



Five-year vegetation control effects on aboveground biomass and nitrogen content and allocation in Douglas-fir plantations on three contrasting sites

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ARTICLE INFO

Article history:

Received 14 June 2011

Received in revised form 2 August 2011

Accepted 4 August 2011

Available online 13 September 2011

Keywords:

Douglas-fir
Competition
Biomass
Nitrogen
Carbon
Plantation

ABSTRACT

Despite widespread use of intensive vegetation control (VC) in forest management, the effects of VC on allocation of biomass and nutrients between young trees and competing vegetation are not well understood. On three Pacific Northwest sites differing in productivity, soil parent material, and understory vegetation community, we evaluated year-5 effects of presence/absence of 5 years of VC on allocation of aboveground biomass and nitrogen (N) between planted Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and competing vegetation. Equations for predicting bole, branch, foliar, and total dry weights based on stem diameter at a height of 15 cm and total tree height did not differ significantly among sites or by presence or absence of VC. This contrasts with previous research, using diameter at breast height rather than at 15 cm, which found that separate equations were warranted for trees with and without competing vegetation. Estimated whole-tree biomass among the six site/VC combinations ranged from 0.8 to 7.5 Mg ha⁻¹, and increases in tree biomass associated with VC ranged from 62% to 173% among sites. Among the three sites, there were positive, linear relationships between soil total N content to a depth of 60 cm and both N content of aboveground vegetation (trees plus competing vegetation) and Douglas-fir foliar N concentration. Tree N content increased by 8.4, 8.2, and 40.0 kg N ha⁻¹ with VC at the three sites, whereas competing vegetation N content decreased with VC by 0.9, 18.8, and 32.0 kg N ha⁻¹, respectively, at the same sites. Thus, VC did not lead to a direct compensatory tradeoff between aboveground N content of trees and other vegetation. However, soil N content was linearly related to N accumulation and plant growth across the three sites. In addition to differences in N availability among sites, the effect of VC on the redistribution of resources among trees and competing vegetation also was influenced by vegetation community composition and efficacy of VC treatments.

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1. Introduction

In forest plantations, the accumulation and distribution of biomass and nutrients are of particular importance in the years be-

tween planting and canopy closure, when trees are capable of achieving exponential growth (Nambiar, 1990). During this period, tree growth rates are tempered by site water and nutrient supply limitations and by vegetation that competes for these same resources (Switzer and Nelson, 1972; Nambiar, 1990; Wagner, 2000). The proportional allocation of biomass and nutrient pools between planted trees and competing vegetation is indicative of the degree to which the trees have achieved site dominance, which is influenced by the type and cover of the competing vegetation (Wagner, 2000). Although rotation-length data on competing vegetation effects are lacking in the Pacific Northwest, limited long-term data and stand growth projections consistently show that

Abbreviations: VC, vegetation control.

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facilitating early dominance of planted trees over competing vegetation using chemical vegetation control (VC) significantly increases the volume of stemwood produced in a given period of time (Wagner et al., 2006; Newton and Cole, 2008; Harrington and Tappeiner, 2009; McFarlane et al., 2009).

Control of competing vegetation is a common practice in management of young forest plantations to increase availability of light, water, and nutrients to crop trees (Wagner et al., 2004). Young-tree growth rates are positively related to intensity of vegetation control, although this relationship is complex and may be non-linear (Harrington et al., 1995; Harrington, 2006; Rose et al., 2006; Maguire et al., 2009; Hoepfing et al., 2011). Competition thresholds have been defined as breakpoints in the relationship between crop performance and competitor abundance (Wagner et al., 1989; Glover and Zutter, 1993; Balandier et al., 2006). For trees, competitor abundance must be below a minimum-response threshold before increasing VC intensity yields an appreciable growth response. Competition thresholds for coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and ponderosa pine (*Pinus ponderosa*) are approximately 20–30% understory vegetation coverage (Oliver, 1984; Dinger and Rose, 2009). The competition threshold for tree survival is generally higher than that for tree growth because of differing sensitivities of these response variables to competitive stress (Wagner et al., 1989). Thresholds also have been developed for duration of competition control necessary to maximize yield of crop trees (critical period threshold) (Maguire et al., 2009; Hoepfing et al., 2011). For planted Douglas-fir, the critical period of vegetation control is 2–4 years, depending on site factors (Maguire et al., 2009).

When plantation trees develop in the absence of overtopping vegetation (i.e., “free to grow”), they compete belowground with other vegetation for nutrients and water (Carter et al., 1984; Morris et al., 1993; Fleming et al., 2006), although in many forests, including those of the Pacific Northwest, it is difficult to determine the relative importance and interactions of water and nutrient limitations to tree growth (Gessel et al., 1990; Nambiar and Sands, 1993; Ares et al., 2007a). Nutrients, specifically nitrogen (N), are growth-limiting on some sites in the coastal Pacific Northwest (Gessel et al., 1990; Chappell et al., 1992); however, the accessibility of N to plants is dependent on soil water availability, especially during the region’s relatively dry summer months. The mineralization rate of organic N is generally correlated positively with soil moisture (Stanford and Epstein, 1973; Walters et al., 2006), and N uptake via diffusion and mass flow also is dependent on the presence of sufficient soil water (Foth and Ellis, 1997; Chapin et al., 2002). Although VC reduces competition for nutrients and generally facilitates increased N availability for crop trees, there has been some concern that intensive or prolonged periods of vegetation control may result in depletion of soil N in young forest plantations (Hoepfing et al., 2011). Reduced vegetative cover creates soil microclimatic conditions favoring decomposition of organic matter and N mineralization (Vitousek and Melillo, 1979). A reduction in vegetative cover reduces N uptake which may lead to increased N leaching (Stevens and Hornung, 1990). The possibility of N loss associated with vegetation control likely depends on soil properties, tree growth rate, and the composition of competing vegetation, with coarse-textured soil and slow tree growth more conducive to N loss (Hoepfing et al., 2011).

Accurate tree biomass estimates are necessary to track nutrient pools and carbon (C) storage over time, as well as to predict yields for energy feedstocks and other wood products. Several studies have published biomass equations for young coast Douglas-fir based on diameter at breast height (DBH) (Gholz et al., 1979; Helgerson et al., 1988; Feller, 1992; Petersen et al., 2008) or basal diameter (Helgerson et al., 1988; Shainsky et al., 1992); however, to our knowledge, biomass equations for young Douglas-fir receiving VC

have only been previously published for one site (Petersen et al., 2008). Equations for predicting aboveground biomass have been created for numerous tree species based on stem diameter (typically at breast height) or on diameter and height, although diameter alone often explains most of the variation in tree biomass (Lambert et al., 2005). Because diameter (i.e., cambial) growth has a lower priority for allocation of photosynthates than shoot growth (Lanner, 1985; Waring and Schlesinger, 1985), it has been found to be more sensitive to the effects of competing vegetation than height growth (Zutter et al., 1986; Harrington et al., 1991; Wagner and Radosevich, 1991). Also, cambial growth of many tree species is relatively indeterminate and occurs over a longer period during the growing season than height growth (Harrington and Tappeiner, 1991). For these and other reasons, cambial growth is widely used as an index of tree response to vegetation management.

The primary objective of this study was to determine how VC affects allocation of aboveground biomass and N between young trees and competing vegetation on contrasting Douglas-fir sites in the US Pacific Northwest. The initial phase of this research included development of allometric equations to predict tree biomass; of particular interest was whether different equations would be warranted for different sites and VC treatments.

2. Methods

2.1. Study sites

The three sites in this study were 5-year-old Douglas-fir plantations in the North American Long-Term Soil Productivity (LTSP) study (Powers et al., 2005). The LTSP network was established to study the effects of various levels of soil compaction, biomass removal, and VC on soil processes, nutrient budgets, and tree growth across a wide range of sites (Powers et al., 2005). The study sites were selected because they are representative of diverse Douglas-fir plantation sites in the Pacific Northwest; the three sites differ substantially in availability of soil resources, understory vegetation communities, climate, and other parameters (Table 1). The Matlock site is in western Washington on the Olympic Peninsula; the Molalla site is in the foothills west of the Cascade Range in northwestern Oregon; the Fall River site is in Washington’s Coast Range.

Soil at Matlock is of the Grove soil series, formed in glacial outwash materials deposited approximately 14,000 years ago. The Grove very gravelly loamy sand is a Dystric Xerorthent and is somewhat excessively drained (Soil Survey Staff, 1999). At Molalla, soil is formed in colluvium and residuum, originating from igneous tuffaceous agglomerate (Soil Survey Staff, 1999). This cobbly loam soil is of the Kinney series (Andic Dystrudept) and is well-drained. The soil at Fall River is formed in residuum of Miocene basalt with volcanic ash present in the surface horizons. This silt loam is of the Boistfort series, a well-drained Typic Fulvudand. Soils at the three sites vary widely in total N content and water-holding capacity (Table 1).

Second-growth Douglas-fir was the predominant stand type at each location prior to harvest and subsequent planting. However, plant associations and understory composition (Peter and Harrington, unpublished data) differed among the three sites. At Matlock, the plant association (Henderson et al., 1989) is western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)/salal (*Gaultheria shallon* Pursh), and at Molalla the plant association (Halverson et al., 1986) is western hemlock/Oregon-grape (*Mahonia nervosa* (Pursh) Nutt.)/swordfern (*Polystichum munitum* (Kaulf.) Presl) and western hemlock/Oregon grape-salal. The plant association (Henderson et al., 1989) at Fall River is western hemlock/swordfern–redwood–sorrel

Table 1
Select physiographic, climate, and soil characteristics of the three study sites.

Variable	Site		
	Matlock	Molalla	Fall River
Latitude	47.21° N	45.20° N	46.72° N
Longitude	123.44° W	122.29° W	123.42° W
Elevation (m)	35	549	334
Slope (percent)	0	0–30	9–16
Aspect	–	NW to SW	W
Annual precipitation (cm) ^a	220	133	181
May–September cumulative precipitation (cm) ^a	32	26	30
Mean January temperature (°C) ^a	3.5	4.0	3.5
Mean July temperature (°C) ^a	16.8	18.0	16.1
Site index, 50-year (m) ^b	36	36	41–43
Water-holding capacity (0–60 cm; mm) ^c	55	142	174
Total soil N (0–60 cm; kg ha ⁻¹) ^c	3300 ± 150	7220 ± 410	10,188 ± 559
Total soil C (0–60 cm; Mg ha ⁻¹) ^c	92.4 ± 5.8	169.5 ± 12.0	193.4 ± 2.3
Soil C: N (0–60 cm)	28.0	23.5	19.0

^a Measured on-site during the study.

^b King (1966) site index for Douglas-fir; values for Matlock and Molalla are from Harrington and Schoenholtz (2010); values for Fall River are from Ares et al. (2007b).

^c Values for Matlock and Molalla are from R.A. Slesak (personal communication, 2010); values for Fall River were calculated from data from Ares et al. (2007a).

(*Oxalis oregana* Nutt.). All three study sites occur in a maritime climate characterized by mild, wet winters and warm, dry summers. Mean growing-season precipitation (May through September), measured on-site, varied by only 6 cm among the three study sites (Table 1).

The previous stands of mature, second-growth Douglas-fir at Matlock and Molalla were clear-cut with chainsaws in April and March of 2003, respectively. Following the 2003 harvests at Matlock and Molalla, trees were yarded using ground-based equipment that followed designated machine trails designed to distribute soil disturbance in a uniform pattern across the study sites. The second-growth Douglas-fir stand at Fall River was clear-cut with chainsaws between May and July 1999; trees were removed using a cable-yarding system. Slash within the tree measurements plots was scattered uniformly using a shovel excavator with a piling-rake head; no ground equipment traffic occurred within the measurement plots.

An initial operational site preparation VC treatment was applied across the study area at Matlock and Molalla. At Matlock, triclopyr was applied using backpack sprayers (September 2003), and at Molalla glyphosate was applied aerially (August 2003). No general site preparation herbicide treatment was necessary at Fall River, given the limited vegetative competition present after the 1999 harvest. Matlock and Molalla were planted with plug + 1 bareroot Douglas-fir seedlings in March and February, 2004, respectively, on a 3 × 3-m grid (1111 trees ha⁻¹). Fall River was planted in March 2000 with 1 + 1 Douglas-fir seedlings on a 2.5 × 2.5-m grid (1600 trees ha⁻¹). Mean seedling heights post-planting were 44, 45, and 36 cm at Matlock, Molalla, and Fall River, respectively. All three study sites were fenced to eliminate confounding effects that could be caused by deer and elk browse. Some of the trees at Matlock had shoot dieback in years 3 and 4, apparently as a result of multiple contributing factors including pest, drought, and frost damage (Harrington and Schoenholtz, 2010); to avoid bias, sampling in this study did not exclude trees that were affected by dieback.

2.2. Experimental design and treatments

At each site, a randomized, complete-block design study with four experimental blocks was installed. Blocking at Matlock and Molalla was based on proximity to logging access roads and, at Molalla, also on aspect. Blocking at Fall River was based on slope position and composition of the previous stand (proportion of Douglas-fir and western hemlock).

At Matlock and Molalla, experimental treatments were applied to 50- × 60-m plots with 30- × 30-m internal measurement plots. Treatments were harvest debris treatment (bole-only harvest with scattered debris and whole-tree harvest) and VC (initial broadcast treatment only (-VC) and initial broadcast treatment plus annual broadcast treatments (+VC)), arranged in a 2 × 2 factorial. In the bole-only treatment, merchantable logs were removed (minimum piece size was 12.7 cm diameter and 3.7 m long); trees were delimiting with chainsaws and all debris was left in place. In the whole-tree treatment, merchantable logs plus all logging debris greater than 5.1 cm diameter were removed from the plots; smaller limbs were left in place. At Matlock, three selective applications of triclopyr (one foliar and two basal-stem treatments) were applied directly to individual plants of the non-native, invasive species Scotch broom (*Cytisus scoparius*) where they occurred across the study area (Harrington and Schoenholtz, 2010). Owing to the highly aggressive nature of Scotch broom, this treatment was necessary to preserve the long-term integrity of the study at that site and was applied wherever the species occurred, regardless of treatment. In the +VC treatment, herbicides were applied annually using backpack sprayers. Average total cover of competing vegetation (sum of the percentage cover of each life form: forbs, grasses, vines, shrubs, and non-planted trees), ocularly estimated within one 176.6-m² circular sample plot per study plot each year and averaged over the 5 years of this study, was 30% and 62% in the +VC treatment at Matlock and Molalla, respectively; in the -VC treatment, total cover of competing vegetation was 69% and 109% at these two sites, respectively.

At Fall River, experimental treatments were applied to 30- × 85-m plots, with 15- × 70-m internal measurement plots. Data for the present study were collected from 2 of the 12 treatments (described in Ares et al. (2007b)): bole-only harvest without and with annual VC. These two treatments were replicated twice within each of the four blocks. In these treatments, merchantable bolewood to an 8- to 13-cm top was removed, and all logging debris was scattered uniformly across the plots. In the -VC treatment, no VC occurred. In the +VC treatment, competing vegetation was controlled annually, from planting through year 5, with a combination of broadcast and spot-applied herbicides; this +VC treatment at Fall River was designed to eliminate all competing vegetation rather than to simulate an operational treatment. Total cover of competing vegetation at Fall River (sum of the percentage cover of each of the five life forms), ocularly estimated as at Matlock and Molalla, was 74% and 4% in the -VC and +VC treatments, respectively. Although the experimental VC treatments differed

among the three sites due to landowner requirements and vegetation community differences, these variations were considered when interpreting the data. Detailed descriptions of the experimental treatments at Matlock and Molalla appear in Harrington and Schoenholtz (2010); those for Fall River appear in Ares et al. (2007b).

2.3. Data collection

Following the fifth growing season post-planting, all trees on the study plots were measured for height (nearest 1 cm) and diameter at 130 cm above ground (DBH). All trees at Matlock and Molalla and 10 trees per plot at Fall River were measured for diameter at a height of 15 cm above ground (D_{15}). Measurement plots at Matlock and Molalla each contained 100 planted trees; those at Fall River each contained 168 planted trees.

In the summer of study year 5, percentage cover of vegetation by species was ocularly estimated at each site within 176.6-m² circular sample plots systematically located within each treatment plot (8 plots at Matlock and Molalla; 16 plots at Fall River) (Peter and Harrington, 2009). Cover was then summed for all herbaceous species and for all woody species (including woody vines) except planted trees.

In February following the year-5 growing season, 10 trees per treatment combination per site were destructively sampled at Matlock and Molalla ($n = 40$ per site), and 59 trees (28 in +VC and 31 in -VC) were sampled at Fall River (Table 2). These sampled trees were randomly selected using stratified sampling to achieve representation across the full range of diameters present among the measurement plot trees in each treatment at each site. The biomass sampling protocol at all sites followed the method used by Petersen et al. (2008) and is briefly described here.

Sample trees were analyzed in three components: bole (including bark), branches, and foliage. After tree height, D_{15} , and DBH were measured, each bole was cut at ground level, and branches were removed and weighed by 1-m bole section. A subsample of three representative branches from each bole section of each tree was weighed, dried to constant weight at 65 °C, and then separated into branch and foliar components, which were also weighed. The ratios of branch to foliar dry weight and of fresh to dry weight were used to estimate per-tree dry branch and foliar weight. The bole of each tree was cut into four sections of equal length which were weighed separately. A 5-cm long cross-sectional subsample of bole wood and bark was removed from the center of each section and weighed, dried to constant weight at 65 °C, and reweighed. The ratio of fresh to dry weight of subsamples was used to estimate bole dry weight by section. For very small trees, the entire bole, branch, and foliar components were oven-dried and weighed separately. Bole, branch, and foliar components were sub-sampled for C and N analysis (dry combustion method; Matejovic, 1995) following the procedure described by Petersen et al. (2008). Matlock and Molalla samples were analyzed using a LECO CNS-2000 Analyzer

(LECO Corporation, St. Joseph, MI) at Central Analytical Laboratory, Oregon State University, Corvallis, OR. Fall River samples were analyzed using a Perkin-Elmer Model 2400 CHN analyzer (Perkin-Elmer, Wellesley, MA) at the School of Forest Resources Soils Laboratory, University of Washington, Seattle, WA. Blind duplicate samples and standards were utilized in each lab's analysis to monitor and control experimental error.

Year-5 aboveground biomass of competing vegetation on each study plot was estimated in August of that year by sampling in 20 randomly located subplots (0.1 m²) per study plot. The 20 samples from each study plot were combined and dried to constant weight. All woody materials greater than 6 mm diameter were grouped separately from other materials. Both groups of material were processed and analyzed for C and N as described above. Plot-level estimates of competing-vegetation C and N concentrations were weighted by the dry-weight fractions of the two analyzed groups (materials greater than 6 mm diameter and other materials) in each plot sample.

2.4. Data analysis

Based on data from the destructively sampled trees, equations were developed to predict the dry weight of bole (including bark), branch, and foliar components, and total aboveground dry weight, of the measurement-plot trees. Preliminary regression analyses showed that log-log ($\ln Y = a + b \ln X$) or log-polynomial ($\ln Y = a + bX + cX^2 + dX^3$) equations fit the data best; thus, both equation forms were tested for each dependent variable. Potential predictor variables tested in these equations were D_{15} and $D_{15}^2 \times \text{height}$ ($D_{15}^2 H$). D_{15} was used rather than DBH as a measure of bole diameter because 24% and 7% of the trees at Matlock and Molalla, respectively, had not reached breast height by year 5. Stepwise variable selection (Sokal and Rohlf, 1995) in PROC REG (SAS Institute, 2005) was used to compare treatment- and site-specific intercepts and slopes to determine whether equations predicting component dry weight differed significantly by VC treatment, harvest debris treatments, or site. Residuals from each model were examined graphically, plotted against predicted values, and tested using PROC REG and PROC UNIVARIATE (White's and Shapiro-Wilk tests) to check variance and normality assumptions (SAS Institute, 2005). All variables not significant at a confidence level of 95% or contributing less than 0.005 to the model R^2 were excluded from the final models. Initially, two-site equations for Matlock and Molalla were created to test the significance of the harvest debris treatment which was not part of the study design at Fall River. The two-site analysis showed no effect of the harvest debris treatment on component dry weight equations, so data from both treatments were used in conjunction with the bole-only harvest treatment data from Fall River in a three-site analysis testing VC and site effects.

For per-hectare analyses of biomass and nutrients, the dry weights of boles, branches, and foliage of all live study trees were

Table 2

Characteristics of destructively sampled trees used to create equations for prediction of component dry weight, and of all trees on measurement plots, for Douglas-fir 5 years post-planting at three study sites. Mean D_{15} and height values are presented with minimum and maximum values in parentheses.

Dataset	Variable	Matlock	Molalla	Fall River
Sampled trees ^a	D_{15} (cm)	3.8 (0.4, 9.5)	4.8 (0.9, 9.6)	7.2 (3.7, 11.3)
	Height (cm)	153 (33, 336)	224 (51, 400)	356 (220, 531)
All study trees	D_{15} (cm)	4.1 (0.4, 9.7)	4.7 (0.6, 10.0)	7.3 (2.5, 11.6) ^b
	Height (cm)	178 (17, 397)	230 (22, 460)	334 (130, 536)
	Survival, -VC (%)	67	91	94
	Survival, +VC (%)	89	93	94

^a Sample size for each component appears in Table 4.

^b At Fall River, D_{15} was measured on a subset of study trees; component dry weight predictions presented in this study were based on DBH equations developed by Petersen et al. (2008).

predicted using the equations shown in Table 3 for Matlock and Molalla. Because DBH, and not D_{15} , was measured at year 5 at Fall River, DBH-based equations developed for Fall River by Petersen et al. (2008) were used for that site. Per-hectare biomass, N-, and C-content estimates include mortality. Because planting density differed among sites (1111 trees ha⁻¹ at Matlock and Molalla; 1600 trees ha⁻¹ at Fall River), all per-hectare tree biomass, N-, and C-content estimates for Fall River were multiplied by a factor of 0.6944 prior to statistical analysis. It is possible that intraspecific competition among trees began earlier at Fall River than at the other sites because of this closer spacing and that this influenced tree development at Fall River prior to the end of year 5. However, we made the assumption that this spacing effect would have been minor owing to high availability of soil N and water at Fall River (Roberts et al., 2005; Ares et al., 2007a) and to the fact that mean crown diameter of trees after year 5 was only 84 and 109 cm in the -VC and +VC treatments, respectively, indicating that crowns of adjacent trees did not contact one another. The different planting densities, and the resulting differences in tree crown cover, likely did have an effect on development of competing vegetation. We did not attempt to quantify the tree density effect on competing vegetation cover or biomass owing to the complex interactions between trees and other vegetation and the fact that tree crown cover changed among and during the five growing seasons. Rather, we present competing vegetation cover and biomass results with the caveat that vegetation development, at least in the -VC treatment, would likely have been greater at Fall River under a lower initial tree density.

Estimated component and total dry weight per hectare, N concentration, estimated N and C contents per hectare, and vegetation cover were analyzed with a generalized, randomized complete-block design (GRCBD) ANOVA model (Hinkelmann and Kempthorne, 1994) using PROC MIXED in SAS (SAS Institute Inc., 2005). Because treatments were replicated on four experimental blocks at each of the three sites, the GRCBD model made it possible to test for interactions between site and VC. Block and block-within-site were random effects, and VC and the site-by-VC interaction were fixed effects. Protected, post-ANOVA comparisons of least-squared treatment means were conducted using Tukey's HSD test (Sokal and Rohlf, 1995). All ANOVA data were checked for heteroscedasticity and normality assumptions; data transformations were not necessary. Significance was set at $\alpha = 0.05$ throughout.

Although the primary focus of this study was the VC treatment and its potential interaction with site, data also were collected in both harvest-debris treatments at Matlock and Molalla. An initial analysis was conducted for these two sites using a GRCBD ANOVA with, as fixed effects, harvest type, VC, the harvest type-by-VC interaction, and interactions between site and the two treatments. Harvest debris treatment (bole-only removal vs. whole-tree removal) at Matlock and Molalla had no significant effect on any of the dependent variables and is not presented here.

3. Results

3.1. Douglas-fir component dry weight equations

Individual-tree equations for prediction of bole, branch, foliar, and total aboveground dry weight appear in Table 3. Bole weight was best predicted by $D_{15}^2 H$ in a log-log equation; branch, foliar, and total dry weights were best predicted by a log-polynomial equation that included linear, quadratic, and cubic forms of D_{15} . Relationships between predictor variables and dry weights for the three sites are shown in Fig. 1. The variables representing the slope and intercept effects of site, VC, and the site-by-VC interaction were non-significant ($P > 0.05$) in each of the four equations, indicating that a single equation per component was sufficient across both VC treatments and all three sites.

3.2. Douglas-fir dry weight estimates

Estimated dry weights per hectare for Douglas-fir bole, branch, and foliar components, and for total aboveground tree weight per hectare, were significantly influenced by site-by-VC interactions ($P < 0.001$). Although the effect of the +VC treatment on dry weight was positive at all sites, the interactions resulted from the absolute magnitude of that increase being greatest at Fall River and least at Molalla (Table 4). Vegetation control was associated with 173%, 144%, and 62% increases in aboveground whole-tree per-hectare dry weights at Matlock, Fall River, and Molalla, respectively. For bole, branch, foliage, and whole-tree dry weight estimates, increases associated with +VC were significant ($P < 0.05$) at each site with one exception: bole weight at Molalla did not differ by VC treatment.

3.3. N concentration by tree component

N concentrations of bole, branch, and foliar components of Douglas-fir trees were significantly affected by site-by-VC interactions ($P < 0.001$). Foliar N concentration at all three sites trended higher in +VC than in -VC, although this effect varied by site (Table 5). The VC treatment significantly increased foliar N concentration at the study level ($P < 0.05$), but we did not detect a statistically significant VC effect within individual sites. Bole and branch N concentrations also did not differ significantly by VC treatment within any of the three sites. Bole and branch N concentrations tended to be higher at Fall River than at Matlock and Molalla; foliar N concentrations followed the sequence: Fall River > Molalla > Matlock.

3.4. Douglas-fir N and C content estimates

Estimated N ha⁻¹ for tree bole, branch, and foliar components, and whole trees, were significantly affected ($P < 0.001$) by site-by-VC interactions. For bole and branch components, N contents were significantly greater for +VC than for -VC at Fall River, but

Table 3

Equations predicting bole, branch, foliar, and whole-tree dry weights for Douglas-fir trees 5 years post-planting for pooled data from the Matlock (MA), Molalla (MO), and Fall River (FR) sites. Predictions and fitted models are illustrated in Fig. 1.

Component	Equation ^a	Adjusted R ²	S _{y,x} ^b	n
Bole with bark	$\ln Y = -0.117 + 0.783 \ln (D_{15}^2 H)$	0.983	0.219	109
Branches	$\ln Y = 1.79 + 1.45 D_{15} - 0.135 D_{15}^2 + 0.00547 D_{15}^3$	0.948	0.334	119
Foliage	$\ln Y = 1.12 + 1.78 D_{15} - 0.177 D_{15}^2 + 0.00674 D_{15}^3$	0.947	0.343	119
Total tree	$\ln Y = 2.67 + 1.60 D_{15} - 0.152 D_{15}^2 + 0.00571 D_{15}^3$	0.974	0.259	89

^a Diameters (D_{15}) and heights (H) were measured in centimeters. Predicted dry weights are in grams.

^b Standard error of the fit.

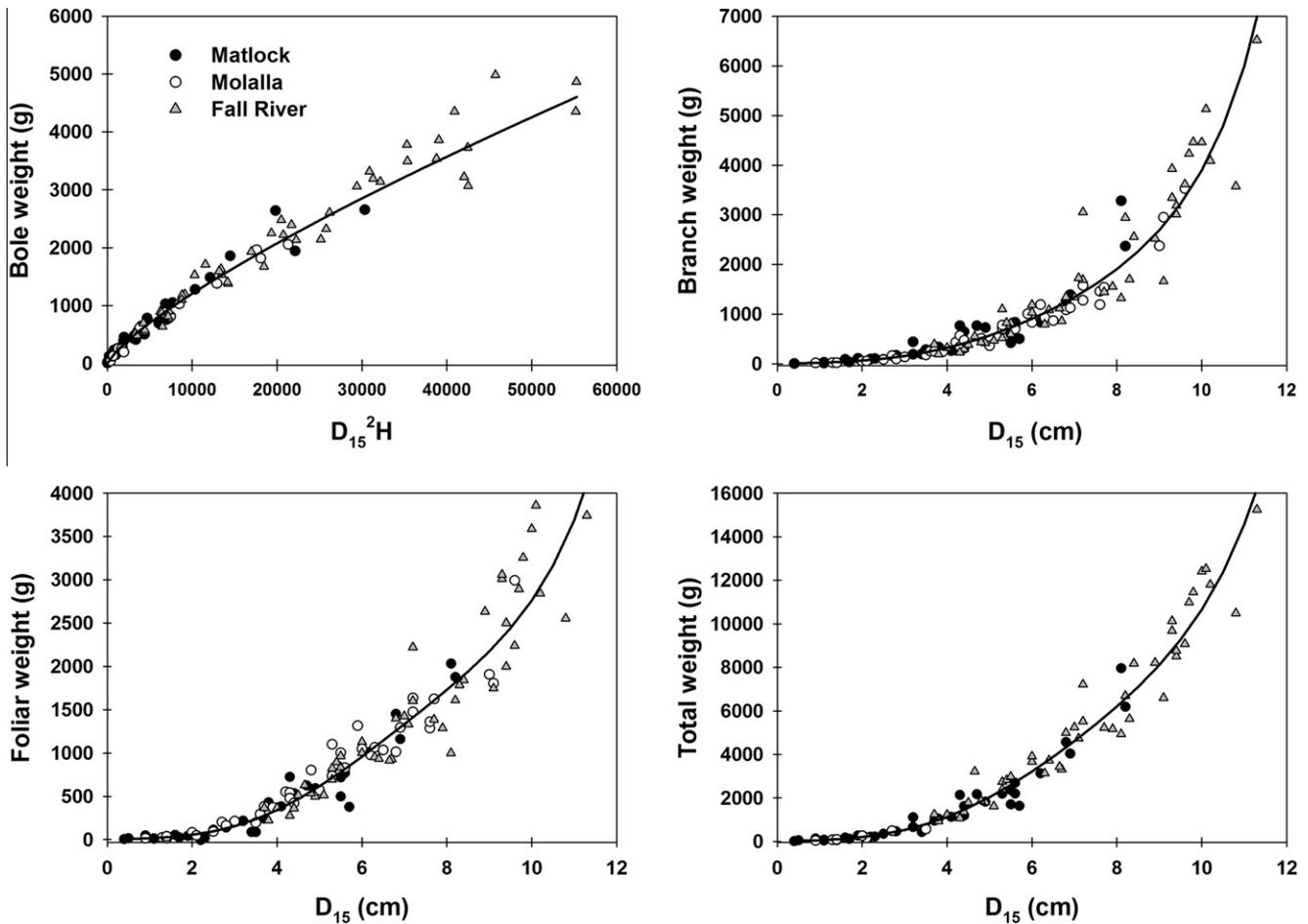


Fig. 1. Relationships between measured stem dimensions and component and total dry weights for destructively sampled trees from 5-year-old Douglas-fir plantations on three sites. Coefficients and model-fit statistics for the three-site equations are listed in Table 3.

Table 4
Least-squared means (\pm standard error) for estimated per-hectare biomass of bole, branches, foliage, and whole trees for 5-year-old Douglas-fir plantations on three sites.

Site	Vegetation control	Bole (kg ha ⁻¹)	Branches	Foliage	Whole tree
Matlock	No	292 \pm 42 d ^a	232 \pm 35 d	235 \pm 38 d	759 \pm 115 d
	Yes	757 \pm 115 c	635 \pm 97 bc	679 \pm 97 bc	2071 \pm 308 bc
Molalla	No	669 \pm 82 cd	486 \pm 54 cd	521 \pm 64 cd	1676 \pm 200 cd
	Yes	998 \pm 210 bc	836 \pm 173 b	882 \pm 171 b	2716 \pm 554 b
Fall River	No	1398 \pm 43 b	825 \pm 28 bc	845 \pm 26 bc	3067 \pm 97 b
	Yes	2694 \pm 46 a	2690 \pm 45 a	2084 \pm 34 a	7469 \pm 125 a

^a Means followed by the same letter within a column do not differ at $\alpha = 0.05$ according to Tukey's test (Sokal and Rohlf, 1995).

the VC treatments did not differ at the other sites (Table 5). For foliar and whole-tree estimates, N ha⁻¹ differed by VC treatment at each of the three sites. Estimated N ha⁻¹ for trees varied dramatically among site and treatment combinations, from 4.6 kg N ha⁻¹ in -VC at Matlock to 67.2 kg N ha⁻¹ in +VC at Fall River. Estimated whole-tree N content increased by 8.4, 8.2, and 40.0 kg N ha⁻¹ in the presence of VC at Matlock, Molalla, and Fall River, respectively.

Estimated C ha⁻¹ for tree boles, branches, foliage, and whole trees, was significantly affected ($P < 0.001$) by site-by-VC interactions. For all four of these dependent variables, +VC was associated with significant ($P < 0.05$) C content increases, relative to -VC at all sites, with the exception of tree bole C content at Molalla (Table 5). Whole-tree C ha⁻¹ in the +VC treatment at Fall River was greater than twice that of any other site/treatment combination. Because patterns in C content closely follow those of dry weight, they are not further discussed.

3.5. Competing vegetation

Year-5 dry weight, N concentration, N content, and C content of competing vegetation were significantly affected ($P < 0.01$) by site-by-VC interactions. Dry weight, N content, and C content of competing vegetation were significantly reduced ($P < 0.05$) by VC at Molalla and Fall River but not at Matlock (Table 6). For Matlock, Molalla, and Fall River, year-5 estimated dry weights of competing vegetation in the +VC treatment were 82%, 31%, and 2%, respectively, of those in the -VC treatment. Estimated N content of competing vegetation was reduced by 0.9, 18.8, and 32.0 kg N ha⁻¹ in the +VC treatment, compared to the -VC treatment, at Matlock, Molalla, and Fall River, respectively.

Year-5 herbaceous, woody, and total cover of competing vegetation each were affected by a significant ($P < 0.001$) site-by-VC interaction. Vegetation control had a similar effect on herbaceous

Table 5

Least-squared means (\pm standard error) for N concentration (g kg^{-1}) and estimated N and C (kg ha^{-1}) of bole, branches, foliage, and whole trees for 5-year-old Douglas-fir plantations on three sites.

Site	Vegetation control	Bole	Branches	Foliage	Whole tree
N (g kg^{-1})					
Matlock	No	3.5 \pm 0.3 abc ^a	5.2 \pm 0.6 b	10.3 \pm 0.6 d	–
	Yes	2.9 \pm 0.6 c	5.1 \pm 0.6 b	11.2 \pm 0.5 cd	–
Molalla	No	2.8 \pm 0.3 c	5.4 \pm 0.4 b	12.5 \pm 0.3 bc	–
	Yes	3.1 \pm 0.3 bc	5.5 \pm 0.6 b	13.1 \pm 0.3 b	–
Fall River	No	4.7 \pm 0.2 a	9.7 \pm 0.3 a	14.9 \pm 0.3 a	–
	Yes	4.2 \pm 0.2 ab	8.7 \pm 0.3 a	15.6 \pm 0.3 a	–
N (kg ha^{-1})					
Matlock	No	1.0 \pm 0.1 d	1.2 \pm 0.2 d	2.4 \pm 0.4 e	4.6 \pm 0.7 e
	Yes	2.2 \pm 0.3 cd	3.2 \pm 0.5 cd	7.6 \pm 1.1 cd	13.0 \pm 1.9 cd
Molalla	No	1.9 \pm 0.2 cd	2.6 \pm 0.3 cd	6.5 \pm 0.8 de	11.0 \pm 1.3 de
	Yes	3.1 \pm 0.7 c	4.6 \pm 1.0 c	11.6 \pm 2.2 bc	19.2 \pm 3.8 bc
Fall River	No	6.6 \pm 0.2 b	8.0 \pm 0.3 b	12.6 \pm 0.4 b	27.2 \pm 0.9 b
	Yes	11.3 \pm 0.2 a	23.4 \pm 0.4 a	32.5 \pm 0.5 a	67.2 \pm 1.1 a
C (kg ha^{-1})					
Matlock	No	143.4 \pm 20.5 d	117.8 \pm 17.7 d	118.2 \pm 19.2 d	379.3 \pm 57.4 d
	Yes	365.8 \pm 55.4 c	318.6 \pm 48.4 bc	341.2 \pm 48.6 bc	1025.6 \pm 152.4 bc
Molalla	No	321.3 \pm 39.2 cd	238.5 \pm 26.6 cd	261.2 \pm 32.1 cd	821.0 \pm 97.8 cd
	Yes	480.8 \pm 101.3 c	412.3 \pm 85.2 b	441.9 \pm 85.7 b	1335.0 \pm 272.1 b
Fall River	No	700.4 \pm 21.5 b	421.0 \pm 14.3 b	437.8 \pm 13.4 b	1559.1 \pm 49.2 b
	Yes	1357.7 \pm 23.0 a	1395.9 \pm 23.4 a	1080.0 \pm 17.6 a	3833.6 \pm 64.0 a

^a Means followed by the same letter within a column do not differ at $\alpha = 0.05$ according to Tukey's test (Sokal and Rohlf, 1995).

Table 6

Estimated dry weight (least-squared means \pm standard error), measured N concentration, and estimated N and C contents of the aboveground portion of all competing vegetation growing in 5-year-old Douglas-fir plantations on three sites. No adjustment have been made for the fact that Fall River had an initial density of 1600 trees ha^{-1} , whereas Matlock and Molalla had initial densities of 1111 trees ha^{-1} .

Site	Vegetation control	Dry weight (kg ha^{-1})	N concentration (g kg^{-1})	N content (kg N ha^{-1})	C content (kg C ha^{-1})
Matlock	No	2502.6 \pm 291.2 ab ^a	7.6 \pm 0.1 c	19.1 \pm 2.3 c	1255.5 \pm 153.6 ab
	Yes	2054.1 \pm 845.4 bc	9.9 \pm 1.2 bc	18.2 \pm 6.5 c	1028.2 \pm 425.7 b
Molalla	No	4773.3 \pm 1053.3 a	9.4 \pm 1.4 bc	40.6 \pm 4.8 a	2398.5 \pm 536.3 a
	Yes	1489.5 \pm 226.2 bc	14.7 \pm 0.5 b	21.8 \pm 3.3 bc	742.0 \pm 107.7 bc
Fall River	No	2940.3 \pm 256.2 ab	11.4 \pm 0.6 bc	33.0 \pm 2.2 ab	1281.9 \pm 109.9 b
	Yes	53.1 \pm 16.6 c	20.4 \pm 1.5 a	1.0 \pm 0.3 d	23.1 \pm 7.4 c

^a Means followed by the same letter within a column do not differ at $\alpha = 0.05$ according to Tukey's test (Sokal and Rohlf, 1995).

cover at Matlock and Molalla, whereas values for both $-VC$ and $+VC$ were more extreme at Fall River (Fig. 5). Woody cover was 30% or less for all sites and VC treatments except $-VC$ at Molalla which had 83% woody cover. The effect of VC on total competing vegetation cover was least at Matlock and greatest at Fall River. A full analysis of vegetation development during this study appears in Peter and Harrington (2009) and Peter and Harrington (unpublished data).

3.6. Total biomass and biomass N content

Total aboveground biomass (planted trees adjusted to 1111 trees ha^{-1} plus unadjusted competing vegetation) did not differ significantly by VC treatment at any of the sites (Fig. 2), although there was a site-by-VC interaction ($P < 0.001$). The interaction resulted from total dry biomass content trending higher for $+VC$ than for $-VC$ at Matlock and Fall River, whereas the reverse pattern occurred at Molalla. Total aboveground vegetation N content also was affected by a site-by-VC interaction ($P < 0.001$) resulting from the same trend that occurred for total aboveground biomass (Fig. 3). The portion of total aboveground vegetation N that was allocated to planted trees was less than 50% for all site/VC combinations, with the exception of $+VC$ at Fall River (98.5%) which also had the lowest percent cover of competing vegetation (3%; Fig. 4).

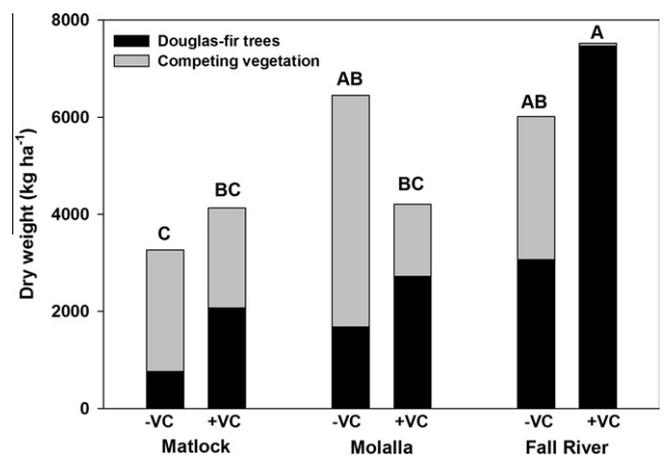


Fig. 2. Aboveground dry weight of Douglas-fir trees and competing vegetation, at plantation age 5 years, without ($-VC$) and with ($+VC$) annual vegetation control at three sites. Site/treatment combinations accompanied by the same letter do not differ in total dry weight (trees plus competing vegetation) at $\alpha = 0.05$ according to Tukey's test (Sokal and Rohlf, 1995). Tree dry weight for Fall River was scaled from an initial density of 1600 trees ha^{-1} to the equivalent of 1111 trees ha^{-1} , the initial density at Matlock and Molalla; competing vegetation dry weight was not scaled.

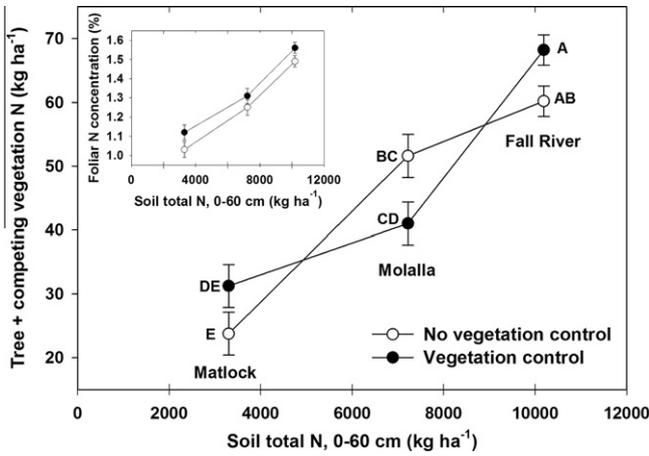


Fig. 3. Total aboveground N in plantation trees and competing vegetation, and Douglas-fir foliar N concentration (inset), in two vegetation control treatments in 5-year-old Douglas-fir plantations on three sites. One standard error is shown. Site/treatment combinations accompanied by the same letter do not differ at $\alpha = 0.05$ according to Tukey's test (Sokal and Rohlf, 1995). Tree N content for Fall River was scaled from an initial density of 1600 trees ha^{-1} to the equivalent of 1111 trees ha^{-1} , the initial density at Matlock and Molalla; competing vegetation N content was not scaled.

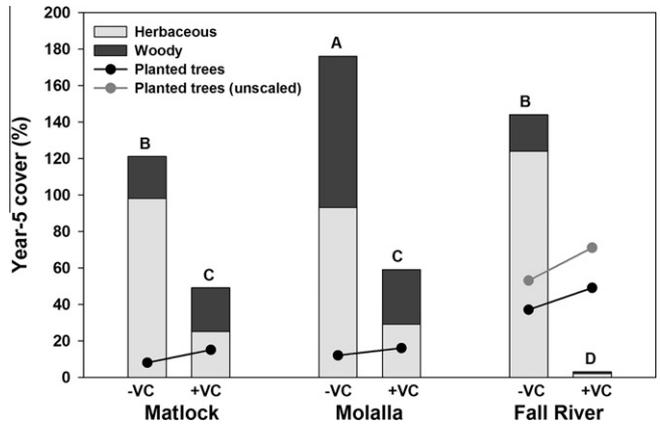


Fig. 5. Percentage cover of herbaceous and woody competing vegetation and crowns of planted trees in 5-year-old Douglas-fir plantations on three sites. Tree crown cover for Fall River was scaled from an initial density of 1600 trees ha^{-1} to the equivalent of 1111 trees ha^{-1} , the initial density at Matlock and Molalla (unscaled values are shown in gray); competing vegetation cover was not scaled. Tree crown cover data are from Peter and Harrington (unpublished data). Bars accompanied by the same letter do not differ in total competing vegetation cover (herbaceous plus woody) at $\alpha = 0.05$ according to Tukey's test (Sokal and Rohlf, 1995).

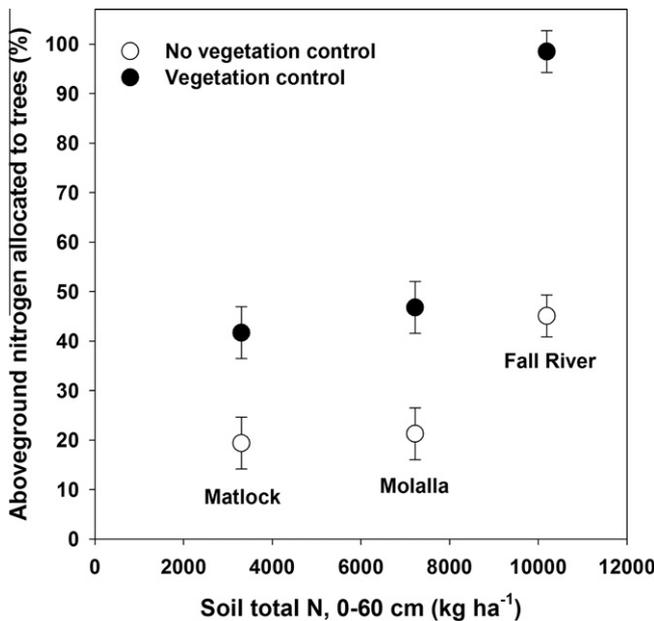


Fig. 4. Aboveground per-hectare N content of plantation trees (as percentage of per-hectare aboveground N content of trees plus competing vegetation) in two vegetation control treatments for 5-year-old Douglas-fir plantations on three sites. Tree N content for Fall River was scaled from an initial density of 1600 trees ha^{-1} to the equivalent of 1111 trees ha^{-1} , the initial density at Matlock and Molalla; competing vegetation N content was not scaled.

4. Discussion

4.1. Prediction of tree biomass

For 5-year-old Douglas-fir, a single allometric equation predicted dry weight across all three sites and both VC treatments, explaining 95–98% of the variation in component or total tree weights. Differences in site productivity and competing vegetation communities, as well as the presence/absence of VC did not warrant separate equations for prediction of individual-tree bole, branch, foliar, or total dry weight. This suggests that basal stem

diameter (D_{15}) can be used broadly to predict aboveground biomass of young Douglas-fir independent of site quality and silvicultural treatment, and that simple equations can be used to predict biomass yields for that stand component. Although numerous diameter-based equations exist for prediction of biomass of mature Douglas-fir trees (Jenkins et al., 2004; Harrison et al., 2009), we are aware of only two previous studies that used diameter near groundline to predict whole-tree biomass of young coast Douglas-fir (Helgerson et al., 1988; Shainsky et al., 1992). However, the equations in these studies are not directly comparable to ours because Shainsky et al. (1992) measured diameter at a 2-cm height and Helgerson et al. (1988) predicted tree biomass excluding a 15-cm stump.

The finding that VC had no effect on the relationship between stem diameter and component dry weight differs from a previous analysis of the sampled year-5 Fall River trees that found, using log-log equations with DBH as the predictor, that equations differed significantly for predicting component weight in -VC and +VC treatments (Petersen et al., 2008). For prediction of bole weight, the difference between our findings and those of Petersen et al. (2008) results from our use of D_{15} instead of DBH. As a predictor of bole weight, D_{15} better accounted for biomass allocation associated with the stem taper of the year-5 trees. Particularly in the +VC treatment, the notable increase in bole diameter near groundline (i.e., nearer a height of 15 cm than breast height) appeared to substantially contribute to total bole weight. For example, at Fall River, the cross-sectional bole area at a 15-cm height averaged 333% and 263% of that at breast height in the +VC and -VC treatments, respectively. This suggests that, compared to DBH, D_{15} is a better predictor of bole volume, and thus bole weight, for 5-year-old Douglas-fir because it better describes the portion of the bole that contributes most to volume and weight. At Fall River, separate biomass equations were needed for +VC and -VC treatments when DBH was used as the predictor (Petersen et al., 2008) because of the difference in lower-bole taper between the +VC and -VC treatments.

Our inclusion of height in the predictor variable D_{15}^2H also may have contributed to making our single bole-weight equation sufficient for both -VC and +VC treatments because the addition of the height variable helps explain differences in stem form (Brand,

1986) and shoot dieback (i.e., at Matlock; Harrington and Schoenholtz, 2010) across VC treatments. The effect of VC on diameter growth, typically measured at breast height, and subsequent height:diameter ratios is well-documented (Zutter et al., 1986; Harrington et al., 1991; Wagner and Radosevich, 1991). Log–log equations using $D_{15}^2 H$ have been used to predict biomass in seedlings of many southern pine species (*Pinus* spp.) (Ruehle et al., 1984). In the study of Petersen et al. (2008), tree height was not used as a predictor of bole weight because it was strongly correlated with diameter and its inclusion did not contribute significantly to model fit. The redundancy of tree height as a predictor in that study was likely at least partially attributable to data collection at a single site, and stem form, specifically the relationship between diameter and height, was likely less variable than it would have been across multiple sites (Weiskittel et al., 2006). By contrast, the fit of our three-site bole equation was improved by the addition of tree height as a predictor.

4.2. Allocation of biomass and N between trees and competing vegetation

Significant increases in tree biomass, N, and $C\ ha^{-1}$ associated with VC at all three sites indicated that non-tree vegetation reduced tree growth through competition for limited soil resources. Differences among sites in composition of competing vegetation, VC treatment protocol (associated with differences in landowner requirements), and availability of soil resources interacted to influence VC efficacy, tree biomass, and tree N and C content. Previous research at these study sites showed that both available soil N and soil water content were significantly increased by the +VC treatment (Ares et al., 2007a; Slesak et al., 2010). Quantifying the relative importance of N and water limitation was beyond the scope of the present study, but inter-annual variation in availability of these resources suggests that the relative importance changes according to growing-season precipitation and other factors (Roberts et al., 2005; Slesak et al., 2010).

Although year-5 estimated biomass for plantation trees in the –VC treatment followed the same numerical sequence among sites as total soil N and soil water-holding capacity (Fall River > Molalla > Matlock), estimated total aboveground living biomass among sites in the –VC treatment was clearly also influenced by species composition of competing vegetation. For total aboveground living biomass, Molalla was similar to Fall River owing to the former site's relatively large amount of competing vegetation biomass (Fig. 2). Much of this competing vegetation consisted of California blackberry (*Rubus ursinus*) (Peter and Harrington, unpublished data), which forms biennial woody stems from a perennial rootstock. However, the closer tree spacing at Fall River, and the greater tree crown cover, likely limited development of competing vegetation in that site's –VC treatment (the +VC treatment had virtually no competing vegetation at Fall River). Thus, our estimates of total aboveground living biomass for Fall River are conservative because tree biomass estimates were adjusted to a lower planting density, but competing vegetation biomass estimates were not adjusted for the effect that the higher tree density had on vegetation development.

The effect of the VC treatments on year-5 total aboveground living biomass accumulation differed by site. Total aboveground biomass at Matlock and Fall River increased with VC as a result of increased biomass production by trees, whereas biomass at Molalla decreased with VC as a result of reduced biomass of competing vegetation. However, the year-4 targeted Scotch broom control in the –VC treatment at Matlock likely affected year-5 biomass estimates in that treatment. Without this Scotch broom control, competing vegetation biomass would have been much greater in the –VC treatment (Harrington and Schoenholtz, 2010), and thus the VC ef-

fect on total aboveground living biomass accumulation would likely have been more similar to that of Molalla (Fig. 2). Although Scotch broom roots are associated with N-fixing bacteria, C:N ratios change little in soils beneath Scotch broom plants (Haubensak and Parker, 2004; Caldwell, 2006); furthermore, Haubensak and Parker (2004) reported that plants growing in soil from Scotch broom sites do not grow faster than those growing in soil from sites without Scotch broom. This suggests that while biomass of Scotch broom plants themselves influenced our biomass estimates, the species may not have increased soil N availability for other plants.

Fall River was the only site at which tree biomass alone in the +VC treatment was greater than total aboveground living biomass in the –VC treatment. This phenomenon may have resulted, at least in part, from several potentially interacting factors: the relatively small amount of understory vegetation left after harvest of the previous stand, the primarily herbaceous composition of competing vegetation, the closer spacing of planted trees, which increased tree cover, and the more complete VC at Fall River relative to the other sites. Intensive management generally limits the realized net primary productivity of young stands by limiting the density of trees and controlling competing vegetation, which results in a total vegetative leaf area (crop trees plus competing vegetation) that is lower than that of an unmanaged stand of the same age (Powers and Reynolds, 1999). This pattern was evident in biomass accumulations between VC treatments at Matlock and Molalla but not at Fall River. At Fall River, a high level of VC shifted the allocation of biomass production predominantly to the planted trees. As woody perennials, they accumulated aboveground biomass over the 5-year study, unlike the competing vegetation at that site which was predominantly herbaceous. At Molalla, by contrast, the woody California blackberry stems contributed substantially in raising the total biomass accumulation in the –VC treatment above that in the +VC treatment. Another factor possibly contributing to the relatively high proportional allocation of biomass to trees at Fall River is that the trees were planted at a closer spacing (2.5 vs. 3.0-m spacing at other sites), which likely reduced the amount of sunlight reaching competing vegetation. Although the per-hectare estimates of tree biomass were adjusted for this spacing difference, the increased shading had an unquantified influence on growth of competing vegetation.

According to nutritional guidelines based on foliar N concentrations of Douglas-fir, the trees at Matlock were likely severely N deficient, while those at Molalla had a moderate to severe deficiency, and those at Fall River had adequate N (Ballard and Carter, 1986). Across sites, there was a strong, near-linear increase in tree foliar N with increasing soil N content (Fig. 3, inset). The trend suggests that, in the absence of VC, 5-year-old planted Douglas-fir trees would have sufficient foliar N (approximated as $14\ g\ kg^{-1}$) on sites with soil N contents of at least 8000–10,000 $kg\ N\ ha^{-1}$. However, owing to the numerous factors influencing N sufficiency, additional data are needed to evaluate this relationship.

The lack of within-site VC effect on foliar N concentration at Fall River is in agreement with prior analyses that also found no significant year-5 VC effect on foliar N concentration in current-year foliage (Ares et al., 2007a) or in samples of whole-crown foliage (Petersen et al., 2008). However, N concentration of current-year foliage was higher in the +VC treatment compared to the –VC treatment from years 2 through 5 at Matlock and Molalla and in years 3 and 4 at Fall River (Ares et al., 2007a; Slesak et al., 2010; T.B. Harrington, unpublished data). This VC effect in the earlier years of the study can be attributed to younger trees (and smaller trees, in the case of Matlock) having less-extensive root systems and greater sensitivity to vegetative competition (Newton and Prest, 1988). As tree root systems develop and tree crowns overtop competing vegetation, this interspecific competition becomes less important.

At each site, the +VC treatment significantly increased year-5 tree foliar N content per hectare compared to the -VC treatment. This was likely an effect, at least in part, of increased N status associated with the +VC treatment, a trend most evident in years prior to year 5 (Ares et al., 2007a; Slesak et al., 2010). Increased N status affects Douglas-fir foliage by increasing: (1) number of needles, (2) needle size and weight, (3) duration of needle retention, and (4) needle N concentration (Turner and Olson, 1976; Brand, 1986; Harrington and Tappeiner, 1991; Devine and Harrington, 2009). The VC treatment effect on foliar weight was strongly influenced by VC effects on tree crown size: larger trees in the +VC treatments had larger crowns (Fig. 5). Given the large increase in foliar weight with +VC, it appears that increased N availability increased tree N status, causing a concurrent increase in needle number, size, and retention (Slesak, 2008). Differences in foliar weight between VC treatments corresponded closely to differences in foliar N content because, in year 5, whole-crown foliar N concentration did not differ widely between VC treatments at a given site.

The shift in aboveground N pools associated with VC treatments varied widely by site and did not appear to be compensatory. Estimated whole-tree N content was increased by 8.4, 8.2, and 40.0 kg N ha⁻¹ in the presence of VC at Matlock, Molalla, and Fall River, respectively, whereas estimated N content of competing vegetation was reduced by 0.9, 18.8, and 32.0 kg N ha⁻¹, respectively, in the presence of VC at the same sites. When a portion of the competing vegetation is eliminated by VC, the remaining competing vegetation may benefit from the resources that would otherwise have been taken up by the eliminated vegetation. An example of this is the trend toward increased N concentration of competing vegetation in the +VC treatment, compared to that in the -VC treatment, at all three sites (Table 5). Thus, a VC treatment may reallocate soil N to young trees and to surviving competing vegetation, and it also increases the amount of plant-available soil N that is lost from the rooting zone through leaching (Slesak et al., 2009).

The observation that less than half of total aboveground N was allocated to planted trees in all but the most intensive VC treatment (Fall River; Fig. 4) indicates the substantial N uptake of competing vegetation, even when annual VC treatments were applied for 5 years. At year 5, the levels of competing vegetation cover in the +VC treatments at Matlock and Molalla were well above the study's target level of less than 20%. Because competing vegetation cover of 20–30% has been reported as a threshold below which tree growth increases dramatically (Oliver, 1984; Dinger and Rose, 2009), it is likely that growth of trees in the +VC treatment at Fall River approached the maximum possible for the site, whereas that of trees at Matlock and Molalla was considerably below the potential maximum.

In the -VC treatment, the portion of aboveground N allocated to trees was apparently affected by differences in competing vegetation composition among sites: at Matlock, Molalla, and Fall River, 19%, 21%, and 45% of N in aboveground living biomass was allocated to planted trees, respectively. The application of a targeted Scotch broom eradication in the -VC treatment undoubtedly influenced N allocation at Matlock, where percentage N in trees would otherwise have been lower. The relatively low portion of N allocated to trees at Molalla was likely influenced by the abundance of California blackberry; substantial accumulations of N per hectare have been measured in stems of *Rubus* (Strik, 2005). At Fall River, the relatively small amount of primarily herbaceous competing vegetation present in the -VC treatment at the time of planting, combined with the closer spacing of the trees and the high productivity of the site, allowed trees to achieve rapid early growth and dominance over competing vegetation (Peter and Harrington, 2009), and capture a greater fraction of available N than at the other sites.

5. Conclusions

Influences of site productivity and VC on aboveground component biomass of trees in 5-year-old Douglas-fir plantations were well-explained by stem diameter at a height of 15 cm. Because diameter growth is greatest at the base of a tree's crown (Larson, 1963), and the crowns of the trees had not yet begun to recede upward, it is not surprising that diameter near groundline was highly predictive of bole weight. Similarly, the components of the crown (i.e., branch and foliar weights) were strongly related to basal diameter, with no differences in that relationship among the three sites. None of the stands in this study had significant amounts of overtopping hardwoods (e.g., red alder (*Alnus rubra*) or big-leaf maple (*Acer macrophyllum*)), so the biomass equations developed here should be used with caution where this type of competition is present or where it was recently removed.

The positive, generally linear relationship between soil N content and both total aboveground N content of trees and other vegetation and Douglas-fir foliar N concentration (Fig. 3) supports the premise that soil N content is strongly linked to N uptake and plant growth at the study sites. Tree N content and biomass were substantially increased by VC at all three sites, whereas year-5 N content of competing vegetation was unchanged, halved, and almost completely eliminated by VC treatments at Matlock, Molalla, and Fall River, respectively. Thus, VC per se did not lead to a direct compensatory tradeoff between aboveground N content of trees and other vegetation. In addition to differences in N availability among sites, these trends in N allocation were certainly influenced by vegetation community composition, efficacy of VC treatments, and the effect of VC on the redistribution of resources among trees and surviving competitors. The three study sites, examples of the diverse soils and plant communities on which Douglas-fir are planted in the coastal Pacific Northwest, provide baseline information of VC effects on young-plantation aboveground biomass and N allocation.

Acknowledgments

This study is a product of the Sustainable Forestry Component of Agenda 2020, a joint effort of the US Department of Agriculture, Forest Service, Research and Development Program and the American Forest and Paper Association. The authors gratefully acknowledge the financial support provided by the National Council for Air and Stream Improvement, Inc. and the Pacific Northwest Stand Management Cooperative. Study sites and support for experimental treatments were provided by Weyerhaeuser Company, Green Diamond Resource Company, and Port Blakely Tree Farms LLC; the authors are particularly grateful to Rodney Meade, Randall Greggs and Jeff Madsen. We are grateful for support from the Oregon State University College of Forestry and the University of Washington School of Forest Resources. We are grateful for study installation and data collection assistance from many employees of these institutions, and of the USDA Forest Service Pacific Northwest Research Station, particularly James Dollins, Barry Flaming, Paul Footen, Irae Guerrini, Diana Livada, Kyle Peterson, Brian Strahm, and David Stephens.

References

- Ares, A., Terry, T., Harrington, C., Devine, W., Peter, D., Bailey, J., 2007a. Biomass removal, soil compaction, and vegetation control effects on five-year growth of Douglas-fir in coastal Washington. *For. Sci.* 53, 600–610.
- Ares, A., Terry, T.A., Piatek, K.B., Harrison, R.B., Miller, R.E., Flaming, B.L., Licata, C.W., Strahm, B., Harrington, C.A., Meade, R., Anderson, H.W., Brodie, L.C., Kraft, J.M., 2007b. The Fall River Long-term Site Productivity Study in Coastal Washington: Site Characteristics, Experimental Design, and Biomass, Carbon and Nitrogen Stores Before and After Harvest. USDA For. Serv. Gen. Tech. Rep. No. PNW-GTR-691, p. 85.

- Ballard, T.M., Carter, R.E., 1986. Evaluating Forest Stand Nutrient Status. Land Management Report No. 20. British Columbia Ministry of Forests, Victoria, Canada.
- Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., Zedaker, S.M., 2006. Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. *Forestry* 79, 3–27.
- Brand, D.G., 1986. Competition-induced changes in developmental features of planted Douglas-fir in southwestern British Columbia. *Can. J. For. Res.* 16, 191–196.
- Caldwell, B.A., 2006. Effects of invasive scotch broom on soil properties in a Pacific coastal prairie soil. *Appl. Soil Ecol.* 32, 149–152.
- Carter, G.A., Miller, J.H., Davis, D.E., Patterson, R.M., 1984. Effect of vegetative competition on the moisture and nutrient status of loblolly pine. *Can. J. For. Res.* 14, 1–9.
- Chapin, F.S., Matson, P.A., Mooney, H.A., 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag, New York.
- Chappell, H.N., Omule, S.A.Y., Gessel, S.P., 1992. Fertilization in coastal northwest forests: using response information in developing stand-level tactics. In: Chappell, H.N., Weetman, G.F., Miller, R.E. (Eds.), *Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests*. College of Forest Resources, University of Washington, Seattle, pp. 98–113.
- Devine, W.D., Harrington, T.B., 2009. Belowground competition from overstory trees influences Douglas-fir sapling morphology in thinned stands. *New For.* 37, 137–153.
- Dinger, E.J., Rose, R., 2009. Integration of soil moisture, xylem water potential, and fall-spring herbicide treatments to achieve the maximum growth response in newly planted Douglas-fir seedlings. *Can. J. For. Res.* 39, 1401–1414.
- Feller, M.C., 1992. Generalized versus site-specific biomass regression equations for *Pseudotsuga menziesii* var. *menziesii* and *Thuja plicata* in coastal British Columbia. *Bioresour. Technol.* 39, 9–16.
- Fleming, R.L., Powers, R.F., Foster, N.W., Kranabetter, J.M., Scott Jr., D.A., Ponder, F., Berch, S., Chapman, W.K., Kabzems, R.D., Ludovici, K.H., 2006. Effects of organic matter removal, soil compaction, and vegetation control on 5-year seedling performance: a regional comparison of Long-Term Soil Productivity sites. *Can. J. For. Res.* 36, 529–550.
- Foth, H.D., Ellis, B.G., 1997. *Soil Fertility*. CRC Press, Boca Raton, FL.
- Gessel, S.P., Miller, R.E., Cole, D.W., 1990. Relative importance of water and nutrients on the growth of coast Douglas fir in the Pacific Northwest. *For. Ecol. Manage.* 30, 327–340.
- Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979. Equations for Estimating Biomass and Leaf Area of Plants in the Pacific Northwest. Research Paper 41. Forest Research Laboratory, Oregon State University, Corvallis, OR.
- Glover, G.R., Zutter, B.R., 1993. Loblolly pine and mixed hardwood stand dynamics for 27 years following chemical, mechanical, and manual site preparation. *Can. J. For. Res.* 23, 2126–2132.
- Halverson, N.M., Topik, C., Van Vickle, R., 1986. *Plant Association and Management Guide for the Western Hemlock Zone: Mt. Hood National Forest*. USDA For. Serv. Pacific Northwest Region.
- Harrington, T.B., 2006. Five-year growth responses of Douglas-fir, western hemlock, and western red cedar seedlings to manipulated levels of overstory and understorey competition. *Can. J. For. Res.* 36, 2439–2453.
- Harrington, T.B., Schoenholtz, S.H., 2010. Effects of logging debris treatments on five-year development of competing vegetation and planted Douglas-fir. *Can. J. For. Res.* 40, 500–510.
- Harrington, T.B., Tappeiner II, J.C., 1991. Competition affects shoot morphology, growth duration, and relative growth rates of Douglas-fir saplings. *Can. J. For. Res.* 21, 474–481.
- Harrington, T.B., Tappeiner II, J.C., Hughes, T.F., 1991. Predicting average growth and size distributions of Douglas-fir saplings competing with sprout clumps of tanoak or Pacific madrone. *New For.* 5, 109–130.
- Harrington, T.B., Wagner, R.G., Radosevich, S.R., Walstad, J.D., 1995. Interspecific competition and herbicide injury influence 10-year responses of coastal Douglas-fir and associated vegetation to release treatments. *For. Ecol. Manage.* 76, 55–67.
- Harrington, T.B., Tappeiner II, J.C., 2009. Long-term effects of tanoak competition on Douglas-fir stand development. *Can. J. For. Res.* 39, 765–776.
- Harrison, R., Terry, T., Licata, C., Flaming, B., Meade, R., Guerrini, I., Strahm, B., Xue, D., Lolley, M., Sidell, A., 2009. Biomass and stand characteristics of a highly productive mixed Douglas-fir and western hemlock plantation in coastal Washington. *West. J. Appl. For.* 24, 180–186.
- Haubensak, K.A., Parker, I.M., 2004. Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington [USA]. *Plant Ecol.* 175, 71–79.
- Helgerson, O.T., Cromack, K., Stafford, S., Miller, R.E., Slagle, R., 1988. Equations for estimating aboveground components of young Douglas-fir and red alder in a coastal Oregon plantation. *Can. J. For. Res.* 18, 1082–1085.
- Henderson, J.A., Peter, D.H., Leshner, R.D., Shaw, D.C., 1989. *Forested Plant Associations of the Olympic National Forest*. R6 Ecology Technical Paper 001–88. USDA Forest Service, Pacific Northwest Region.
- Hinkelmann, K., Kempthorne, O., 1994. *Design and Analysis of Experiments*, Vol. 1: Introduction to Experimental Design. Wiley, New York.
- Hoeping, M.K., Wagner, R.G., McLaughlin, J., Pitt, D.G., 2011. Timing and duration of herbaceous vegetation control in northern conifer plantations: 15th-year tree growth and soil nutrient effects. *For. Chron.* 87, 398–413.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2004. *Comprehensive Database of Diameter-based Biomass Regressions for North American Tree Species*. USDA Forest Service, Northeastern Research Station. Gen. Tech. Rep. NE-GTR-319.
- King, J.E., 1966. *Site Index Curves for Douglas-fir in the Pacific Northwest*. Weyerhaeuser Forestry Paper No. 8. Weyerhaeuser Co., Forestry Research Center, Centralia, WA.
- Lambert, M.-C., Ung, C.-H., Raulier, F., 2005. Canadian national tree aboveground biomass equations. *Can. J. For. Res.* 35, 1996–2018.
- Lanner, R.M., 1985. On the insensitivity of height growth to spacing. *For. Ecol. Manage.* 13, 143–148.
- Larson, P.R., 1963. Stem form development of forest trees. *For. Sci. Monographs* 5, 1–42.
- Maguire, D.A., Mainwaring, D.B., Rose, R., Garber, S.M., Dinger, E.J., 2009. Response of coastal Douglas-fir and competing vegetation to repeated and delayed weed control treatments during early plantation development. *Can. J. For. Res.* 39, 1208–1219.
- Matejovic, I., 1995. Total nitrogen in plant material determined by means of dry combustion: a possible alternative to determination by Kjeldahl digestion. *Comm. Soil Sci. Plant Anal.* 26, 2217–2229.
- McFarlane, K.J., Schoenholtz, S.H., Powers, R.F., 2009. Plantation management intensity affects belowground carbon and nitrogen storage in northern California. *Soil Sci. Soc. Am. J.* 73, 1020–1032.
- Morris, L.A., Moss, S.A., Garbett, W.S., 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. *For. Sci.* 39, 166–187.
- Nambiar, E.K.S., 1990. Interplay between nutrients, water, root growth and productivity in young plantations. *For. Ecol. Manage.* 30, 213–232.
- Nambiar, E.K.S., Sands, R., 1993. Competition for water and nutrients in forests. *Can. J. For. Res.* 23, 1955–1968.
- Newton, M., Cole, E.C., 2008. Twenty-six-year response of ponderosa pine and Douglas-fir plantations to woody competitor density in treated stands of madrone and whiteleaf manzanita. *For. Ecol. Manage.* 256, 410–420.
- Newton, M., Preest, D.S., 1988. Growth and water relations of Douglas fir (*Pseudotsuga menziesii*) seedlings under different weed control regimes. *Weed Sci.* 36, 653–662.
- Oliver, W.W., 1984. *Brush Reduces Growth of Thinned Ponderosa Pine in Northern California*. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Research Paper PSW-RP-172, p. 7.
- Peter, D.H., Harrington, C.A., 2009. Six years of plant community development after clearcut harvesting in western Washington. *Can. J. For. Res.* 39, 308–319.
- Peter, D.H., Harrington, T.B., unpublished data. Relations of Native and Exotic Species Five Years after Clearcutting With and Without Herbicide and Logging Debris Treatments. USDA Forest Service, Pacific Northwest Research Station, Research Paper PNW-RP-XXX (in review).
- Petersen, K.S., Ares, A., Terry, T.A., Harrison, R.B., 2008. Vegetation competition effects on aboveground biomass and macronutrients, leaf area, and crown structure in 5-year old Douglas-fir. *New For.* 35, 299–311.
- Powers, R.F., Reynolds, P.E., 1999. Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. *Can. J. For. Res.* 29, 1027–1038.
- Powers, R.F., Scott, D.A., Sanchez, F.G., Voldseth, R.A., Page-Dumroese, D., Elioiff, J.D., Stone, D.M., 2005. The North American long-term soil productivity experiment: findings from the first decade of research. *For. Ecol. Manage.* 220, 31–50.
- Roberts, S.D., Harrington, C.A., Terry, T.A., 2005. Harvest residue and competing vegetation affect soil moisture, soil temperature, N availability, and Douglas-fir growth. *For. Ecol. Manage.* 205, 333–350.
- Rose, R., Rosner, L.S., Ketchum, J.S., 2006. Twelfth-year response of Douglas-fir to area of weed control and herbaceous versus woody weed control treatments. *Can. J. For. Res.* 36, 2464–2473.
- Ruehle, J.L., Marx, D.H., Muse, H.D., 1984. Calculated nondestructive indices of growth response for young pine seedlings. *For. Sci.* 30, 469–474.
- SAS Institute Inc., 2005. *The SAS System for Windows*. Version 9.1. Cary, NC.
- Shainsky, L.J., Newton, M., Radosevich, S.R., 1992. Effects of intra- and inter-specific competition on root and shoot biomass of young Douglas-fir and red alder. *Can. J. For. Res.* 22, 101–110.
- Slesak, R.A., 2008. *Soil Respiration, Carbon and Nitrogen Leaching, and Nitrogen Availability in Response to Harvest Intensity and Competing Vegetation Control in Douglas-fir (Pseudotsuga menziesii) Forests of the Pacific Northwest*. Oregon State University, Corvallis, OR.
- Slesak, R.A., Schoenholtz, S.H., Harrington, T.B., Strahm, B.D., 2009. Dissolved carbon and nitrogen leaching following variable logging-debris retention and competing-vegetation control in Douglas-fir plantations of western Oregon and Washington. *Can. J. For. Res.* 39, 1484–1497.
- Slesak, R.A., Harrington, T.B., Schoenholtz, S.H., 2010. Soil and Douglas-fir (*Pseudotsuga menziesii*) foliar nitrogen responses to variable logging-debris retention and competing vegetation control in the Pacific Northwest. *Can. J. For. Res.* 40, 254–264.
- Soil Survey Staff, 1999. *Soil Taxonomy, a Basic System of Soil Classification for Making and Interpreting Soil Surveys*, second ed. USDA Natural Resources Conservation Service.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, third ed. W.H. Freeman and Company, New York.
- Stanford, G., Epstein, E., 1973. Nitrogen mineralization–water relations in soils. *Soil Sci. Soc. Am. J.* 38, 103–107.

- Stevens, P.A., Hornung, M., 1990. Effect of harvest intensity and ground flora establishment on inorganic-N leaching from a Sitka spruce plantation in North Wales. UK. *Biogeochem.* 10, 53–65.
- Strik, B.C., 2005. A review of nitrogen nutrition of *Rubus*. *Acta Horticult.* (ISHS) 777, 403–410.
- Switzer, G.L., Nelson, L.E., 1972. Nutrient accumulation and cycling in loblolly pine (*Pinus taeda*) plantation ecosystems: the first 20 years. *Soil Sci. Soc. Am. Proc.* 36, 143–147.
- Turner, J., Olson, P.R., 1976. Nitrogen relations in a Douglas-fir plantation. *Ann. Bot.* 40, 1185–1193.
- Vitousek, P.M., Melillo, J.M., 1979. Nitrate losses from disturbed forests: patterns and mechanisms. *For. Sci.* 25, 605–619.
- Wagner, R.G., 2000. Competition and critical-period thresholds for vegetation management decisions in young conifer stands. *For. Chronicle* 76, 961–967.
- Wagner, R.G., Little, K.M., Richardson, B., McNabb, K., 2006. The role of vegetation management for enhancing productivity of the world's forests. *Forestry* 79, 57–79.
- Wagner, R.G., Newton, M., Cole, E.C., Miller, J.H., Shiver, B.D., 2004. The role of herbicides for enhancing forest productivity and conserving land for biodiversity in North America. *Wildlife Soc. Bull.* 32, 1028–1041.
- Wagner, R.G., Petersen, T.D., Ross, D.W., Radosevich, S.R., 1989. Competition thresholds for the survival and growth of ponderosa pine seedlings associated with woody and herbaceous vegetation. *New For.* 3, 151–170.
- Wagner, R.G., Radosevich, S.R., 1991. Neighborhood predictors of interspecific competition in young Douglas-fir plantations. *Can. J. For. Res.* 21, 821–828.
- Walters, M.B., Lajzerowicz, C.C., Coates, K.D., 2006. Soil resources and the growth and nutrition of tree seedlings near harvest gap-forest edges in interior cedar-hemlock forests of British Columbia. *Can. J. For. Res.* 36, 62–76.
- Waring, R.H., Schlesinger, W.H., 1985. *Forest Ecosystems: Concepts and Management*. Academic Press, Inc., New York, pp. 32–37.
- Weiskittel, A.R., Maguire, D.A., Monserud, R.A., Rose, R., Turnblom, E.C., 2006. Intensive management influence on Douglas fir stem form, branch characteristics, and simulated product recovery. *New Zealand J. For. Sci.* 36, 293–312.
- Zutter, B.R., Glover, G.R., Gjerstad, D.H., 1986. Effects of herbaceous weed control using herbicides in a young loblolly pine plantation. *For. Sci.* 32, 882–899.