

Performance of Four Planted Conifer Species Within Artificial Canopy Gaps in a Western Washington Douglas-Fir Forest

Timothy B. Harrington and Warren D. Devine

Research Forester, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, Olympia, WA; Data Management Specialist, Washington State Department of Natural Resources, Forest Resources Division, Olympia, WA

Abstract

Regeneration performance of planted grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.), coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) seedlings was studied for 3 years within artificial canopy gaps in a mature Douglas-fir forest near Tacoma, WA. Third-year survival of Douglas-fir and western redcedar did not vary with gap size, but peak survival of grand fir and western hemlock occurred at gap sizes of 0.13 and 0.14 ha (0.32 and 0.35 ac), respectively. Peak values of stem diameter occurred within a narrow range of gap sizes for all species. Because of their larger initial size and superior performance across a range of gap sizes, Douglas-fir and western redcedar were concluded to be the most suitable species for group selection on droughty, glacial-origin soils of western Washington.

Introduction

Coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) began to colonize the prairies of Joint Base Lewis-McChord (JBLM), a U.S. military installation near Tacoma, WA, in the mid-1800s after suspension of burning by Native Americans. From about 1878 to 1938, Douglas-fir density at JBLM increased in waves associated with low-intensity fires having return intervals of 10 to 91 years (Peter and Harrington 2014). Today, many of the 12,000 ha (29,640 ac) of prairie-colonization forests at JBLM have developed secondary forest characteristics, including a diverse understory of herbaceous, shrub, and hardwood species and a forest floor of decomposing tree litter and coarse

woody debris (Foster and Schaff 2003). Because these prairie-colonization forests developed on droughty, glacial-origin soils, natural regeneration of conifers is often variable in distribution and development.

The diverse array of management objectives associated with the mission of JBLM (e.g., diverse cover types needed for military training, wildlife habitat, and timber management) has prompted land managers to preferentially select uneven-aged regeneration methods over even-aged methods. Light availability, however, can be an important factor limiting growth of conifer seedlings in uneven-aged methods because of the inherent juxtaposition of mature trees and seedlings (Brodie and DeBell 2013, Harrington 2006). Creation of artificial canopy gaps using the uneven-aged, group-selection method of regeneration avoids some of the light limitations, because much of the regeneration will occur near the center of the openings where shading from overstory trees is less (Tappeiner et al. 2015). Hence, species exhibiting a wide range of shade tolerances can be regenerated with group selection. Isaac (1943) recommended openings of 0.4 ha (1 ac) or larger for natural regeneration of Douglas-fir.

From a silvicultural perspective, shade tolerances of common Northwestern conifers can be ranked as follows: Douglas-fir $\leq$ grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) $\ll$ western redcedar (*Thuja plicata* Donn ex D. Don) $<$ western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) (Burns and Honkala 1990, Daniel et al. 1979, Minore 1979). Douglas-fir seedlings need greater than 20 percent of full sunlight to survive, at least 40 percent for continued morphological development (Mailly and Kimmins 1997), and full sunlight for maximum growth rates (Drever and Lertzman 2001). In contrast, western redcedar seedlings require

only 10 percent of full sunlight to survive (Wang et al. 1994), and their maximum growth rates can occur at only 30 percent of full sunlight (Drever and Lertzman 2001). Western hemlock is considered among the most shade tolerant of Northwestern conifers (Packee 1990). However, Douglas-fir, western hemlock, and western redcedar may exhibit greater shade tolerance on sites of lower soil water availability (Carter and Klinka 1992), such as those having glacial-origin soils.

A study was initiated in 2007 to quantify performance of planted conifer seedlings in artificially created canopy gaps ranging in size from 0.1 to 0.4 ha (0.25 to 1.0 ac) and embedded within mature Douglas-fir stands thinned at two intensities. The objectives of the research were to determine 3-year responses to gap size and thinning intensity for (1) survival and growth of planted grand fir, Douglas-fir, western redcedar, and western hemlock seedlings, (2) survival and growth of naturally regenerated Douglas-fir seedlings, and (3) forest floor coverage in herbaceous and woody vegetation, exposed mineral soil, and coarse woody debris. Variation in gap size resulted in a wide range of light environments from diffuse to full sunlight, enabling the testing of the following hypotheses. H1: The gap size that supports maximum seedling performance will decrease as a species' shade tolerance increases (i.e., shade tolerance of Douglas-fir ≤ grand fir << western redcedar < western hemlock). H2: Species responses to gap size will vary between the two thinning intensities because of differences in diffuse light availability. H3: Relationships of stem basal area growth to light availability will vary among conifer species according to their respective shade tolerances.

Methods

Study Sites and Treatments

In fall 2007, we selected six mature stands of Douglas-fir prairie-colonization forest at JBLM on which to replicate the study (Peter and Harrington 2014). Devine and Harrington (2016) reported on Douglas-fir seedfall and seed viability in a subset of these stands. Soils are primarily gravelly sandy loams of the Spanaway series, which is a deep, somewhat excessively drained soil formed in glacial outwash

and volcanic ash (USDA NRCS 2018). About one-half of one study site (East Nollerath) had a loamy sand of the Nisqually series, which is also a deep, somewhat excessively drained glacial outwash soil (USDA NRCS 2018). Topography of the study sites is primarily flat, with occasional slopes up to 30 percent. Elevations range from 106 to 139 m (348 to 456 ft) above sea level. Long-term (1981–2010) predicted annual precipitation ranges from 1,040 to 1,190 mm (40.9 to 46.8 in), only 26 percent of which falls during the growing season (April to September) (PRISM 2018).

Two treatment areas, each 12 ha (29.6 ac) in size (256 by 475 m [840 by 1558 ft]) and containing relatively uniform forest cover, were designated within each stand. We randomly assigned two thinning intensities to the treatment areas at each site corresponding to retention of either 20 or 30 percent of the maximum Stand Density Index for Douglas-fir (Reineke 1933). During winter 2007–2008, a pre-thinning stand survey was conducted within each treatment area of four of the study sites, and the remaining two sites were surveyed during winter 2008–2009. A grid of 14 sample points was located systematically throughout each treatment area. At each sample point, we measured basal area by tree species (via prism count; 5 m²/ha [21.8 ft²/ac]) basal area factor), stem diameter at breast height (dbh; 1.3 m [4.3 ft] above ground) of every tree counted via prism, and height, height to crown base, and age of one dominant tree per sample point to use for estimation of site index_{50-year} (King 1966). Table 1 shows average stand characteristics of the overstory Douglas-fir at the six study sites.

Table 1. Average stand characteristics with standard errors for six prairie colonization stands of Douglas-fir at Joint Base Lewis-McChord.

Stand characteristic	Average	Standard error
Height	47.0 m (154.2 ft)	1.7 m (5.6 ft)
Height to crown base	26.7 m (87.6 ft)	1.2 m (3.9 ft)
Breast-height age	92.4 yr	5.6 yr
Site index _{50 year} ¹	36.3 m (119.1 ft)	1.4 m (4.6 ft)
Quadratic mean diameter	65.1 cm (25.6 in)	3.8 cm (1.5 in)
Stand Density Index ²	36.8 percent	1.6 percent
Stem density	166 trees ha ⁻¹ (67 trees ac ⁻¹)	15 trees ha ⁻¹ (6 trees ac ⁻¹)

¹ King (1966)
² Percent of maximum; Reineke (1933)

After each stand was marked for thinning at the two intensities, we systematically selected 8 of the 14 sample points within each treatment area. Selected sample points were spaced approximately 110 m (361 ft) apart and were at least 73 m (240 ft) from the edge of the stand. Four of the sample points within each treatment area were randomly assigned a gap area of either 0.1, 0.2, 0.3, or 0.4 ha (0.25, 0.5, 0.75, or 1.0 ac), and the remaining four sample points were assigned to the thinned matrix of the treatment area, hereafter designated as having a gap size of 0.0 ha (0.0 ac). The four matrix sample points were included within each treatment area to sample the inherent variability of the thinned stands. Centered on each designated sample point, the gaps were marked to be circular in shape such that every tree having the center of its stem rooted within the radius of the assigned gap size was marked for cutting. Thinning and gap treatments on four of the study sites were conducted during winter 2008–2009 (i.e., South Perry, Rodomsky, East Nollerath, and Midway), and the treatments on the remaining two sites were conducted during winter 2009–2010 (i.e., Holliday Woods and Cheadle) (figure 1).

At each sample point (i.e., either at gap center or within forest matrix), four plots, each 12.2 by 12.2 m (40 by 40 ft) in dimension, were located in a 2-by-2 cluster with boundaries oriented in cardinal directions. One of the following conifer species was randomly assigned to each plot: grand-fir, Douglas-fir, western redcedar, and western hemlock. Two-year-old seedlings (2+0, 1+1, plug+1, and plug+1 stock types for grand fir, Douglas-fir, western redcedar, and western hemlock, respectively) of the assigned species were planted at 2.4-m (8-ft) spacing in each plot, providing a total of 25 seedlings in a 5-by-5 planting grid at each sample point. Four study sites were planted in early 2009 (i.e., South Perry, Rodomsky, East Nollerath and Midway), and two sites were planted in early 2010 (i.e., Holliday Woods and Cheadle). No treatments were applied to reduce abundance of competing vegetation.

Light Measurements

Intensity of photosynthetically active radiation was quantified in mid-July during the first year after planting at each study site. We used an AccuPAR®



Figure 1. Douglas-fir forest thinned to 30 percent of maximum Stand Density Index (Reineke 1933) at the Cheadle site, Joint Base Lewis-McChord. Subjects in the photograph are walking toward a 0.4-ha (1-ac) canopy gap in the background. (Photo by James P. Dollins, USDA Forest Service, Pacific Northwest Research Station, 2010)

LP80 ceptometer (Meter Group, Inc., Pullman, WA) to measure light intensity at 1.3-m (4.3-ft) height above each of nine subsample points systematically located within the grid of planted conifer seedlings. Readings were taken on cloudless days within 2 hours of solar noon. To record reference conditions, a LI-190 quantum sensor (LI-COR Biosciences, Lincoln, NE) was mounted at 1.3-m (4.3-ft) height near the center of the nearest 0.4-ha (1-ac) canopy gap and connected to a LI-1400 data-logger (LI-COR Biosciences, Lincoln, NE) to take readings of light intensity every 60 seconds in full sun conditions. Data from each instrument were merged according to the nearest minute, and a ratio was calculated to quantify proportion of full sun (i.e., relative light intensity [RLI]). The coefficient of variation (CV) was calculated for RLI to provide a measure of variability among sample points.

Vegetation Measurements

Immediately after planting, stem diameter at 15-cm (6-in) height (nearest mm [0.04 in]) was measured on each seedling. During three subsequent winters after planting each site, we recorded survival, stem diameter at 15-cm (6-in) height, total height (nearest cm [0.39 in]), and injury information for each planted seedling. Three types of seedling damage incidence (i.e., percentage of seedlings) were measured: overtopping by woody vegetation that exceeded 75 percent (Howard and Newton 1984), stem dieback, and stem browsing by deer or elk. An average value for each variable was then calculated for the forest matrix sample points within each treatment area. Up to 10 naturally regenerated Douglas-fir seedlings (≥ 0.5 m [1.6 ft] in height but < 2.5 cm [1 in] dbh) rooted within 18 m (59 ft) of each grid point (i.e., the approximate radius of the smallest gap size) were tagged. For each naturally regenerated seedling, we recorded its location (i.e., azimuth and distance from the sample point), stem diameter, height, and injury information. Survival and growth of the tagged natural regeneration seedlings were recorded annually.

Mean values of stem basal area for years 0 (initial measurement; BA_0) and 3 (BA_3) were calculated for each sample point and species and used in the following equation to estimate relative growth rate (RGR; after Hunt [1990]) of the planted conifer seedlings.

$$RGR = [\log_e(BA_3) - \log_e(BA_0)]/3$$



Figure 2. Visual estimation of forest-floor cover in herbaceous and woody vegetation, exposed mineral soil, and coarse woody debris within a 0.1-ha (0.25-ac) gap at the Holliday Woods site, Joint Base Lewis-McChord. (Photo by Timothy B. Harrington, USDA Forest Service, Pacific Northwest Research Station, 2011)

At each of five subsample points located systematically within the grid of planted conifer seedlings, we used a 1 by 1 m (3.3 by 3.3 ft) sample frame as a guide to visually estimate forest-floor cover (nearest 5 percent) for each of the following categories: herbaceous species (grasses, forbs, and ferns), woody species (vines, shrubs, and tree species < 2.5 cm [1 in] dbh), exposed mineral soil, and coarse woody debris. Cover estimates were taken in mid-summer, near the peak of vegetation development, during each of 3 years after planting the conifer seedlings (figure 2).

Data Analyses

The experimental design of the study is a randomized complete block with six replicate sites (blocks) and a split-plot arrangement of treatments. The main-plot treatment is thinning intensity and the split-plot treatment is gap size. For each sample point and measurement year, we calculated average values for (1) RLI, (2) cover by forest floor category, and (3) survival, stem diameter, height, and injury incidence of each species of planted conifer seedlings and of the Douglas-fir natural regeneration. Analysis of variance (ANOVA) was applied to mean values of RLI using PROC Mixed in SAS version 9.4 (SAS Institute 2013) to test the significance ($\alpha = 0.05$) of the fixed effects of thinning intensity, gap size, and their interaction, while adjusting for the random effect of blocks. ANOVA was applied similarly to data for initial stem diameter with the

inclusion of conifer species as an additional factor. Repeated-measures ANOVA was applied to each conifer and forest floor variable to test the significance of the fixed effects, thinning intensity, gap size, measurement year, and their interactions, while adjusting for the random effect of blocks. Species was included as an additional nested factor (split-split plot experimental design) in the repeated-measures ANOVA for the planted-conifer variables. Initial stem diameter was not included as a covariate in the ANOVAs for stem diameter or height or in other analyses because of potential confounding of this variable with species.

To homogenize the residual variation prior to ANOVA, an angular transformation (arc-sine, square root) was applied to the proportionate variables of RLI, conifer survival, conifer damage incidence, and forest-floor cover, and a logarithmic transformation was applied to conifer stem diameter and height. When a significant F-test was detected in the ANOVA for gap size or its interaction with thinning intensity, measurement year, or conifer species, we conducted polynomial contrasts to test for potential linear or quadratic effects of gap size as affected by the interacting variable. A first-order derivative was taken for each fitted quadratic regression model to predict maximum values for third-year survival, stem diameter, and height of the planted conifers and the gap sizes associated with each predicted maximum (hypothesis 1). Effects of thinning intensity on the planted-conifer variables were tested by conducting ANOVA both for data containing all gap sizes and for data only from the matrix plots (hypothesis 2). When a year-by-gap-size or year-by-species interaction was detected, we focused on third-year responses. ANOVA of stem diameter and height of naturally regenerated Douglas-fir was conducted only on third-year data. This avoided complications from a changing sample population as new trees were recruited each year as they reached the threshold size for selection.

Indicator variables were specified to represent each species, and the pooled data were subjected to linear regression in PROC Reg to test for species' differences in intercepts and slopes for the relationship of RGR versus RLI (hypothesis 3), using the extra-sums-of-squares approach (Neter et al. 1989).

Results and Discussion

Light Availability

RLI and the CV for RLI each varied significantly among gap sizes ($p < 0.01$). However, matrix thinning intensity and its interaction with gap size did not have a significant effect on RLI ($p = 0.36$ and 0.09 , respectively) or the CV for RLI ($p = 0.35$ and 0.10 , respectively), indicating similarity in the light environments for the two thinning intensities. Both RLI and CV for RLI had quadratic relationships with gap size (figure 3). At gap sizes of 0.2 ha (0.5 ac) and greater, average RLI varied from 91 to 98 percent, indicating that near-full sun conditions existed during mid-day for these gap sizes. Relative light intensities were 68 and 39 percent for 0.1-ha gaps and forest matrix, respectively, demonstrating how proximity of overstory trees limited light availability in the understory.

The diameters of the 0.1- and 0.4-ha (0.25- and 1.0-ac) gaps were equal to 0.76 and 1.52 times the average height of dominant trees (47 m [154 ft]), respectively. These ratios of gap diameter to canopy height (D:H) indicate that light conditions within the treatment areas ranged from the virtual absence of direct sunlight in the forest matrix and in 0.1-ha gaps to increasing proportions of gap area illuminated by direct sunlight (Pickett and White 1985). A D:H ratio of 1.52 in 0.4-ha (1-ac)

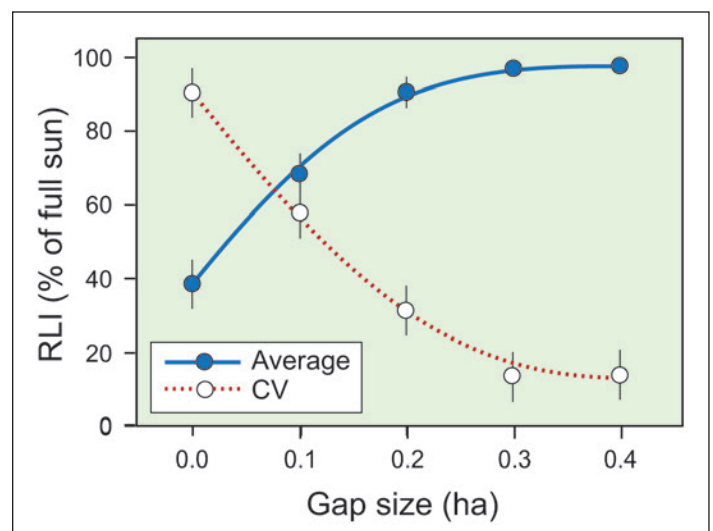


Figure 3. Relationships of first year average relative light intensity (RLI) and the coefficient of variation (CV) for RLI ($\pm$ standard error) to gap size in six prairie colonization stands of Douglas-fir at Joint Base Lewis-McChord. Lines represent the following quadratic regression models: average RLI = $0.658 + 3.92(\text{GAP}) - 4.96(\text{GAP}^2)$ ($n = 60$, $s_{y,x} = 0.225$, $R^2 = 0.62$); CV of RLI = $91.6 - 412(\text{GAP}) + 536(\text{GAP}^2)$ ($n = 60$, $s_{y,x} = 23.4$, $R^2 = 0.61$). The model for average RLI predicts angular-transformed values. Conversion: 1 ha = 2.47 ac.

gaps indicates that gap center—around which seedlings were planted—would not be fully illuminated by direct sunlight. Marquis (1965) demonstrated that the proportion of a gap receiving direct sunlight increases with gap size, and that gap shape and orientation are important determinants of light availability for gaps of about 0.2 ha (0.5 ac).

The CV for RLI declined from 90 to 14 percent as gap size increased from 0.0 to 0.4 ha (0.0 to 1.0 ac), indicating that variation in RLI decreased dramatically with increasing gap size. Variability in RLI was highest in the forest matrix because of inherent variation in structure of the natural stands after thinning. The high variability in the light environment of the forest matrix was likely the reason why the understory conifer seedlings were able to survive and grow reasonably well for the duration of this 3-year study (discussed in the following paragraphs). Those seedlings that survived may have been growing in locations where direct sunlight penetrated during part of the day.

Forest Floor Coverage

The three-way interaction of thinning intensity, gap size, and measurement year was significant for herbaceous species cover in years 2 and 3 ($p = 0.02$). In addition, the interaction of thinning intensity and gap size was significant for both herbaceous and woody covers ($p \leq 0.03$). In the lower thinning intensity (30 percent retention), herbaceous cover increased and woody cover decreased, with increasing gap size such that they were approximately equal to the cover in 0.2-ha (0.5-ac) gaps (figure 4). In the higher thinning intensity (20 percent retention), however, herbaceous and woody coverages were similar regardless of gap size.

Two explanations are possible for the differing vegetation responses to gap size for the two thinning intensities. First, the low-intensity thinning resulted in less ground disturbance within 0.1-ha (0.25-ac) gaps, thereby preserving existing woody cover and enabling it to respond to the moderated growing conditions associated with the small gap. Second, the low-intensity thinning limited availability of side light within 0.1-ha gaps, and this limitation, combined with the effects of competition with woody vegetation, restricted herbaceous cover development in smaller gaps. The ratio of gap diameter to canopy height in 0.1-ha gaps was

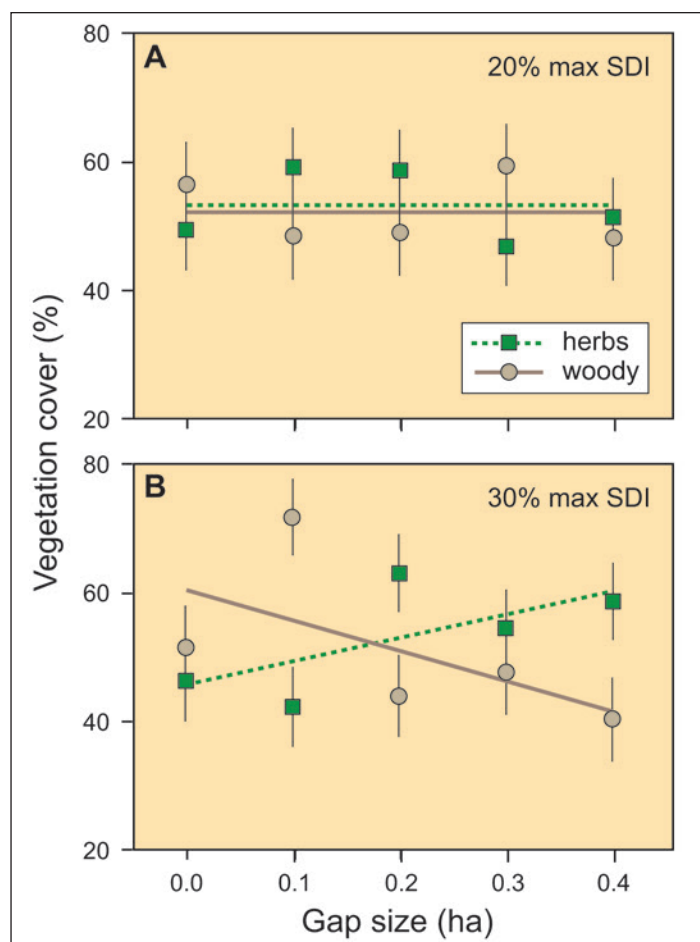


Figure 4. Relationships of average cover ($\pm$ standard error) of herbaceous and woody vegetation to gap size and forest matrix thinning intensity (20 or 30 percent of maximum Stand Density Index [SDI]; Reineke 1933) during 3 years in six prairie colonization stands of Douglas-fir at Joint Base Lewis-McChord. Lines represent linear regression models that were fitted to each vegetation group. Conversion: 1 ha = 2.47 ac.

less than 1.0, and therefore, little or no direct sunlight reached the forest floor (Pickett and White 1985). Hence, all vegetation growing within gaps of this size were forced to rely on diffuse light for growth. In both Pacific Northwestern and Midwestern forests, niche differentiation of understory species has been shown to increase with gap size and forest-floor disturbance because of strengthening resource gradients and increased likelihood of ruderal invasion (Fahey and Puettmann 2007, Kern et al. 2013). Therefore, in our study, it is likely that resource gradients were stronger for the lower thinning intensity (30 percent retention) than for the higher thinning intensity (20 percent retention), resulting in the observed inverse relationship between woody and herbaceous cover that was observed with increasing gap size.

Abundance of woody vegetation increased significantly ($p < 0.01$) each year of the study, as it recovered from disturbances associated with thinning (37, 50, and 54 percent cover in years 1, 2, and 3, respectively). Cover of exposed mineral soil had linear ($p < 0.01$) and quadratic ($p < 0.01$) relationships with gap size in years 1 and 2, respectively. In year 1, soil cover increased proportionately from 3 to 9 percent, as gap size increased from 0.0 ha (nongap forest matrix) to 0.4 ha (0.0 to 1.0 ac), respectively. By year 2, only forest matrix and 0.4-ha (1.0 ac) gaps had detectable levels of exposed soil (1 percent), and in year 3, none of the gap sizes or forest matrix had exposed mineral soil at a detectable level. Visible coverage of coarse woody debris decreased with years since treatment ($p < 0.01$)—12, 4, and 1 percent in measurement years 1, 2, and 3, respectively—as recovering herbaceous and woody vegetation obscured it.

Responses of Planted Conifer Seedlings

The interaction of gap size and conifer species was significant for survival of the planted seedlings ($p = 0.02$). Grand fir and western hemlock each had a quadratic relationship of survival to gap size, whereas survival of Douglas-fir and western redcedar was unaffected by gap size (figure 5A; table 2). Brodie and DeBell (2013) compared performance of planted Douglas-fir, western redcedar, and western hemlock under different levels of overstory retention in western Washington and found that western hemlock had the lowest second-year survival (76 to 85 percent) of any species when overstory retention was less than 16 percent of full stocking (i.e., full stocking equals relative density 65; Curtis 1982), presumably due to increased sunlight exposure.

Initial stem diameters varied significantly among species ($p < 0.01$) and were ranked as follows: Douglas-fir (5 mm [0.20 in]) > western redcedar (4 mm [0.16 in]) > grand fir (3 mm [0.12 in]) = western hemlock (3 mm [0.12 in]). Note that the two species having the lowest survival, grand fir and western hemlock, also had the smallest initial stem diameters. Initial diameter, an indicator of root biomass, has been strongly associated with field survival and growth of planted Douglas-fir (Long and Carrier 1993, Rose et al. 1991, Roth and Newton 1996).

Based on the fitted regressions for year 3, average peak values of stem diameter were ranked as 11, 10, 8, and 8 mm (0.43, 0.39, 0.31, and 0.31 in) for Douglas-fir,

western hemlock, western redcedar, and grand fir, respectively (figure 5B; table 2). In year 3, quadratic relationships were also detected for height of grand fir, Douglas-fir, and western hemlock, but no significant regression relationship was detected for western redcedar (figure 5C; table 2).

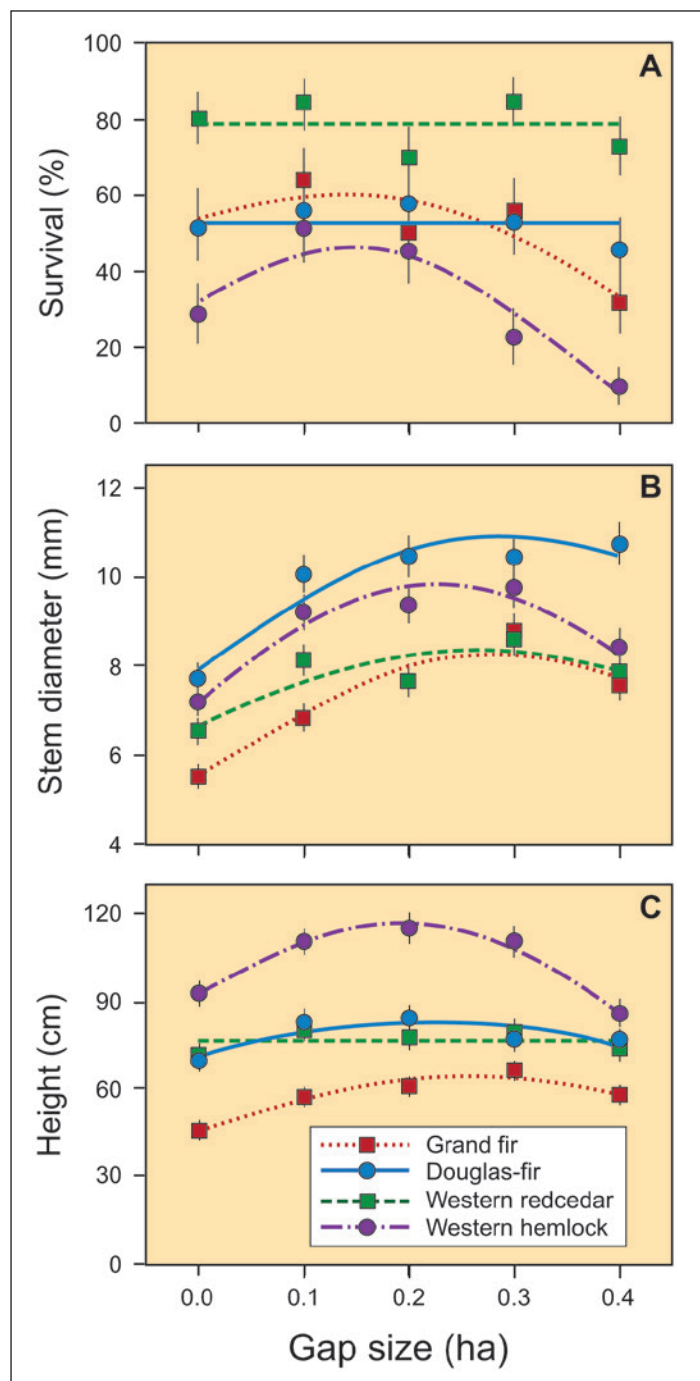


Figure 5. Relationships of third-year average (a) survival, (b) stem diameter, and (c) height ($\pm$ standard error) of planted grand fir, Douglas-fir, western redcedar, and western hemlock seedlings to gap size in six prairie colonization stands of Douglas-fir at Joint Base Lewis-McChord. Lines represent quadratic regression models that were fitted to each conifer species (see table 2). Conversions: 1 ha = 2.47 ac; 1 mm = 0.0394 in; 1 cm = 0.394 in.

Table 2. Quadratic regression models for predicting effects of gap size on third-year survival, stem diameter, and height of planted conifer seedlings in six prairie colonization stands of Douglas-fir at Joint Base Lewis-McChord.

Response variable	Species ^a	Regression model ^b	R ²	n	S _{y.x}	Y _{max} ^c	X at Y _{max} ^d
Survival (%)	ABGR	$Y = 0.825 + 0.962X - 3.70X^2$	0.09	60	0.270	60	0.13
	PSME	$Y = 0.812$	n.s. ^e	60	0.242	— ^f	—
	THPL	$Y = 1.09$	n.s.	60	0.269	—	—
	TSHE	$Y = 0.599 + 2.08X - 7.22X^2$	0.25	60	0.277	46	0.14
Stem diameter (mm)	ABGR	$Y = 1.70 + 2.91X - 5.08X^2$	0.37	60	0.193	8	0.29
	PSME	$Y = 2.07 + 2.17X - 3.68X^2$	0.38	60	0.146	11	0.29
	THPL	$Y = 1.90 + 1.67X - 3.09X^2$	0.13	60	0.186	8	0.27
	TSHE	$Y = 1.98 + 2.65X - 5.84X^2$	0.13	56	0.258	10	0.23
Height (cm)	ABGR	$Y = 3.82 + 2.62X - 4.96X^2$	0.33	60	0.168	64	0.26
	PSME	$Y = 4.27 + 1.42X - 3.24X^2$	0.09	60	0.159	84	0.22
	THPL	$Y = 4.33$	n.s.	60	0.183	—	—
	TSHE	$Y = 4.52 + 2.49X - 6.56X^2$	0.12	56	0.262	116	0.19

^a ABGR = grand fir. PSME = Douglas-fir. THPL = western redcedar. TSHE = western hemlock.

^b Y = response variable. X = gap size (ha). The regression models predict angular-transformed values of survival and Log_e-transformed values of stem diameter and height. Conversion: 1 ha = 2.47 ac.

^c The maximum value of Y predicted from the regression model.

^d The gap size (ha) at which the maximum value of Y is predicted from the regression model. Conversion: 1 ha = 2.47 ac.

^e Indicates that the regression was not statistically significant ($p > 0.05$).

^f Y_{max} or X at Y_{max} cannot be computed for a non-significant regression.

The predicted gap sizes at which seedling performance peaked were not ranked among species according to their respective shade tolerances, resulting in rejection of hypothesis 1. Western hemlock had maximum performance in the smaller gap sizes, but the other three also had peak performance at similar gap sizes. The absence of a discrete ranking of performance according to species' shade tolerances supports the findings of Carter and Klinka (1992) in which Douglas-fir, western hemlock, and western redcedar all exhibited greater shade tolerance on sites of lower soil water availability. In a meta-analysis of previous studies of the interactive effects of light and soil water availability, Holmgren et al. (2012) demonstrated that intermediate levels of shade provide plants with relief from soil drought that is not experienced at either higher or lower levels of shade. The net effect of this response is for plant species to exhibit greater tolerance of intermediate shade in dry soils because of the ameliorative effects to drought that shade provides.

Species' growth responses to gap size are in general agreement with previous research, showing an asymp-

totic increase with gap size with the largest changes occurring between gap sizes of 0 (forest matrix) and 0.1 ha (0.25 ac) (Coates 2000, Gray and Spies 1996, York et al. 2004). Similar to our findings, Brodie and DeBell (2013) found that Douglas-fir had the greatest average stem diameter, western hemlock had the greatest average height, and western redcedar had the smallest diameter and height 9 years after planting seedlings under a full range of overstory retention levels in western Washington. In another study, de Montigny and Smith (2017) found that gap sizes of 0.2 to 0.3 ha (0.50 to 0.75 ac) were suitable for conifer regeneration, because they provided adequate light to support stem and height growth of each species.

Thinning intensity did not have a detectable effect on performance of the planted conifer seedlings when data from the forest matrix and gap sample points were combined into the same ANOVA. Therefore, hypothesis 2 was rejected. Furthermore, analysis of only the data from the forest matrix plots did not detect significant effects from thinning intensity or its

interactions with species or measurement year for survival, stem diameter, or height ($p \geq 0.06$). Although stand density could potentially influence performance of seedlings planted near the stand edge (Coates 2000, Gray and Spies 1996, York et al. 2004), our study focused on seedlings planted near gap center.

In year 3, a quadratic relationship was detected between woody overtopping and gap size, because the peak value occurred in 0.1-ha (0.25-ac) gaps (9 percent of seedlings) with lower values in the forest matrix (6 percent) and in larger gaps (3 to 7 percent). For each species, overtopping decreased linearly with increasing gap size. In year 3, overtopping of hemlock seedlings (2 percent of seedlings) was less than that of the other species (6 to 8 percent), likely because of the species' superior height growth. Stem dieback

varied among gap sizes and according to a species-by-year interaction ($p < 0.01$). Dieback declined from 3 percent of seedlings in forest matrix to 1 percent of seedlings in all other gap sizes. In years 1 and 2, Douglas-fir had the highest percentage of seedlings with dieback (7 and 4 percent, respectively, compared with 0 to 2 percent for the other species). By year 3, however, dieback did not differ among species ($p = 0.39$). Very little browsing occurred on grand fir or western hemlock seedlings during the study (< 1 percent). Browsing on Douglas-fir varied little among years (7 to 8 percent); whereas, browsing on western redcedar peaked in year 2 (19 percent) but was similar in years 1 and 3 (11 percent).

RGR of stem basal area had a significant linear relationship with RLI using the pooled data for the four

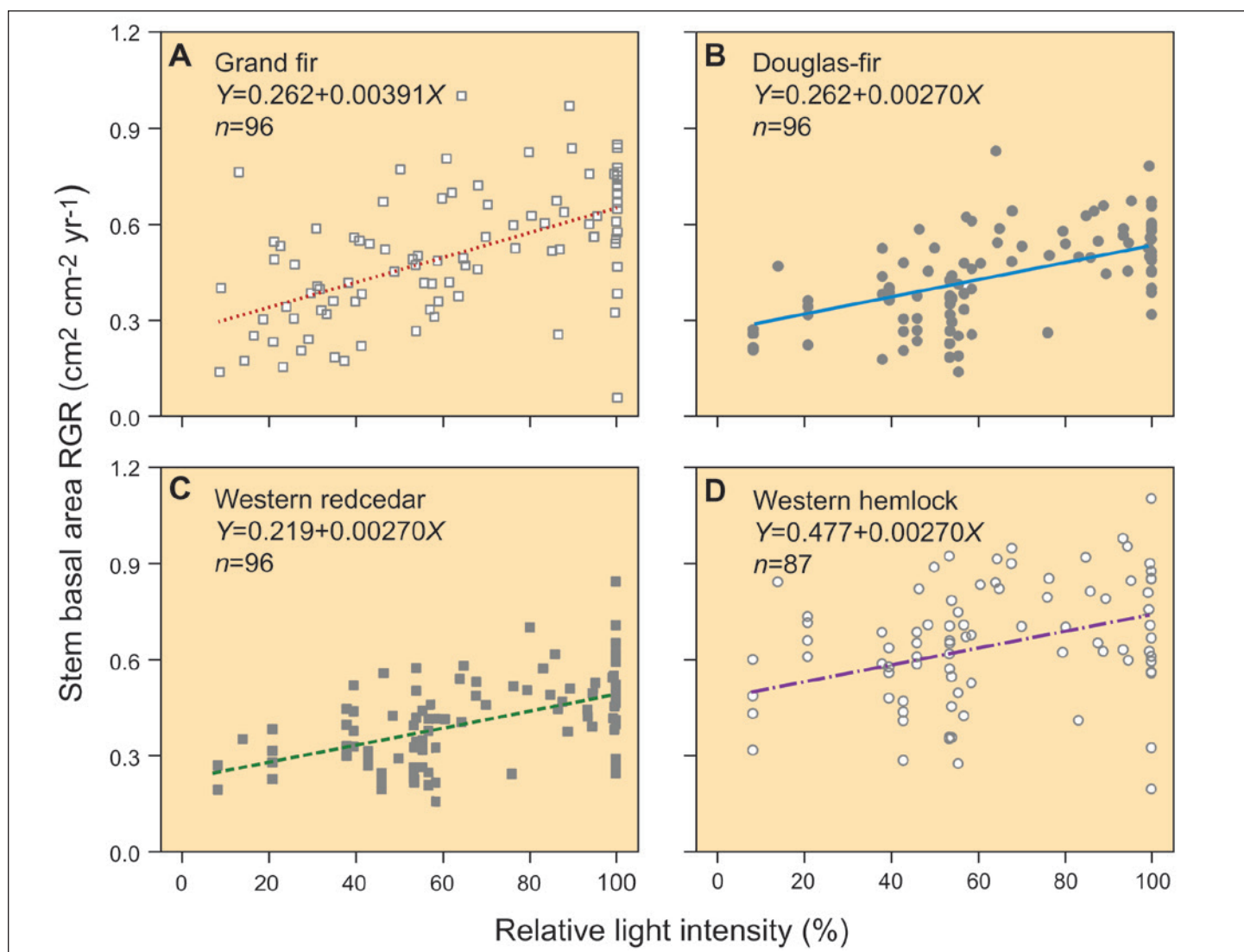


Figure 6. Relationships of 3-year relative growth rate of stem basal area to relative light intensity for planted (a) grand fir, (b) Douglas-fir, (c) western redcedar, and (d) western hemlock in six prairie colonization stands of Douglas-fir at Joint Base Lewis-McChord. Regression equations are from a linear model that was fitted to pooled data from the four conifer species (adjusted $R^2 = 0.41$, $s_{y,x} = 0.152$). Conversion: 1 cm² cm⁻² yr⁻¹ = 1 in² in⁻² yr⁻¹.

conifer species ($R^2 = 0.41$, $s_{y,x} = 0.152$; figure 6), indicating that light was a common factor limiting stem growth. Western hemlock had a significantly larger regression intercept than the other species, indicating greater stem growth in nongap (i.e., forest matrix) areas. Grand fir had a significantly larger regression slope than the other species, indicating greater stem growth per unit RLI. Hypothesis 3 was rejected because RGR responses to RLI were not ranked according to species' shade tolerances, presumably because each species became more shade tolerant due to the ameliorative effects of intermediate shade on the droughty, glacial-origin soil (Carter and Klinka 1992, Holmgren et al. 2012).

Responses of Naturally Regenerated Douglas-fir

During the 3-year study, 185 naturally regenerated Douglas-fir seedlings were tagged to monitor their survival and growth responses. Ten of these seedlings (5 percent) died as a result of injury from deer antler rubbing. Third-year stem diameter and height of these seedlings did not vary significantly as a result of thinning intensity, gap size, or their interaction ($p \geq 0.08$), averaging 17 mm and 133 cm (0.67 in and 52 in), respectively. Note that forest-harvesting operations likely destroyed much of the existing Douglas-fir natural regeneration.

Management Implications and Future Directions

In this 3-year study, species having the smallest initial sizes (grand fir and western hemlock) were at a disadvantage relative to those with larger initial sizes (Douglas-fir and western redcedar). Research is needed to compare differences in regeneration performance of Northwestern conifer species with the same initial size at planting.

The relatively low survival of Douglas-fir in this study (53 percent), compared with that observed by other land management organizations, suggests that other factors besides the light environment caused seedling mortality. Competing vegetation, no doubt, played an important role in limiting seedling survival, and intensity of competition increased with gap size because of greater abundance of herbaceous species, especially grasses (figure 7). To fully understand how gap size influenc-



Figure 7. High abundance of grasses within a 0.4-ha (1.0-ac) gap at the Rodomsky site, Joint Base Lewis-McChord. (Photo by Jessyka Williams, USDA Forest Service, Pacific Northwest Research Station, 2011)

es regeneration performance of Northwestern conifer species, controlled studies are needed to eliminate confounding effects of competing vegetation.

Nonetheless, research results indicate that, in the absence of competing vegetation control, Douglas-fir is the best choice of conifer species for regenerating glacial-origin soils via group selection because of its superior stem growth. Western redcedar also is a viable choice for regeneration under these conditions because of its higher survival (79 percent) and reasonably good growth. However, susceptibility to browsing places western redcedar at a disadvantage relative to the other species. Gaps of 0.2 ha (0.5 ac) and larger are likely to provide adequate growing conditions for regenerating both species.

Address Correspondence To—

Timothy B. Harrington, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue Southwest, Olympia, WA 98512; email: tharrington@fs.fed.us; phone: 360-753-7674.

Acknowledgments

Joint Base Lewis-McChord (JBLM), Environmental and Natural Resources Division, provided financial support for this research. The authors thank Jeffrey Foster, Allan Derickson, and JBLM staff for logistical support. The authors also thank the staff of the Olympia Forestry Sciences Laboratory for assistance with the field measurements, including James Dollins, Dave Peter, David Stephens, and Jessyka Williams.

REFERENCES

- Brodie, L.C.; DeBell, D.S. 2013. Residual densities affect growth of overstory trees and planted Douglas-fir, western hemlock, and western redcedar: results from the first decade. *Western Journal of Applied Forestry*. 28(3): 121–127.
- Burns, R.M.; Honkala, B.H., tech. coords. 1990. *Silvics of North America*. 1: Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.
- Carter, R.E.; Klinka, K. 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. *Forest Ecology and Management*. 55(1–4): 87–105.
- Coates, K.D. 2000. Conifer seedling response to northern temperate forest gaps. *Forest Ecology and Management*. 127(1–3): 249–269.
- Curtis, R.O. 1982. A simple index of stand density for Douglas-fir. *Forest Science*. 28(1): 92–94.
- Daniel, T.W.; Helms, J.A.; Baker, F.S. 1979. *Principles of silviculture*. Second ed. New York: McGraw-Hill: 292–298.
- de Montigny, L.E.; Smith, N.J. 2017. The effects of gap size in a group selection silvicultural system on the growth response of young, planted Douglas-fir: a sector plot analysis. *Forestry*. 90(3): 426–435.
- Devine, W.D.; Harrington, T.B. 2016. Seedfall and seed viability within artificial canopy gaps in a western Washington Douglas-fir forest. *Tree Planters' Notes*. 59(1): 23–32.
- Drever, C.R.; Lertzman, K.P. 2001. Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. *Canadian Journal of Forest Research*. 31(12): 2124–2133.
- Fahey, R.T.; Puettmann, K.J. 2007. Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *Journal of Ecology*. 95(5): 1098–1109.
- Foster, J. R.; Shaff, S.E. 2003. Forest colonization of Puget Lowland grasslands at Fort Lewis, Washington. *Northwest Science*. 77(4): 283–296.
- Gray, A.N.; Spies, T.A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *Journal of Ecology*. 84(5): 635–645.
- Harrington, T.B. 2006. Five-year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition. *Canadian Journal of Forest Research*. 36(10): 2439–2453.
- Holmgren, M.; Gómez-Aparicio, L.; Quero, J.L.; Valladares, F. 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. *Oecologia*. 169(2): 293–305.
- Howard, K.M.; Newton, M. 1984. Overtopping by successional Coast-Range vegetation slows Douglas-fir seedlings. *Journal of Forestry*. 82(3): 178–180.
- Hunt, R. 1990. *Basic growth analysis*. London: Unwin Hyman: 25–27.
- Isaac, L. 1943. *Reproductive habits of Douglas-fir*. Washington, DC: Charles Lathrop Pack Forestry Foundation. 107 p.
- Kern, C.C.; Montgomery, R.A.; Reich, P.B.; Strong, T.F. 2013. Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest. *Journal of Plant Ecology*. 6(1): 101–112.
- King, J.E. 1966. *Site index curves for Douglas-fir in the Pacific Northwest*. Weyerhaeuser Forestry Paper No. 8. Centralia, WA: Weyerhaeuser Company. 49 p.
- Long, A.J.; Carrier, B.D. 1993. Effects of Douglas-fir 2+0 seedling morphology on field performance. *New Forests*. 7(1): 19–32.
- Maily, D.; Kimmins, J.P. 1997. Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* seedlings along a light gradient: resource allocation and morphological acclimation. *Canadian Journal of Botany*. 75(9): 1424–1435.
- Marquis, D.A. 1965. *Controlling light in small clearcuttings*. Research Paper NE-39. U.S. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 16 p.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. Gen. Tech. Rep. PNW-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 72 p.
- Neter, J.; Wasserman, W.; Kutner, M.H. 1989. *Applied linear regression models*. 2nd ed. Homewood, IL: Richard D. Irwin: 271–284.
- Packee, E.C. 1990. *Tsuga heterophylla* (Raf.) Sarg., Western hemlock. In: Burns, R.M.; Honkala, B.H., tech coords. *Silvics of North America*. 1: Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 613–622.
- Peter, D.H.; Harrington, T.B. 2014. Historic colonization of South Puget Sound Prairies by Douglas-fir at Joint Base Lewis McChord, Washington. *Northwest Science*. 88(3): 186–205.
- Pickett, S.T.A.; White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. New York: Academic Press: 19, 220–221.
- PRISM Climate Group (PRISM). 2018. Prism climate data. Corvallis, OR: Oregon State University. <http://prism.oregonstate.edu>. (March 2018).
- Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research*. 46(7): 627–638.

Rose, R.; Atkinson, M.; Gleason, J.; Sabin, T. 1991. Root volume as a grading criterion to improve field performance of Douglas-fir seedlings. *New Forests*. 5(3): 195–209.

Roth, B.E.; Newton, M. 1996. Survival and growth of Douglas-fir relating to weeding, fertilization, and seed source. *Western Journal of Applied Forestry*. 11(2): 62–69.

SAS Institute. 2013. Base SAS 9.4 procedures guide: statistical procedures. 2nd ed. Cary, NC: SAS Institute, Inc. 550 p.

Tappeiner, J.C., II; Maguire, D.A.; Harrington, T.B.; Bailey, J.D. 2015. *Silviculture and ecology of western U.S. forests*. 2nd ed. Corvallis, OR: Oregon State University Press: 225–227, 362–363.

U.S. Department of Agriculture, Natural Resources Conservation Service (USDA NRCS). 2018. Official soil series descriptions.

http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/class/?cid=nrcs142p2_053587. (March 2018).

Wang, G.G.; Qian, H.; Klinka, K. 1994. Growth of *Thuja plicata* seedlings along a light gradient. *Canadian Journal of Botany*. 72(12): 1749–1757.

York, R.A.; Heald, R.C.; Battles, J.J.; York, J.D. 2004. Group selection management in conifer forests: relationships between opening size and tree growth. *Canadian Journal of Forest Research*. 34(3): 630–641.