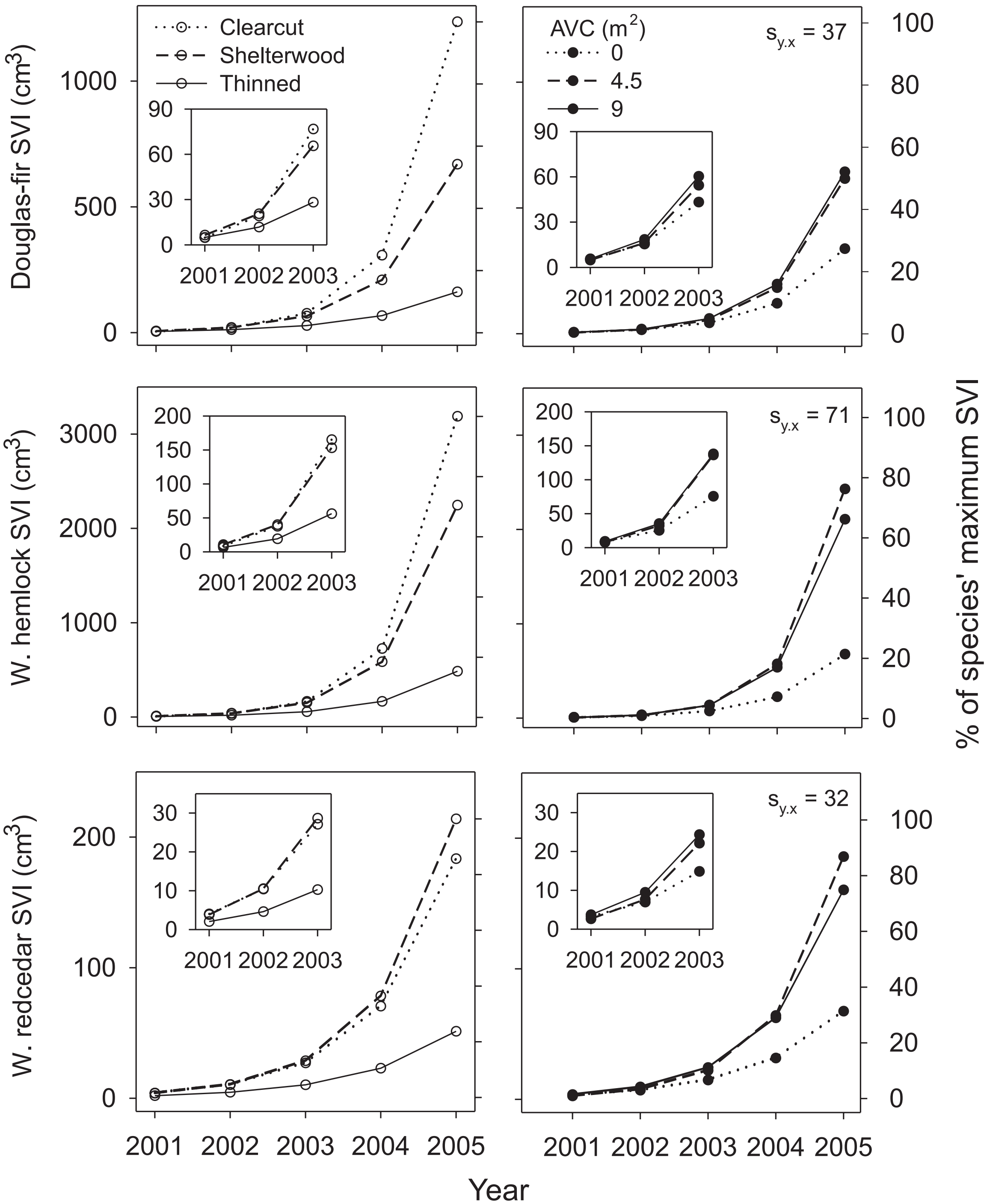
from those given in hypothesis 1, in which hemlock was ranked to be more tolerant of shade and root competition than redcedar.

For each species, variation in SVI was largely attributable to interactions of measurement year with either overstory level or AVC, indicating that the two factors had additive effects on RGR (Table 4). For Douglas-fir and hemlock, RGR was greater in the absence versus presence of overstory trees, and it was greater in shelterwoods versus thinned stands. Although not statistically significant (P = 0.075), RGR of redcedar was greater in shelterwoods than in thinned stands. RGR of each species was greater in the presence versus absence of vegetation control but it did not differ between 4.5 and 9 m^2 AVC ($P \geq 0.282$). In clearcuts, RGR of Douglas-fir was greater in the presence versus absence of vegetation control (1.5 vs. 1.2 $cm^3 \cdot cm^{-3} \cdot year^{-1}$, respectively), whereas it differed little in shelterwoods and thinned stands (1.1 vs. 1.0 $cm^3 \cdot cm^{-3} \cdot year^{-1}$, respectively) ($P$ = 0.037 for orthogonal contrast 5).

Resource responses

The interaction of overstory level and AVC was significant (P = 0.013) for PAR (Table 5). In thinned stands, PAR increased from 26% to 39% of full sunlight in the absence versus presence of vegetation control, whereas in shelterwoods it decreased (from 67% to 60%, respectively) (P = 0.006 for orthogonal contrast 6). Despite this interaction, PAR varied primarily as a result of overstory level with values of 62% and 34% in shelterwoods and thinned stands, respectively. Annual rainfall (averages of sites 1 and 3) was 1417, 1387, 1116, and 1403 mm in 2002, 2003, 2004, and 2005, respectively. From July 2002 to October 2004, soil water content differed between shelterwoods and thinned stands and between the presence and absence of vegetation control. Soil water content in shelterwoods was 1%–2% greater than in thinned stands during approximately the first 12 months of measurements, and it was 1%–2% greater in the presence versus absence of vegetation control in the summers of 2002 and 2003 (Fig. 3). Based on relative reductions in soil water content, the intensity of summer drought was least in 2002 and greatest in 2003. The interaction of overstory level and measurement date was marginally significant (P = 0.053) for soil water content, whereas the interaction of overstory level and AVC approached statistical significance (P = 0.071). Average soil water content in clearcuts increased from 32.1% to 32.6% as AVC increased from 4.5 to 9 m^2, whereas in shelterwoods and thinned stands it decreased from 33.0% to 32.2% (P = 0.017 for orthogonal contrast 7). Therefore, in agreement with hypothesis 2, increases in soil water availability from vegetation control became smaller as overstory level increased. Note also that, in the absence of vegetation control, average soil water content was practically identical among clearcuts (31.6%), shelterwoods (31.9%), and thinned stands (31.9%). Midday water potential of Douglas-fir during late summer 2005 was greater in the presence versus absence of vegetation control (–1.19 vs. –1.44 MPa, respectively), but it did not differ between 4.5 and 9 m^2 AVC (–1.25 vs. –1.13 MPa, respectively) (P = 0.159) (Table 5). Although not statistically significant (P = 0.069), midday water potential was

Fig. 2. Predicted average stem volume index (SVI) of Douglas-fir, western hemlock, and western redcedar in response to the main effects of overstory level and area of vegetation control (AVC). $S_{y.x}$ is the standard error of estimate.



greater in the absence versus presence of overstory trees (–1.10 vs. –1.36 MPa, respectively). In shelterwoods, midday water potential decreased from –1.29 to –1.44 MPa as AVC increased from 4.5 to 9 m^2, whereas in thinned stands it increased from –1.45 to –1.04 MPa (P = 0.013 for orthogonal contrast 8).

Dry mass, nitrogen concentration, and nitrogen content of Douglas-fir foliage were greater in the absence versus presence of overstory trees, but only dry mass and nitrogen content were greater in shelterwoods than in thinned stands (Tables 6 and 7). All three foliage variables were greater in the presence versus absence of vegetation control, but they did not differ between 4.5 and 9 m^2 AVC ($P \geq 0.446$). In clearcuts, nitrogen content was greater in the presence versus absence of vegetation control (9.4 vs. 6.1 mg, respectively), whereas in shelterwoods and thinned stands, they differed little (5.5 vs. 4.5 mg, respectively) (P = 0.007, for orthogonal contrast 5). Although not statistically significant (P = 0.063, for orthogonal contrast 5), dry mass in clearcuts was greater in the presence (0.47 g) versus absence (0.37 g)

Table 4. Results of the analysis of variance for the natural logarithm of stem volume index of Douglas-fir, western hemlock, and western redcedar in response to overstory level (OL), area of vegetation control (AVC), and measurement year; contrasts involving OL or AVC interactions with measurement year test for treatment effects on relative growth rates of stem volume index.

			Prob. > F		
Source[a]	Numerator df[b]	Denominator df	Douglas-fir	Western hemlock	Western redcedar
OL	2	18	0.174	0.533	0.655
Year	1	99	<0.001	<0.001	<0.001
OL × year contrasts	(2)	99			
(1) CC vs. (SH and TH)	1	99	<0.001	<0.001	0.589
(2) SH vs. TH	1	99	<0.001	0.001	0.075
AVC	2	18	0.591	0.352	0.634
AVC × year contrasts	(2)	99			
(3) AVC: 0 vs. (4.5 and 9 m^2)	1	99	0.004	<0.001	0.012
(4) AVC: 4.5 vs. 9 m^2	1	99	0.640	0.318	0.282
OL × AVC	4	18	0.863	0.857	0.992
OL × AVC × year	4	99	0.338	0.381	0.987

[a]Overstory levels: CC, clearcut; SH, shelterwood; TH, thinned.
[b]Parentheses indicate degrees of freedom that were partitioned into orthogonal contrasts.

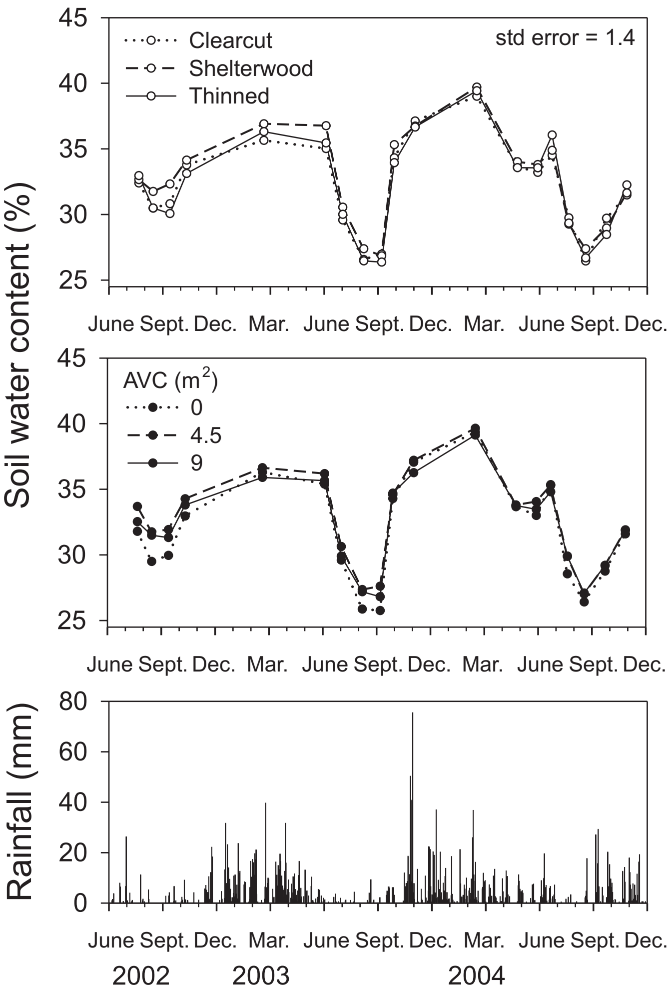
Table 5. Results of the analysis of variance for photosynthetically active radiation (PAR), soil water content, and Douglas-fir midday water potential in response to overstory level (OL), area of vegetation control (AVC), and measurement date.

Variable	Source[a]	Numerator df[b]	Denominator df	Prob. > F
PAR	OL contrast	(1)	2	
	(2) SH vs. TH	1	2	0.029
	AVC contrasts:	(2)	8	
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	8	0.286
	(4) AVC: 4.5 vs. 9 m^2	1	8	0.372
	OL × AVC	2	8	0.013
Soil water content	OL contrasts	(2)	18	
	(1) CC vs. (SH and TH)	1	18	0.162
	(2) SH vs. TH	1	18	0.035
	Date	18	323	<0.001
	OL × date	36	323	0.053
	AVC contrasts	(2)	18	
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	18	0.002
	(4) AVC: 4.5 vs. 9 m^2	1	18	0.091
	AVC × date	36	323	0.528
	OL × AVC	4	18	0.071
	OL × AVC × date	72	323	0.964
	MAXSWC[c]	1	323	<0.001
Midday water potential	OL contrasts	(2)	4	
	(1) CC vs. (SH and TH)	1	4	0.069
	(2) SH vs. TH	1	4	0.452
	AVC contrasts	(2)	12	
	(3) AVC: 0 vs. (4.5 and 9 m^2)	1	12	0.004
	(4) AVC: 4.5 vs. 9 m^2	1	12	0.159
	OL × AVC	4	12	0.077

[a]Overstory levels: CC, clearcut; SH, shelterwood; TH, thinned.
[b]Parentheses indicate degrees of freedom that were partitioned into orthogonal contrasts.
[c]MAXSWC, maximum soil water content per sample point, was used as a covariate in the analysis of variance to adjust for within-site variation in soil bulk density.

of vegetation control, but in shelterwoods and thinned stands it differed little (0.33 vs. 0.31 g, respectively). Results of the vector analysis indicated that the greatest changes in the foliar variables occurred in response to overstory level (Fig. 4), as found for SVI responses. In thinned stands, all three foliage variables decreased relative to the reference treatment (seedlings growing in clearcuts with 0 m^2 AVC), especially dry mass and nitrogen content. In shelterwoods, the values for the foliage variables were similar to those of the reference treatment. Regression analysis indicated that

Fig. 3. Average volumetric soil water content at 0–12 cm depth in response to the main effects of overstory level and area of vegetation control (AVC).



the relationship of nitrogen concentration versus nitrogen content was similar for all treatments except shelterwoods with 0 or 4.5 m^2 AVC (R^2 = 0.77). For seedlings in shelterwoods with 0 or 4.5 m^2 AVC, nitrogen responses exhibited mild "dilution" effects because foliage dry mass either increased slightly or remained constant relative to the reference treatment, but nitrogen concentration decreased. In contrast, seedlings in clearcuts with vegetation control experienced 19%–27% increases in dry mass and nitrogen concentration resulting in 49%–59% increases in nitrogen content.

Seedling growth versus resource availability

Stepwise regression analyses identified significant relationships of RGR versus basal area of overstory trees (R^2 = 0.48), PAR (R^2 = 0.38), competing vegetation cover (R^2 = 0.47–0.62), nitrogen content (R^2 = 0.71), and midday water potential (R^2 = 0.60). The relationship of RGR versus overstory basal area was not significant for redcedar (P = 0.218), and the regression intercept was 11% greater for hemlock than for Douglas-fir (Fig. 5A). Thus, for a given overstory basal area, RGR was greater for hemlock than for Douglas-fir. The relationship of RGR to PAR was only significant for seedlings in thinned stands, and it did not differ among species or levels of AVC (Fig. 5B). Contrary to hypothesis 3, the rate at which RGR declined with decreasing light availability (i.e., the regression slope) was not affected by differences in soil water availability because of variation in AVC. The relationship of RGR versus herbaceous or woody cover was not significant ($P \geq 0.072$) for thinned stands. In shelterwoods and clearcuts, RGR of Douglas-fir and redcedar was most strongly related to herb cover (R^2 = 0.47), and the regression intercept was 26% greater for Douglas-fir (Fig. 5C). This indicates that, for a given level of herb cover, RGR of Douglas-fir was greater than that of redcedar. RGR of hemlock was most strongly related to woody cover (R^2 = 0.62) (Fig. 5D).

The strongest predictor of Douglas-fir RGR was foliar nitrogen content; separate regression intercepts or slopes for overstory level or vegetation control were not significant ($P \geq 0.15$) (Fig. 5E). The measure of resource availability having the strongest relationship with foliar nitrogen content of Douglas-fir seedlings in clearcuts and shelterwoods was midday water potential (R^2 = 0.63, $P < 0.001$, n = 18, $s_{y \cdot x}$ = 1.08); whereas, for seedlings in thinned stands it was PAR (R^2 = 0.34, P = 0.058, n = 9, $s_{y \cdot x}$ = 0.81) (regression relationships not shown). In the relationship of Douglas-fir RGR versus midday water potential, the regression intercept was 27% greater for clearcuts and shelterwoods than for thinned stands (Fig. 5F). This indicates that, for a given level of water potential, RGR was greater in clearcuts and shelterwoods than in thinned stands.

Discussion

This study compared seedling and resource responses among manipulated levels of competition from overstory trees and understory vegetation, and it identified mechanisms explaining species' growth responses, especially those of Douglas-fir. Fifth-year SVI in clearcuts was four to eight times that observed in thinned stands, and with vegetation control it was two to four times that observed without it. Increasing the AVC from 4.5 to 9 m^2 did not stimulate further increases in SVI. On two of three study sites, Rose et al. (1999) observed a similar diminishing gain in growth of Douglas-fir seedlings, as AVC in clearcuts increased from 4.5 to 9 m^2.

In general, effects of overstory level and vegetation control on seedling and resource responses were additive and they did not interact. Brandeis et al. (2001) observed similarly that growth of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) seedlings was increased only by reductions in overstory density, while growth of hemlock seedlings was increased only by vegetation control. Likewise, Mitchell et al. (2004) observed increases in growth of western hemlock and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) seedlings following either overstory density reduction or vegetation control. Despite the presence of additive effects of competition for most of the response variables, several noteworthy interactions were detected. First, PAR was increased by vegetation control, but only in thinned stands. Second, as AVC around seedlings increased from 4.5 to 9 m^2, soil water content in clearcuts increased, but in shelterwoods or

Table 6. Results of the analysis of variance for Douglas-fir foliage variables in response to overstory level (OL) and area of vegetation control (AVC).

			Prob. > F^c		
Source[a]	Numerator df[b]	Denominator df	Foliage mass	N concn.	N content
OL contrasts	(2)	4			
(1) CC vs. (SH and TH)	1	4	0.003	0.008	0.002
(2) SH vs. TH	1	4	0.003	0.264	0.009
AVC contrasts	(2)	12			
(3) AVC: 0 vs. (4.5 and 9 m^2)	1	12	0.019	0.002	0.003
(4) AVC: 4.5 vs. 9 m^2	1	12	0.446	0.520	0.598
OL × AVC	4	12	0.384	0.370	0.071

[a]Overstory levels: CC, clearcut; SH, shelterwood; TH, thinned.
[b]Parentheses indicate degrees of freedom that were partitioned into orthogonal contrasts.
[c]Foliage mass is the dry mass of 100 needles, nitrogen concentration (N concn.) is mass of nitrogen expressed as a percentage of dry mass, and nitrogen content is the mass of nitrogen per 100 needles.

Table 7. Average values and standard errors for Douglas-fir foliage variables by the main effects of overstory level and area of vegetation control (see Table 6 for significance levels of specific contrasts among treatment means).

	Overstory level[b]			Area of vegetation control (m^2)			
Variable[a]	CC	SH	TH	0	4.5	9	SE
Foliage mass (g)	0.44	0.39	0.26	0.33	0.39	0.37	0.02
N concn. (%)	1.9	1.6	1.5	1.5	1.7	1.8	0.05
N content (mg)	8.3	6.4	3.9	5.1	6.9	6.7	0.40

[a]Foliage mass is the dry mass of 100 needles, nitrogen concentration (N concn.) is mass of nitrogen expressed as a percentage of dry mass, and nitrogen (N) content is the mass of nitrogen per 100 needles.
[b]Overstory levels: CC, clearcut; SH, shelterwood; TH, thinned.

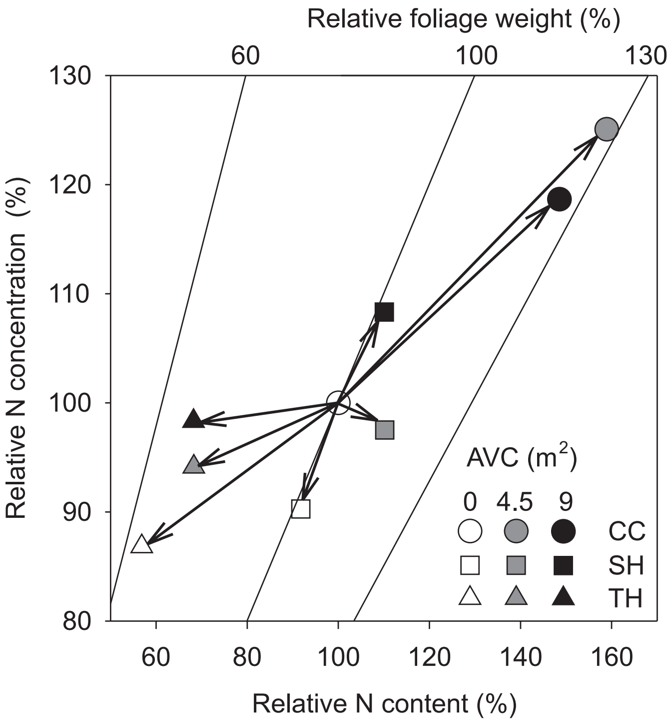
thinned stands it decreased, suggesting that roots of overstory trees had consumed the surplus water made available by vegetation control. Third, increases in both RGR and foliar nitrogen content of Douglas-fir from vegetation control were greater in clearcuts than in shelterwoods or thinned stands. Mitchell et al. (2004) found similarly that growth of Pacific silver fir and western hemlock seedlings did not differ significantly between clearcuts and shelterwoods if understory vegetation was not controlled. A fourth interaction response suggests a potential benefit from overstory trees. As AVC increased from 4.5 to 9 m^2, midday water potential of Douglas-fir in thinned stands increased, but in shelterwoods it changed very little, suggesting that the combination of shade and vegetation control in thinned stands allowed Douglas-fir seedlings to encumber less midday water stress.

The high level of seedling survival observed in this study (≥94%) suggests that competition effects did not exceed species' threshold values. PAR in thinned stands (34% of full sunlight) exceeded the 20% required for survival of Douglas-fir and it approached the 40% required for continued morphological development (Mailly and Kimmins 1997). However, survival threshold values probably were exceeded in the study by Brandeis et al. (2001). Third-year survival of Douglas-fir, hemlock, and redcedar was 22%–38%, 41%–53%, and 78%–97%, respectively, for RDs of 2.3–4.5 (RDs in the current study ranged from 0 to 3.8). For stands of similar basal area (26 $m^2 \cdot ha^{-1}$), 4th-year (conical) stem volume of Douglas-fir, hemlock, and redcedar seedlings in the current study averaged two times, six times, and one-third of that reported by Brandeis et al. (2001), respectively. Differences in seedling growth between the two studies may be attributable to the lower annual rainfall (about 1143 mm) of the Brandeis et al. (2001) study site and the increased frequency of browse on redcedar at low levels of overstory and understory observed in the present study. Deer browse on conifer seedlings differed little among levels of overstory density or vegetation control in the study by Brandeis et al. (2002).

Seedling growth responses were in general agreement with accepted tolerance classifications (Barnes et al. 1998) with a few exceptions. Because of its narrower range of growth responses, redcedar was considered more tolerant to both shade and root competition than hemlock, contrary to hypothesis 1. Note, however, that increased frequency of deer browsing on redcedar in clearcuts and with vegetation control may have compressed the range of its growth responses, resulting in an erroneous tolerance ranking. Douglas-fir was identified as the species least tolerant of shade and most tolerant of root competition, in agreement with its general tolerance classification.

Minimum values of average soil water content were about 25% by volume, approximately equal to the midpoint in available water between field capacity and permanent wilting point for silty loam and clay loam soils of the Pacific Northwest (Ley et al. 1994). Therefore, soil water availability never became severely limiting to seedling growth in any of the treatments, and this conclusion is supported by the

Fig. 4. Relative responses of Douglas-fir foliage dry mass, nitrogen concentration, and nitrogen content to the combined effects of overstory level and area of vegetation control (AVC). CC, clearcut; SH, shelterwood; TH, thinned. Plotted values are expressed relative to the reference treatment (seedlings in clearcuts with 0 m^2 AVC) and vectors (arrows) indicate the magnitude of responses to overstory level and AVC.



low to moderate values of midday water potential observed at the peak of summer drought in 2005. Shelterwoods averaged slightly greater in soil water content than thinned stands, similar to the findings of Kranabetter and Coates (2004). As noted previously, the increase in soil water content from vegetation control was less in shelterwoods or thinned stands than in clearcuts (hypothesis 2), suggesting that overstory trees had consumed the surplus water. Conversely, in the absence of vegetation control, average soil water content was nearly identical among overstory levels, similar to the findings of Mitchell (2001) and Barg and Edmonds (1999). Thus, if overstory density and understory vegetation abundance are not varied independently, observed effects of root competition will be similar for a wide range of overstory densities, because roots of residual overstory trees or understory vegetation will consume the surplus water made available by reductions in overstory density.

Results of regression analyses indicated that, for all three conifer species, light was the factor most limiting to seedling growth in thinned stands where PAR averaged 34%, similar to the findings of Carter and Klinka (1992). The slope of the regression did not differ among species or in the presence versus absence of vegetation control, indicating that shade tolerance (i.e., the relative change in growth rate per unit change in light availability) was not influenced by soil water availability. This finding is contrary to hypothesis 3 and the research results presented in Carter and Klinka (1992), where a much wider range of soil moisture conditions was studied. The foliar analysis and midday water potential measurements on Douglas-fir shed further light on factors limiting seedling growth in shelterwoods and clearcuts. Foliar nitrogen content was a strong predictor of Douglas-fir RGR for all overstory levels (R^2 = 0.71), probably because foliar nitrogen concentration is an indicator of potential photosynthesis (Mitchell and Hinckley 1993). In thinned stands, PAR was the strongest predictor of foliar nitrogen content, whereas in clearcuts and shelterwoods midday water potential was the strongest predictor.

Vector analysis revealed that, for most levels of overstory and AVC, foliar nitrogen concentration of Douglas-fir seedlings was tightly linked to nitrogen uptake and biomass accumulation. The exceptions to this relationship were for seedlings in shelterwoods in which nitrogen concentration was diluted by an increase in foliage mass (4.5 m^2 AVC) or a decrease in nitrogen content (uptake) (0 m^2 AVC). This suggests that, for seedlings in shelterwoods growing without vegetation control, availabilities of soil water and nitrogen were inadequate to enable them to sustain their nitrogen concentration at the reference level because of root competition from overstory trees and understory vegetation. In contrast, availability of soil water for shelterwood seedlings at 4.5 m^2 AVC apparently was adequate to enable them to increase their foliage mass relative to the reference treatment, but availability of soil nitrogen was inadequate to enable them to sustain their nitrogen concentration at the reference level because of root competition from overstory trees. In the 2nd year after harvesting old-growth stands of western hemlock, Prescott (1997) observed lower amounts of mineralizable nitrogen in the forest floor of partial overstory retention stands versus clearcuts. However, differences in nitrogen availability among these overstory levels may no longer exist by the 10th year after harvest (Kranabetter and Coates 2004). Thus, presence of overstory trees can result in short-term reductions in nitrogen availability relative to clearcuts.

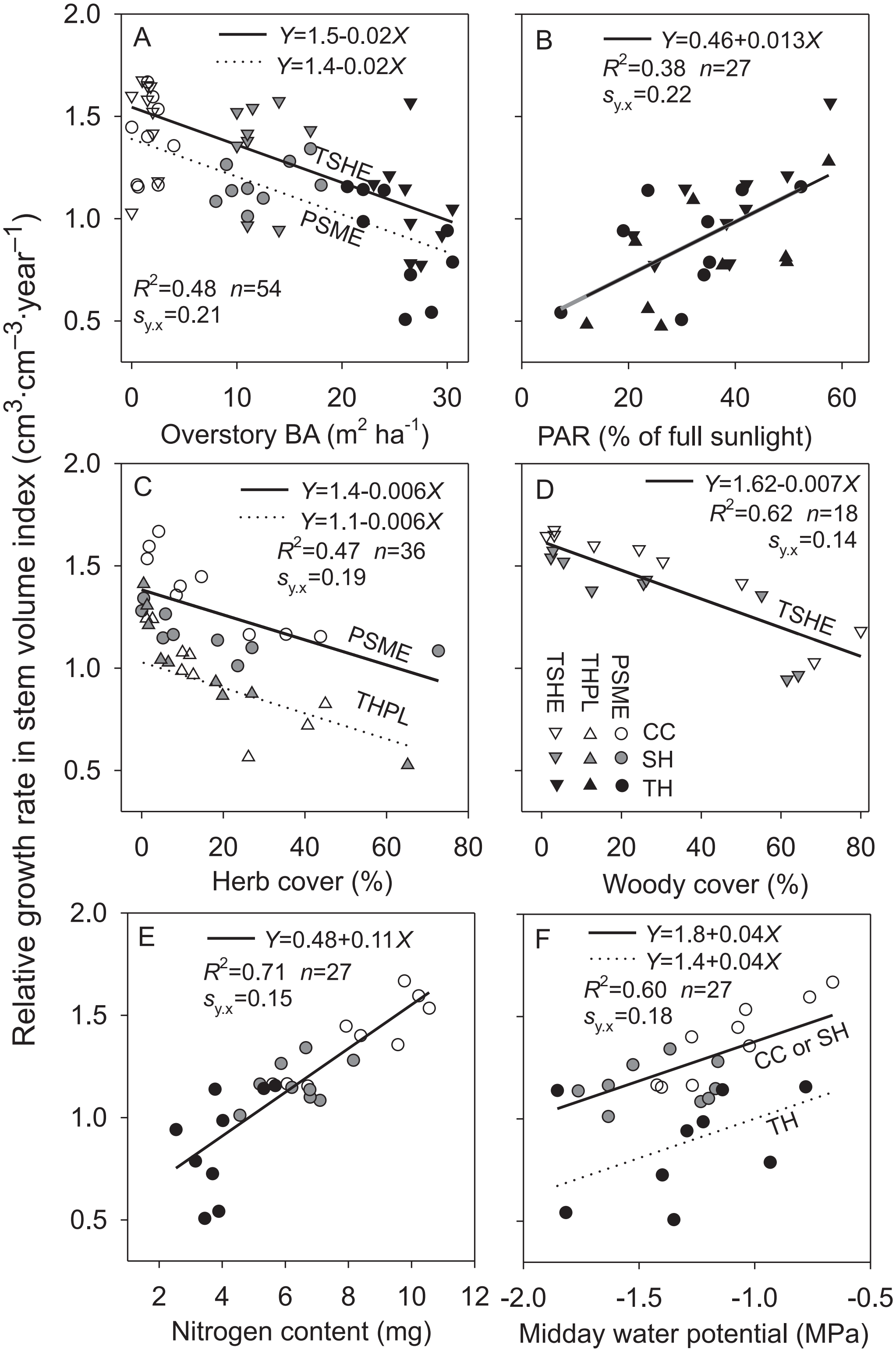
Because foliar analyses and water potential measurements were not conducted on hemlock and redcedar, the mechanisms by which these species responded to competition in shelterwoods and clearcuts remain unclear. However, similarities in their relationships of RGR versus understory cover suggest that, like Douglas-fir, competition for soil water, and concomitantly nutrients, limited their growth in shelterwoods and clearcuts. Hemlock RGR was most strongly related to woody cover, which was dominated by salal (10% average cover). Recent research by Mallik and Prescott (2001) demonstrated that competition for soil resources, and not allelopathy, was the primary means by which salal inhibited growth of western hemlock. The two species compete directly, because their fine roots are concentrated in the upper forest floor (Bennett et al. 2002).

Silvicultural implications

Given the stage of stand development and range of overstory and understory conditions in this research, the results have the following silvicultural implications.

(1) Up to 5 years after planting, survival of Douglas-fir, hemlock, and redcedar seedlings is likely to remain high (>90%) in clearcuts and in shelterwoods or thinned stands of similar overstory density.

Fig. 5. Regression relationships of conifer seedling relative growth rate in stem volume index to (A) overstory basal area, (B) photosynthetically active radiation (PAR) in thinned stands, (C) herb cover, (D) woody cover, (E) Douglas-fir foliar nitrogen content, and (F) Douglas-fir midday water potential. CC, clearcut; SH, shelterwood; TH, thinned; PSME, Douglas-fir; THPL, western redcedar; and TSHE, western hemlock. Regression equations are shown with values for the coefficient of determination adjusted for degrees of freedom (R^2), sample size (n), and standard error of estimate ($s_{y.x}$). Legend in (D) indicates symbols for species and overstory levels.



(2) An overstory density similar to that of thinned stands (RD = 3.8) will severely limit stem volume growth of Douglas-fir, hemlock, and redcedar seedlings because of restricted light availability. Independent of vegetation control, 5th-year SVI can be increased by a factor of 4 to 5, if overstory densities are reduced to those of a shelterwood (RD = 1.5–2.3), and they can be increased by a factor of 4 to 8, if overstory trees are eliminated via clearcutting.
(3) Competition from overstory trees, even at shelterwood densities (RD = 1.5–2.3), will limit growth responses of Douglas-fir seedlings to vegetation control; whereas, hemlock and redcedar responses to vegetation control will be relatively unaffected.
(4) Independent of overstory density, 5th-year SVI can be increased by a factor 2–4, if vegetation control is applied within an area of 4.5 m^2 or greater of the seedling's growing space.
(5) Browsing frequency on redcedar will increase as seedlings become more visible to black-tailed deer through reductions in overstory density or vegetation control. Under these conditions, intensive efforts should be made to suppress browsing if vigorous seedling growth is desired.
(6) On sites dominated by salal, competition for soil resources will be especially intense for hemlock. Either an alternative conifer species or vegetation control should be considered if vigorous seedling growth is desired.

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