

Effects of post-harvest treatments on high-elevation forests in the North Cascade Range, Washington

Ella Elman¹ and David L. Peterson²

Abstract

We studied the effects of post-harvest treatments on regeneration and forest composition 13–27 years following harvest in high-elevation forests of the North Cascade Range, Washington. Eighteen sites encompassing three common post-harvest treatments were examined at elevations ranging from 830 m to 1460 m. Treatments included: (1) sites broadcast burned and planted with *Abies amabilis* or *Abies procera*; (2) unburned sites seeded with *A. amabilis* or *A. procera*; and (3) unburned sites mostly planted with *A. amabilis*. Overstorey and understorey species composition was determined and compared to agency records of mature forest stands in the area. Burned-planted sites contained a smaller proportion of *A. amabilis* than unburned sites. Burned sites also contained less advance regeneration than unburned sites. Two understorey vegetation communities were segregated by elevation—an *Epilobium angustifolium*–*Rubus* spp. community dominated lower-elevation sites, and a *Vaccinium* spp. community dominated higher-elevation sites. To date, widespread planting and seeding of *A. amabilis* have not had significant effects on overstorey species composition, although future stand composition is difficult to predict. Comparison of understorey composition showed a contrast between shade-tolerant understorey species in mature stands and shade-intolerant pioneer species in clearcut sites. Advance regeneration in these systems may be enhanced by not using fire to treat slash.

KEYWORDS: *Abies amabilis*, Cascade Range, high-elevation forest, overstorey, *Tsuga heterophylla*, understorey.

Contact Information

- 1 Research Scientist, University of Washington, College of Forest Resources, Box 352100, Seattle, WA 98195, USA. Email: eelman@u.washington.edu
- 2 Research Biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 400 N. 34th Street, Suite 201, Seattle, WA 98103, USA. Email: peterson@fs.fed.us

Introduction

Over the last 150 years, forest harvest practices in the Pacific Northwest region of North America have altered the structural complexity and biodiversity of forest landscapes (Franklin and Forman 1987; Peterson *et al.* 1997). Clearcut logging has been extensive on United States Department of Agriculture (USDA) Forest Service and private lands, starting in low-elevation forests in the late 1800s and extending to high-elevation forests in the 1950s. Highly productive low-elevation forests were harvested first followed by less productive and less accessible high-elevation stands. In the Willamette National Forest (Oregon, USA), 90% of harvesting before the 1930s occurred on low-elevation sites (below 1200 m); during the 1970s, 65% of harvesting occurred above 1200 m (Harris 1984). In a portion of the Mt. Baker–Snoqualmie National Forest in the North Cascade Range (Washington, USA), harvest in the *A. amabilis* zone began in the early 1960s. Twenty years later, 2225 ha were harvested per year, 30% of which were located in the *A. amabilis* zone (Boecksteigel 1982).

When harvesting shifted to high-elevation forests, management techniques were similar to those used in low-elevation forests. Slash burning for site preparation and planting *Pseudotsuga menziesii* (Mirb.) Franco was formerly standard practice in low-elevation coniferous forests, but proved ineffective at high elevations because of high tree mortality, stem and form defects, and slow post-harvest growth (Boecksteigel 1982; Arnott *et al.* 1995; J. Henderson, USDA Forest Service Pacific Northwest Region, pers. comm., 2002).

Prescribed burning can be deleterious to the long-term site fertility of high-elevation stands, removing nutrients such as nitrogen, potassium, and magnesium through volatilization and leaching (DeByle 1974; Vogt *et al.* 1989). Short growing seasons and deep snowpack are responsible for slow regeneration rates of forests at high elevations, sometimes taking up to 150 years to reach the stem exclusion phase (Agee and Smith 1984; Vogt *et al.* 1989).

The effects of forest management activities on high-elevation forests have not been adequately studied, due in part to the lower commercial value of these forests for wood production compared to low-elevation forests. The Mt. Baker–Snoqualmie National Forest was selected to study the effects of harvesting and post-harvest management treatments in a montane forest. Logging in the montane forest began after 1945. By the early 1980s, approximately 55% of the original mature forest remained, most of it in higher elevation *A. amabilis* stands

The effects of forest management activities on high-elevation forests have not been adequately studied, due in part to the lower commercial value of these forests for wood production.

(Boecksteigel 1982). Logging continued at a steady pace until 1993, when Forest Service lands in the Mt. Baker Ranger District were classified as late-successional reserves by the Northwest Forest Plan (Tuchman and Brookes 1996). By the mid-1990s when harvesting in the area ceased, approximately 43% of the original late-successional forest remained (J. Henderson, USDA Forest Service Pacific Northwest Region, pers. comm., 2002).

According to historical records of the USDA Forest Service Tree Resource Inventory, most high-elevation clearcuts had some sort of slash treatment either by pile burning or broadcast burning, and were then reseeded with *A. amabilis*. Many sites were replanted 1 or 2 years after harvest, primarily with *A. amabilis*, but with a small component of *A. procera*. Many of these sites had to be replanted several years later, however. Following cessation of timber harvest and silvicultural treatments in the mid-1990s, monitoring of the harvest areas was discontinued. Under the Northwest Forest Plan (Forest Ecosystem Management Assessment Team 1993), these areas are currently managed as late-successional reserves.

The objectives of this study were to quantify the effects of clearcutting and post-harvest management treatments on tree regeneration and species composition in montane forests. Key questions guiding this research were:

- How have various post-harvest treatments (burned-planted, unburned-planted, unburned-seeded) affected regeneration?
- Have post-harvest treatments, such as the seeding and planting of *A. amabilis*, influenced species composition of regenerating stands?
- Due to current management objectives to manage forests for late-successional status, is regeneration sufficient to return forests to pre-harvest stand structure and species composition?

Empirical data relevant to these questions will provide insights on the degree to which past harvest treatments affect the current, and possible future, composition of these forests.

Methods

Study Area

The study area is located in the watershed of the North Fork of the Nooksack River, Mt. Baker–Snoqualmie National Forest, in the North Cascade Range (Figure 1), and has rugged topography that results in a wide range of environmental conditions over relatively short distances. Average monthly air temperatures range from 0°C in January to 14°C in August, although minimum temperatures of -15°C in January and maximum temperatures of 25°C in August have been recorded (USDA Natural Resources Conservation Services, Washington State Cooperative Snow, Water and Climate Services Program SNOTEL data from Wells Creek, Washington, within the study area, 1996–2001). Mean annual precipitation is 233 cm, with over 80% typically falling as snow.

This portion of the North Cascade Range contains steep, highly dissected terrain composed of sedimentary and metamorphic formations that have been glacially modified. The landscape is a mosaic of broad valleys, cirques, arêtes, and morainal and outwash deposits containing numerous streams. Soils in this area, primarily Spodosols, Inceptisols, and Entisols, have developed in hillslope sediments and tephra, and are subject to colluvial activity.

In high-elevation areas (above 800 m) where the study was conducted, overstorey vegetation is composed mainly of *A. amabilis* and *Tsuga heterophylla* (Rafn.) Sarg., along with the codominants *Tsuga mertensiana* (Bong.) Carr. and *Chamaecyparis nootkatensis* (D. Don in Lamb.) Spach. Understorey species include *A. amabilis*, *T. heterophylla*, and *Vaccinium* spp.

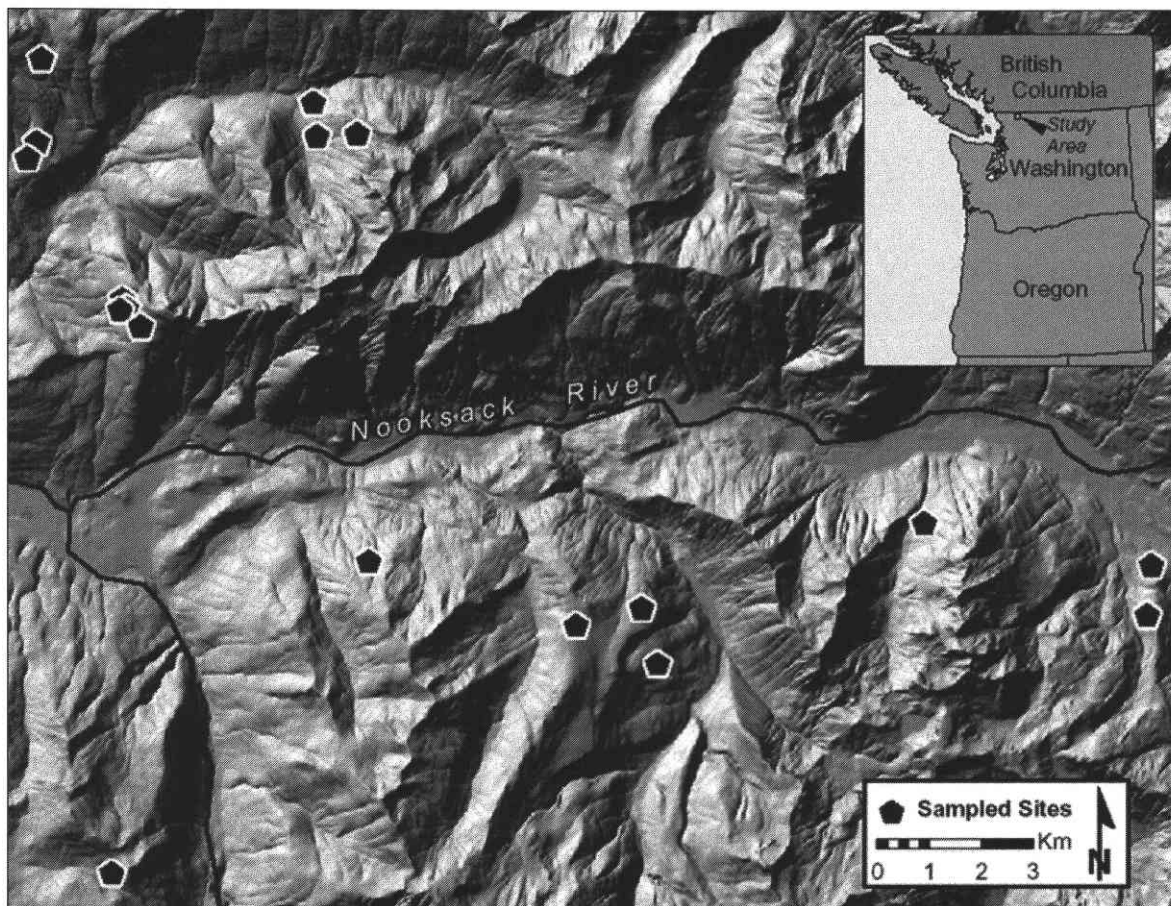


FIGURE 1. Study area, North Fork of the Nooksack River, expanded.

Site Selection

Complete historical records of forest harvest practices are archived at the Mt. Baker–Snoqualmie National Forest (Mt. Baker Ranger District Office, Sedro-Woolley, Washington). Records show that a large number of high-elevation forest sites with similar harvest and post-harvest treatments exist in the study watershed. Harvest activities and active management stopped in the mid-1990s, which allows study of regeneration conditions on many sites that otherwise would have been routinely thinned.

A geospatial database of forest management activities was provided by the Mt. Baker–Snoqualmie National Forest. From the database, six random “replicates” were selected from each of three post-harvest treatments.

1. Sites that were broadcast burned and planted with *A. amabilis* or *A. procera*. These sites were burned uniformly to dispose of slash.

2. Unburned sites that were seeded with *A. amabilis* or *A. procera*. In many cases, slash was piled in one or two locations on site and spot-burned.
3. Unburned sites that were planted with *A. amabilis*. Trees were planted at approximately 1200–2000 stems per hectare.

Sites were selected to cover a wide range of geographic points in the watershed, at elevations above 800 m and with similar stand age (13–27 years). Where possible, sites were located near functional roads for ease of access. Site characteristics are summarized in Table 1.

Vegetation Data

Sampling was conducted during August and September 2000. Three, 100 × 5 m belt transects were sampled on each site to capture spatial variability of vegetation. Transects were positioned throughout the clearcut to

TABLE 1. Characteristics of study sites in the North Fork of the Nooksack River, Mt. Baker–Snoqualmie National Forest, Washington

Sites	Year harvested	Year planted or seeded	Elevation (m)	Aspect	Slope (°)
<i>Burned-planted</i>					
BP1	1977	1978	1042	SW	13
BP2	1980	1981	891	W	31
BP3	1979	1981	967	W	15
BP4	1976	1978	829	NW	30
BP5	1977	1977	1113	SE	21
BP6	1977	1980	1364	SW	25
<i>Unburned-planted</i>					
UP1	1973	1974	1095	SW	29
UP2	1979	1980	1256	W	25
UP3	1978	1980	1282	W	29
UP4	1987	1988	992	NW	33
UP5	1977	1978	1276	N	8
UP6	1978	1978	1459	E	9
<i>Unburned-seeded</i>					
US1	1983	1983	1215	S	13
US2	1983	1983	1190	SW	29
US3	1983	1985	1211	W	39
US4	1983	1985	1120	SW	25
US5	1986	1986	1019	NW	16
US6	1987	1988	1159	N	25

sample as much of the clearcut as possible and were located at least 30 m from forest and road edges to avoid edge effects. Transect starting points were randomly selected. All trees and seedlings (any tree below the shrub canopy layer) along the transect were tallied and identified. Trees were measured with calipers or diameter tape, and placed into 3-cm classes under 16 cm DBH and into 5-cm classes thereafter, due to the small number of larger trees found in the study area. The largest size class measured was 41–46 cm DBH. A total of 7374 trees were surveyed. All large woody debris greater than 7.5 cm DBH within the boundaries of the transect was measured, including its end diameter, mid-diameter, and length. Measurements also included the diameter and height of all stumps remaining from harvests.

Six, 2 × 2 m vegetation plots were established in each transect. Plots were spaced 20 m apart along the transect, with the first plot placed at the beginning of the transect. In each plot, percent cover of herbaceous and shrub layers was recorded. In addition, depth of the O horizon and any evidence of soil erosion and compaction were recorded. Diameter at breast height and height of three trees closest to each vegetation plot were measured and increment cores extracted to determine age of regeneration on the site. Height and age data were obtained from 835 trees.

Statistical Analysis

One-way analysis of variance (ANOVA) tests were used to detect differences between post-harvest treatments (Zar 1999). Due to the high level of variation present in the data, tests were considered significant at $p < 0.1$. Proportional data were transformed using the arcsin square-root transformation (Zar 1999). Linear regression was used to model:

- the effects of elevation on overstorey tree and seedling abundance,
- the effects of elevation on overstorey and understorey species distribution,
- the effects of plot size on overstorey tree and seedling abundance, and
- possible interactions between elevation and treatment effects for *A. amabilis* and *T. heterophylla*.

To normalize data and reduce variance, a square-root transformation was applied to the total stem density on each site. Tests were considered significant if the regression coefficient was significantly different from 0 at $p < 0.1$. Mean DBH and height of advance regeneration and planted trees across sites were compared using *t*-tests. Aspect data were converted from degrees to

cosines for statistical testing (Zar 1999). Large woody debris volume was calculated using Smalian's formula:

$$\text{Volume (m}^3\text{)} = (((\text{Diameter (cm) at end 1} \times \Pi) + 10\,000 \text{ (cm}^2\text{/m}^2\text{)} + (\text{Diameter (cm) at end 2} \times \Pi + 10\,000 \text{ (cm}^2\text{/m}^2\text{)})) \div 2) \times \log \text{length (m)}$$

$$\text{Volume per plot area (m}^3\text{/ha)} = \text{Volume (m}^3\text{)} \div (500 \text{ m}^2 \div 10\,000 \text{ (m}^2\text{/ha)})$$

Density of decayed logs = 0.3 g/cm (R. Edmonds, University of Washington, pers. comm., 2002)

$$\text{Biomass (Mg/ha)} = \text{Volume per plot area (m}^3\text{/ha)} \times \text{Density (0.3 g/cm}^3\text{)} \times 10^6 \text{ (cm}^3\text{/m}^3\text{)} \times (\text{kg}/10^3 \text{ g)} \times (\text{Mg}/10^3 \text{ kg)}$$

Large woody debris biomass was transformed using the square-root transformation to equalize variances between groups, and was then tested using ANOVA. Data on depth of the O horizon were compared using a Kruskal-Wallis test (Zar 1999) due to unequal variances between groups. A Chi-square test was used to test for differences between population variances in O-horizon data.

Historical Data

Records obtained from the Mt. Baker–Snoqualmie National Forest were used to reconstruct pre-harvest overstorey species composition of mature forests in the study area. Pre-harvest cruise information was obtained for each site when available. Records were difficult to locate for several sites, so adjacent stand records were used. Because of inconsistency between recorders, actual stand composition may vary from these estimates. *Abies amabilis*, *T. heterophylla*, and *T. mertensiana* were considered the most merchantable species and were therefore best represented in records. *Tsuga mertensiana* and *T. heterophylla* were often grouped into one category as hemlocks; the designation “hemlock and others” was frequently used. Therefore, some minor subcomponents of species composition were often lost, and the amount of *Tsuga* spp. on the sites may have been overestimated. Several comments in the stand records also indicate that on sites where it was recorded, *C. nootkatensis* was combined with *Thuja plicata* Donn ex D. Don, and therefore no separate records exist. No historical data record the presence of *A. procera* in these stands.

Many stands were selected for harvest because they were considered “overmature,” and many of the trees were rotten or otherwise unsuitable for use after harvest and were considered “cull,” or unmerchantable. Stand cruises often do not mention the existence of these cull

trees although other comments in the records lead us to believe that additional species were present, but not noted. Therefore, although records exist for many of the sites, information on historical stand composition in Table 2 only approximates actual stand composition. Paired *t*-tests were used to compare historic and current species composition across all sites.

Understorey data for the sampled sites were not available from historical records. Vegetation information for the entire North Fork of the Nooksack River watershed was obtained from the USDA Forest Service Area Ecology Program. These data were collected using 0.2-ha plots in selected stands that were greater than 75 years old and relatively undisturbed. Visual estimates of cover were made for all species, including herbs, shrubs, regenerating trees (< 3.5 m tall) and mature trees (> 3.5 m tall). To accurately compare data from our sites to those obtained from the Forest Service, only data within the elevation limits of our sampled plots were used to compare pre-harvest understorey conditions with present conditions. It is reasonable to assume that the understorey species composition of mature stands sampled by the Area Ecology Program resembles that of pre-harvest conditions of stands sampled in this study.

Results

Overstorey Data

In all sites, *A. amabilis* and *T. heterophylla* combined represented 68–100% of trees present. *Pseudotsuga menziesii* was common, but not abundant, on most sites, with the exception of US4, where it dominated the overstorey (Table 3). Other species that occurred in low relative abundance were *A. procera*, *C. nootkatensis*, *Thuja plicata*, *T. mertensiana*, and *Prunus emarginata* (Dougl.) Walp. (Table 3).

The relative abundance of *A. amabilis* contributed to most of the difference in overstorey composition found between treatments. Overstorey *A. amabilis* had significantly lower density in burned-planted sites than in unburned-planted sites ($p = 0.085$, $n = 18$). Although the proportions of *T. heterophylla* on burned-planted sites were higher when compared to unburned sites, this difference was not significant (Figure 2). Burned-planted sites also had a slightly higher subcomponent of *C. nootkatensis* and *T. plicata* than other treatments. Tree density varied from 1000 to 5305 trees per hectare and was similar between treatments ($p > 0.1$) (Figure 3). Tree height and DBH were also similar across treatments ($p > 0.1$) (Figures 4 and 5).

TABLE 2. Historical stand composition reconstruction of the proportion (%) of overstorey species found on sampled sites (rows add to 100%) (USDA Forest Service, Sedro-Woolley, Washington)

Treatment	<i>Abies amabilis</i>	<i>Pseudotsuga menziesii</i>	<i>Thuja plicata</i>	<i>Tsuga heterophylla</i>	<i>Tsuga mertensiana</i>
BP1	60	—	—	40	—
BP2	30	—	—	70	—
BP3	56	—	—	44	—
BP4	39	—	4	57	—
BP5	19	—	—	81	—
BP6	58	—	—	11	31
UP1	37	10	6	47	—
UP2	47	—	—	43	10
UP3	24	39	10	27	—
UP4	45	—	—	55	—
UP5	66	—	—	34	—
UP6	84	—	—	—	16
US1	22	—	—	12	66
US2	1	61	13	25	—
US3	90	1	—	9	—
US4	39	—	—	61	—
US5	36	—	23	41	—
US6	44	—	13	43	—

EFFECTS OF POST-HARVEST TREATMENTS ON HIGH-ELEVATION FORESTS

TABLE 3. Proportion (%) of overstorey species found on all sampled sites (rows add to 100%)

Treatment	<i>Abies amabilis</i>	<i>Abies procera</i>	<i>Chamaecyparis nootkatensis</i>	<i>Prunus emarginata</i>	<i>Pseudotsuga menziesii</i>	<i>Thuja plicata</i>	<i>Tsuga heterophylla</i>	<i>Tsuga mertensiana</i>	Density (stems per hectare)
<i>Burned-planted</i>									
BP1	36.4	2.4	0.1	—	0.9	6.3	53.9	—	4660
BP2	7.4	—	—	—	—	—	92.3	0.3	5307
BP3	26.1	—	0.8	—	0.3	9.0	63.4	0.5	2660
BP4	61.4	—	—	—	1.4	—	36.1	1.1	2867
BP5	2.1	—	—	—	0.5	24.4	73.0	—	1847
BP6	64.5	—	16.7	—	0.4	—	3.6	14.7	1673
<i>Unburned-planted</i>									
UP1	67.6	—	—	0.1	0.1	3.7	28.4	—	4853
UP2	34.7	—	0.7	—	—	0.7	62.7	1.3	1000
UP3	75.2	—	—	2.9	7.4	0.4	14.1	—	1807
UP4	43.5	—	—	—	—	0.9	55.6	—	1440
UP5	71.6	—	—	—	—	—	28.2	0.3	2273
UP6	84.1	—	—	—	—	—	15.9	—	2887
<i>Unburned-seeded</i>									
US1	85.5	0.6	—	—	—	—	2.4	11.5	3547
US2	69.4	—	—	3.1	8.6	4.7	14.3	—	2567
US3	35.9	—	—	—	4.7	5.1	54.3	—	1573
US4	24.7	—	—	0.7	20.9	7.5	46.2	—	1947
US5	46.6	—	—	4.3	0.2	2.1	46.8	—	3533
US6	69.9	—	—	—	—	—	29.2	0.9	2720

Proportion of stems (%)

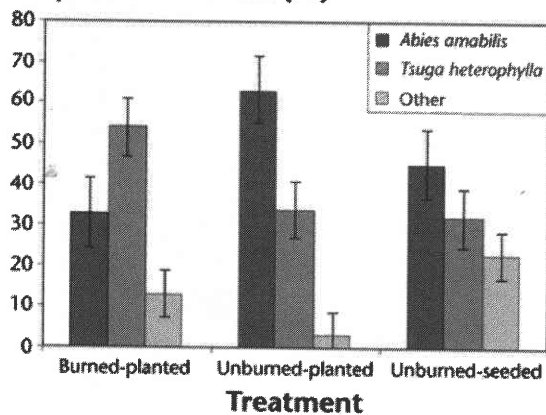


FIGURE 2. Mean percent of *Abies amabilis* and *Tsuga heterophylla* in the overstorey across treatments. Error bars represent one standard error of the mean.

Density (stems per hectare)

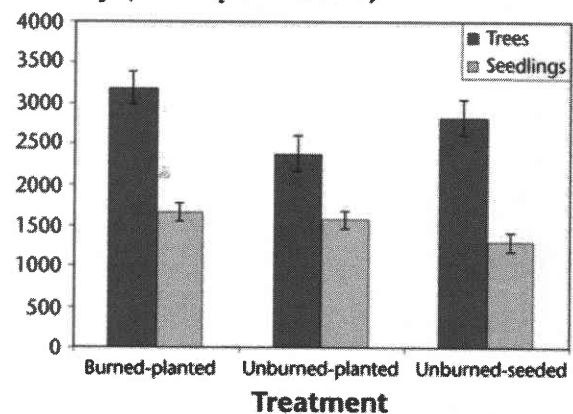


FIGURE 3. Mean tree and seedling density across treatments. Error bars represent one standard error of the mean.

No. of trees

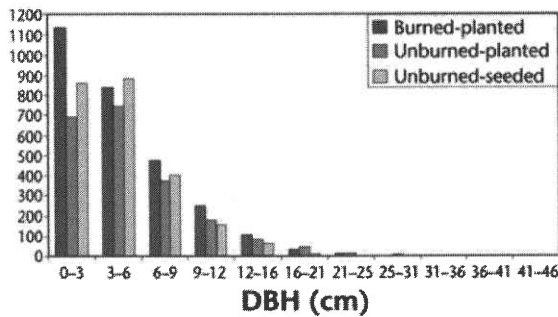


FIGURE 4. DBH distribution of all sampled individuals by post-harvest treatment.

No. of trees

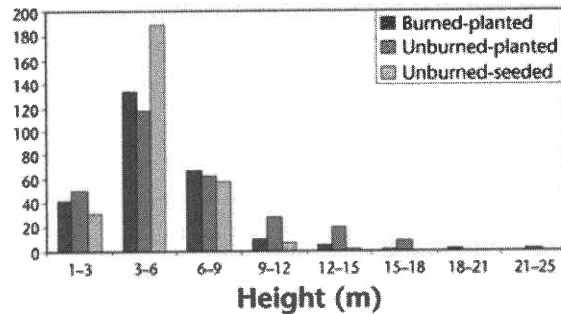


FIGURE 5. Height distribution of all sampled individuals by post-harvest treatment.

Overstorey age distribution differed somewhat among treatments due to advance regeneration on many sites. In this study, advance regeneration was considered to be any tree present on the site that had been released after harvest and was older than the harvest date. Although advance regeneration was present across all treatments, there were significantly fewer instances of it on sites that were broadcast burned compared to unburned sites

TABLE 4. Age distribution of trees across treatments

Treatment	Proportion of trees that were advance regeneration (%)	Mean age (yr) + SE of the mean
Burned-planted	3.1	16.9 + 0.53
Unburned-planted	37.2	24.0 + 1.14
Unburned-seeded	48.0	21.1 + 1.07

No. of trees

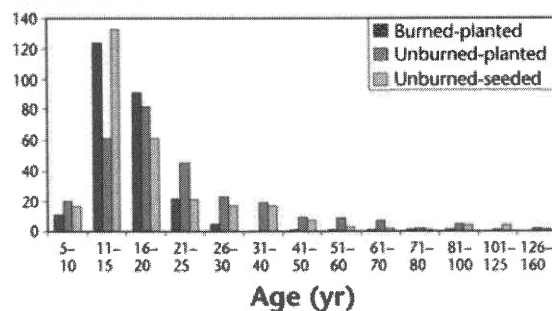


FIGURE 6. Age distribution of all sampled individuals by post-harvest treatment.

($p < 0.001$, $n = 18$), leading to a lower mean age on burned sites (Table 4). Only two of the burned-planted sites had advance regeneration (3.1% of all trees cored); 37.2% and 48.0% of the trees on unburned-planted and unburned-seeded sites, respectively, were of advance regeneration origin. Advance regeneration ages ranged from 1 year after the stand establishment to 158 years (Figure 6). Both height ($p = .007$, $n = 12$) and DBH ($p = .002$, $n = 12$) of advance regeneration were significantly larger than planted trees on non-burned sites. Burned sites were not compared due to lack of advance regeneration.

Understorey Data

Seedling density ranged from 213 to 5567 seedlings per hectare and was similar between treatments (Figure 3). Sampling was conducted in August and September 2000, which was the only time the sites were accessible. Several understorey species had already flowered and fruited before data collection, making it difficult to identify some of them. A total of 91 species were identified to species and 16 others were identified to genus or family. The number of species at planted sites was lower than at seeded sites (Table 5). *Epilobium angustifolium*, *Rubus* species (*R. parviflorus*, *R. pedatus*, and *R. spectabilis*), and two *Vaccinium* species (*V. membranaceum*, *V. ovalifolium*) comprised a large proportion of cover in the three treatments (Figure 7). Mean height of the understorey shrub layer ranged from 77 to 86 cm across all treatments. No significant differences were evident in understorey species cover between treatments (Table 5).

EFFECTS OF POST-HARVEST TREATMENTS ON HIGH-ELEVATION FORESTS

TABLE 5. Percent cover of major understorey species across three treatments (overall species percent cover 1% or greater for any treatment), *n* = no. of species

Species	Common name	Burned-planted (%) (<i>n</i> = 63)	Unburned-planted (%) (<i>n</i> = 65)	Unburned-seeded (%) (<i>n</i> = 85)
<i>Abies amabilis</i>	Amabilis fir	5.6	6.1	5.2
<i>Anaphalis margaritacea</i>	Pearly everlasting	6.3	3.9	5.8
<i>Athyrium filix-femina</i>	Ladyfern	3.4	6.7	5.4
<i>Blechnum spicant</i>	Deerfern	1.8	0.6	0.2
<i>Clintonia uniflora</i>	Queens' cup	0.3	0.7	2.1
<i>Cornus canadensis</i>	Bunchberry	6.4	2.6	4.4
<i>Dryopteris expansa</i>	Shield fern	0.0	1.8	0.0
<i>Epilobium angustifolium</i>	Fireweed	11.3	15.8	14.0
<i>Equisetum</i> spp.	Horsetails	0.0	1.0	0.3
<i>Gymnocarpium dryopteris</i>	Oak fern	0.1	1.6	0.1
<i>Lactuca muralis</i>	Wall lettuce	0.7	0.7	0.1
<i>Linnaea borealis</i>	Twinflower	0.1	0.1	3.7
<i>Oplopanax horridum</i>	Devil's club	0.1	0.6	1.4
Poaceae	Grass	1.8	2.7	2.9
<i>Ribes viscosissimum</i>	Sticky currant	0.0	0.0	1.3
<i>Rubus parviflorus</i>	Thimbleberry	9.8	1.1	3.8
<i>Rubus pedatus</i>	Strawberry-leaf blackberry	3.0	2.7	2.7
<i>Rubus spectabilis</i>	Salmonberry	6.2	3.2	6.9
<i>Salix sitchensis</i>	Sitka willow	0.1	1.1	0.0
<i>Sambucus racemosa</i>	Elderberry	0.9	0.7	0.5
<i>Smilacina stellata</i>	Star-flowered false Solomon's-seal	0.1	0.7	2.3
<i>Sorbus sitchensis</i>	Sitka mountain ash	0.3	1.5	0.4
<i>Tiarella trifoliata</i>	Three-leaved coolwort	1.3	5.0	1.5
<i>Tsuga heterophylla</i>	Western hemlock	6.8	3.8	3.0
<i>Vaccinium membranaceum</i>	Big huckleberry	16.5	3.3	2.5
<i>Vaccinium ovalifolium</i>	Oval-leaf huckleberry	11.5	16.8	19.1
<i>Vaccinium parvifolium</i>	Red huckleberry	0.3	0.1	1.7
<i>Valeriana sitchensis</i>	Sitka valerian	0.0	7.0	0.1

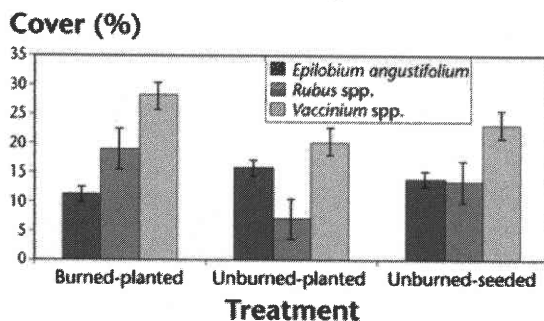


FIGURE 7. Percent cover of major understorey species among treatments. Error bars represent one standard error of the mean.

Large Woody Debris and Forest Floor Characteristics

Biomass of large woody debris varied, but not significantly, between treatments. Mean large woody debris biomass ranged from 291 ± 115 Mg/ha (± 1 SD) in burned-planted sites to 390 ± 199 Mg/ha in unburned-planted sites. The highest variability in biomass was observed on unburned-seeded sites. For depth of the O horizon, Chi-square tests showed significant differences between unburned-seeded and burned-planted sites ($p < 0.05$). No significant differences between treatment means were found using a Kruskal-Wallis test. Mean depth of the O horizon was similar in all treatments and

ranged from 4.3 cm in burned-planted sites to 6.8 cm in unburned-planted sites.

Clearcut Size

Clearcut size was examined for possible interaction with tree and seedling density as a significant independent variable. Clearcut sizes varied from 0.7 to 20.0 ha. Tree and seedling densities were similar across all clearcut areas, which indicated that clearcut size had no apparent effect on seed dispersal. Similarly, no statistical differences in cover of understorey species existed for different clearcut sizes. It was determined that seedling regeneration resulted from seed dispersal from adjacent stands, as most trees growing on the study sites were too young to produce seed, with the possible exception of some of the older advance regeneration.

Environmental Factors

Several environmental factors, including aspect and elevation, were evaluated for possible interactions with management treatments. Aspect was examined as a possible influence on vegetation distribution on the sites. Because of constraints of site selection, it was difficult to allocate sites equally among aspects. For this analysis, north and east aspects were grouped, and south and west aspects were grouped. Overall, no differences in tree density, seedling density, or overstorey composition were detected due to aspect. The relationship between treatments and elevation as a whole was examined and no interaction was found. In addition, the relationship between densities for individual treatments and elevation was examined and found not to be significant.

Elevation of harvest units varied from 830 to 1460 m and had a strong influence on overstorey and understorey species abundance and distribution. Density of *A. amabilis* was higher at higher elevations ($r^2 = 0.22$, $p = 0.049$), and density of *T. heterophylla* was lower ($r^2 = 0.61$, $p < 0.001$). *Tsuga mertensiana* was more common at higher elevations than at lower elevations. *Abies amabilis* seedling density was positively correlated with elevation ($r^2 = 0.34$, $p = 0.010$), and *T. heterophylla* seedlings and established trees had a negative distribution with respect to elevation. No relationships existed between elevation and treatment effects for *A. amabilis* and *T. heterophylla*.

Understorey species composition was also affected by elevation. Understorey *T. heterophylla* seedlings decreased in density with increasing elevation ($r^2 = 0.51$, $p < 0.001$). *Rubus spectabilis* and *R. parviflorus* density

was also negatively correlated with elevation ($r^2 = 0.28$, $p = 0.023$ and $r^2 = 0.22$, $p = 0.048$ respectively). *Vaccinium membranaceum* was the only understorey species with a positive correlation between density and elevation ($r^2 = 0.41$, $p = 0.004$).

Historical Comparisons

Based on paired *t*-tests, no statistical difference was evident between the current and historical proportion of total stems of *A. amabilis* and *T. heterophylla*. The amount of *T. plicata* present in the past appeared to be less than current densities. It is possible, however, that the presence of *T. plicata* was not recorded in the historical if the tree was not present in merchantable quantities.

Because of the differing methods by which current and historical data were collected, understorey data obtained from the Forest Service Area Ecology survey were not subjected to statistical tests. The Forest Service Area Ecology data consisted of 60 plots located in mature forest within the geographic co-ordinates of the study area. Overall, species lists for Forest Service data and current species composition are comparable, although many species occurring in small amounts do not overlap (Table 6). *Dryopteris expansa* was the only species present in our data, but absent from the Forest Service data. *Rhododendron albiflorum* and *Taxus brevifolia* Nutt. were present only in the Forest Service data.

Discussion

Effects of Treatments on Overstorey Species Composition

A key finding in this study is that burned-planted sites have less *A. amabilis* than unburned-planted sites. The slightly higher densities of *T. heterophylla* and *T. plicata* on burned-planted sites may indicate that these species compete favourably with *A. amabilis*, possibly due to higher soil temperatures at burned sites (Zabowski *et al.* 2000). In general, *A. amabilis* is most productive on soils with deep organic horizons and does not establish well on burned sites (Koppelaar and Mitchell 1992). In contrast, *T. heterophylla* establishes well on mineral soil at burned sites, although sites with exposed mineral soil can have high temperatures and low soil moisture near the surface (Hetherington 1965; Gray and Spies 1997). In general, unburned sites contained higher amounts of *A. amabilis*, most likely due to the higher amounts of natural regeneration present (Table 4), which tends to have higher vigour than planted stock in terms of growth and nutrient accumulation (Arnott *et al.* 1995; Koppelaar *et al.* 1995).

EFFECTS OF POST-HARVEST TREATMENTS ON HIGH-ELEVATION FORESTS

TABLE 6. Historical understorey species composition of mature stands and current understorey conditions in the North Fork of the Nooksack River watershed (Jan Henderson, USDA Forest Service)

Species	Historical data (% cover)	Current data (% cover)
<i>Abies amabilis</i>	27.0	5.7
<i>Acer circinatum</i>	0.6	0.0
<i>Anaphalis margaritacea</i>	0.1	5.2
<i>Athyrium filix-femina</i>	0.5	5.2
<i>Blechnum spicant</i>	0.2	0.8
<i>Clintonia uniflora</i>	0.8	1.0
<i>Cornus canadensis</i>	0.3	4.3
<i>Dryopteris expansa</i>	0.0	0.7
<i>Epilobium angustifolium</i>	1.7	13.6
<i>Gymnocarpium dryopteris</i>	0.5	0.7
<i>Lactuca muralis</i>	0.2	0.5
<i>Linnaea borealis</i>	0.2	1.3
<i>Menziesia ferruginea</i>	1.8	0.1
<i>Oplopanax horridum</i>	0.9	0.7
Poaceae	0.0	2.6
<i>Pseudotsuga menziesii</i>	6.0	0.2
<i>Rhododendron albiflorum</i>	1.3	0.0
<i>Rubus parviflorus</i>	0.1	4.7
<i>Rubus pedatus</i>	3.9	2.8
<i>Rubus spectabilis</i>	1.0	5.3
<i>Sambucus racemosa</i>	0.1	0.7
<i>Sorbus sitchensis</i>	0.4	0.8
<i>Streptopus roseus</i>	0.5	0.1
<i>Taxus brevifolia</i>	1.0	0.0
<i>Thuja plicata</i>	2.9	0.4
<i>Tiarella trifoliata</i>	0.0	2.7
<i>Tiarella unifoliata</i>	1.2	0.0
<i>Tsuga heterophylla</i>	18.8	4.5
<i>Tsuga mertensiana</i>	5.9	0.5
<i>Vaccinium membranaceum</i>	5.5	7.1
<i>Vaccinium ovalifolium</i>	8.7	15.9
<i>Vaccinium parvifolium</i>	0.2	0.6
<i>Valeriana sitchensis</i>	0.2	2.6

Unburned-seeded sites do not have significantly different amounts of *A. amabilis* than burned-planted sites, but have higher overall stem densities (Table 4). Because trees were not directly planted on unburned-seeded sites, the original seed bank had a larger influence on species composition. For instance, *P. menziesii* is more prevalent on these sites than the other treatments. *Thuja plicata* also has relatively high densities on unburned-seeded sites, although it is found in highest concentrations on burned-planted sites. *Thuja plicata*

may regenerate better on burned forest floor than in a thick layer of litter and duff (Feller and Klinka 1998).

Effects of Treatments on Overstorey Regeneration

A second main finding of this study is that burned sites have significantly less advance regeneration than unburned sites. Of the unburned treatments, unburned-seeded sites have a slightly higher amount of advance regeneration than unburned-planted sites, most likely

because less disturbance occurred during site preparation for seeding.

Burned-planted sites are the oldest sites, established 21.5 years ago, followed by unburned-planted sites, (20.0 years), and unburned-seeded sites (15.6 years). Trees on burned sites, however, are the youngest of the three (mean age of 16.9 years), and trees on the unburned treatments are older on average than the stand itself (24.0 years for unburned-planted sites and 21.1 years for unburned-seeded sites).

The burned sites experienced a lag of approximately 4.5 years between harvest and stand establishment. Almost all trees, other than *A. amabilis* on the burned sites, have regenerated from seed, which can require several years for germination and successful establishment. Data from the Mt. Baker-Snoqualmie National Forest indicate that at least 3 years are required to grow *A. amabilis* seedlings to plantable stock in the nursery (Boecksteigel 1982). On high-elevation sites, where conditions are less favourable than in a nursery and growth is slow, it can take longer for seedlings to establish, as was the case on these sites. In addition, advance regeneration on unburned sites has significantly larger height and DBH than on burned sites. Retaining a healthy stock of advance regeneration appears to greatly reduce the time for stand establishment.

Effects of Environmental Factors on Overstorey and Understorey Species Composition

In addition to being influenced by silvicultural treatments, the overstorey species in this study are also influenced by an elevation gradient of over 600 m. *Abies amabilis* tree and seedling densities are positively correlated with elevation ($r^2 = 0.22$, $p = 0.049$) and *T. heterophylla* tree density is negatively correlated with elevation ($r^2 = 0.61$, $p < 0.001$). *Tsuga heterophylla* seedling density in overstorey site tallies has a non-significant negative correlation with elevation; *T. heterophylla* seedlings in understorey vegetation tallies have a strong negative relationship with elevation ($r^2 = 0.51$, $p < 0.001$). These findings corroborate well-established concepts on the current distribution of *T. heterophylla* and *A. amabilis*, namely that the distribution of *A. amabilis* extends to much higher elevations than *T. heterophylla*, although they overlap considerably (Franklin and Dyrness 1988). *Tsuga heterophylla* has lower frost tolerance than *T. mertensiana* and is replaced by *T. mertensiana* at higher elevations (Minore 1979).

It appears that two separate understorey communities dominate the study sites. Most of the sites show some segregation between *E. angustifolium* and *Vaccinium* spp. dominance, although both communities are often present along the same transect. *Vaccinium membranaceum* cover significantly increases with elevation ($r^2 = 0.41$, $p = 0.004$), and *R. parviflorus* and *R. spectabilis* cover decreases significantly ($r^2 = 0.28$, $p = 0.023$ and $r^2 = 0.22$, $p = 0.048$ respectively). *Epilobium angustifolium* cover also shows a non-significant decreasing trend with elevation, supporting observations that the study sites are located in a transition zone between a *Rubus* spp. and *E. angustifolium* community prevalent at lower elevations and a *Vaccinium* spp. community prevalent at higher elevations.

Competition between understorey vegetation and tree seedlings has been the subject of considerable research (Comeau 1988; Haeussler *et al.* 1990; Coates *et al.* 1991; Koppenaal and Mitchell 1992). In British Columbia, the Ministry of Forests considers brush to be one of the main agents hindering tree regeneration (B.C. Ministry of Forests 1992). Each of the three main components in the understorey, *E. angustifolium*, *Rubus* spp., and *Vaccinium* spp., are potential competitors with conifer seedlings and are a source of concern for forest regeneration.

Epilobium angustifolium is a very competitive, rhizomatous, wind-dispersed colonizer that quickly develops high densities in natural or human-made clearings, and has historically been associated with fires and other disturbances (Haeussler *et al.* 1990; Oswald and Brown 1993; Mitich 1999; USDA Forest Service 2001). Its seeds can travel up to 300 km within several days, allowing individuals to colonize openings from distant seed sources (Solbreck and Andersson 1987). In a management context, this plant is often considered a "weed" and has been shown to compete with conifer seedlings for nutrients, water, and light resources (Oswald and Brown 1993; Bell *et al.* 2000; Thevathasan *et al.* 2000). Although it can pose problems for seedling establishment, *E. angustifolium* tends to reach a peak in density during the first several years after an opening is created and then declines rapidly. In addition, this species can persist in lower abundance for many years (Haeussler *et al.* 1990; Messier and Kimmins 1991; Oswald and Brown 1993).

Although *Vaccinium* also spreads through rhizomes, its seedlings establish more slowly than those of *E. angustifolium* because of its considerable early investment in below-ground growth; it may require up to

7 years to dominate a site (Tappeiner and Alaback 1989; Alaback and Tappeiner 1991). Over time, *Vaccinium* can form dense thickets that impede seedling growth by limiting light and creating cold soil conditions underneath shrubs (Coates *et al.* 1991). *Vaccinium* also competes for nutrients on low-fertility sites (Koppelaar and Mitchell 1992).

Rubus spectabilis and other *Rubus* species are early colonizers that initiate from buried seeds that can remain viable for up to 100 years (Haeussler *et al.* 1990; Alaback and Tappeiner 1991). *Rubus* spp. spread through rhizomes and can form dense stands, shading out seedlings and other shrubs by allowing as little as 10% of light to penetrate to the forest floor (Franklin and Pechanec 1968; Comeau 1988). *Rubus spectabilis* requires 15–20 years to reach peak biomass in the absence of overstorey competition and can suppress tree regeneration for several decades (Franklin and Pechanec 1968; Tappeiner *et al.* 1991).

The only definitive way to determine the effects of understorey competition on conifer regeneration is to conduct a long-term study with a control area and an understorey exclusion area on each site. Only a few such studies have been conducted (Coates *et al.* 1991; Duns-worth and Arnott 1995; Bell *et al.* 2000; Kübner *et al.* 2000), but none were long term. Furthermore, at high elevations, conifer growth and regeneration are relatively slow, making it difficult to distinguish between climatic effects and possible competitive pressure. Forest Service records show that some sites had as much as 75% *E. angustifolium* cover at the time of planting, but do not mention *Vaccinium* or *Rubus*, which usually take longer to establish. Oswald and Brown (1993) studied a burned and planted clearcut at high elevation in southeastern British Columbia and recorded significant *E. angustifolium* and *V. membranaceum* cover, but concluded that *E. angustifolium* did not pose a threat to seedlings in the first 2 years.

Shrubs and other vegetation can also provide benefits to shade-tolerant conifers, such as the overstorey species in the present study, by providing shade and reducing soil temperatures (Simard and Nicholson 1990; Little *et al.* 1994). Shrubs can protect seedlings from ice and wind damage, and reduce erosion and snow movement (Agee and Smith 1984). Deciduous *Vaccinium* can provide different microsite conditions throughout the year, moderating high temperatures and moisture stress in the summer, and providing higher solar penetration in spring and autumn (Little *et al.* 1994). Coates *et al.* (1991) found that seedling diameter growth was more strongly affected

by increased shrub and herb competition than either seedling survival or height growth.

Low air and soil temperatures were found to be the primary factors inhibiting conifer seedling growth (Coates *et al.* 1991). It is likely that, during the early stages of development, tall shrubs and herbaceous vegetation may benefit seedling survival; however, that same vegetation would also shade the tree and reduce growth until the stem emerges above the shrub canopy. Average shrub height on sites in this study (ranging from 77 to 86 cm) likely affects the light environment sufficiently that conifer growth is inhibited.

Current conditions on our study sites indicate that *Vaccinium* may be a greater competitive influence than *E. angustifolium*, which does not form dense thickets. Some sites have vigorous overstorey growth that is beginning to shade out understorey species, but many of the sites have little canopy cover. Because of the patchy distribution of trees, most sites contain large areas with no canopy cover, interspersed with areas of heavy cover. It is clear that *E. angustifolium* and *Vaccinium* and *Rubus* species will persist on these sites for many years.

Historical Comparisons

Planting and seeding following harvest do not appear to have altered overstorey species composition when compared with historical records. Although *A. amabilis* was planted and seeded extensively, large amounts of *T. heterophylla* and smaller amounts of other species are present on the study sites. Species composition currently is similar to the historical composition, with the exception of two stands that contain planted *A. procera* (north of its natural range). In a study of post-harvest treatments that included natural regeneration, reseeding, and replanting in a high-elevation forest in Oregon, most seedlings were of natural origin regardless of treatment, and species composition was similar to that of the surrounding stands (Minore and Dubrasich 1981). Similar conclusions were reached in this study because current seedlings appear to originate from the surrounding stands. Due to the young age of stands, it is difficult to speculate on species composition 50–100 years in the future. Several decades of monitoring will be necessary to accurately assess the effects of timber harvest and post-harvest management activities.

Unlike overstorey species composition, understorey composition differs between clearcuts and historical data. Not surprisingly, historical data show a higher

percentage of shade-tolerant understorey tree and shrub species present in mature forests versus clearcuts. *Abies amabilis*, *T. heterophylla*, *T. mertensiana*, *P. menziesii*, *T. plicata*, *Menziesia ferruginea*, *R. albiflorum*, *T. brevifolia*, and *Acer circinatum* Pursh are all present in higher proportions in the historical data. Of those species, the largest disparities between the proportions of seedlings present in mature stands and clearcuts were found in *A. amabilis* (27% vs. 5.7%, respectively) and *T. heterophylla* (18.8% vs. 4.5%, respectively) (Table 6).

Many of the shade-intolerant species and those species that grow well in forest openings are found in higher densities in clearcut sites. *Anaphalis margaritacea*, *Athyrium filix-femina*, *Cornus canadensis*, *E. angustifolium*, Poaceae, *R. parviflorus*, *Tiarella trifoliata*, *V. ovalifolium*, and *Valeriana sitchensis* are all present in higher quantities in clearcuts, although in forested and clearcut areas the largest differences were found in *E. angustifolium* (1.7% vs. 13.6%, respectively) and *V. ovalifolium* (8.7% vs. 15.9%, respectively) (Table 6).

Species with similar cover in historical data and our data tend to be generalist species that grow well in both forests and clearings. Most of these generalist species (*Blechnum spicant*, *Clintonia uniflora*, *Gymnocarpium dryopteris*, *Lactuca muralis*, *Oplopanax horridum*, *Vaccinium parvifolium*) are present in very small quantities (Table 6). A few species, such as *Rubus pedatus* and *V. membranaceum*, have relatively high cover in both historical records and our data.

Management Implications

Over the past 30 years, high-elevation forests in the Pacific Northwest region of North America have been increasingly relied upon to supply timber, both by government agencies and by private companies. At the same time, under the Northwest Forest Plan in the United States, there has been a growing recognition of high-elevation forests as valuable habitat for numerous

species. Although the forested areas included in this study are considered late-successional reserves under the Northwest Forest Plan, timber harvest is still occurring on adjacent private and public lands. Sustainable approaches for managing timber production and late-successional forest are needed when considering management implications for these sites in particular and for regenerating high-elevation forests in the Pacific Northwest in general.

Managing High-elevation Stands for Timber

To have minimum impact on the ecological functions of high-elevation forests, it is important to incorporate management practices appropriate for these forest ecosystems into harvest and post-harvest management. Several inferences and recommendations emerge from this study.

Regeneration and growth are slow in high-elevation forests. True firs grow very slowly in the juvenile phase and can take up to 20 years to reach breast height (Harrington and Murray 1982). After about 20 years post-harvest, trees at our study sites have a mean height of only 5.6 m and a mean DBH of only 4.4 cm. Slow rates of regeneration and growth mean that several decades may be needed to achieve desired stand (stocking) density.

Because of the prevalence of regeneration problems, alternative harvest methods, including partial cutting, shelterwood cutting, and green tree retention, have been evaluated in high-elevation areas. Spruce-fir forests in Utah, Wyoming, and Idaho regenerated faster over 20 years under a partial cutting system as opposed to a clearcut (McCaughey *et al.* 1991). In British Columbia, no height differences were found for *A. amabilis* and *T. heterophylla* growth among a clearcut, green tree retention area, and patch cut, but slower growth was recorded in the shelterwood system, which had the highest canopy cover of all treatments (Mitchell 2001).

Based on these studies, it appears that alternative harvest systems that leave partial tree cover can improve regeneration and growth of shade-tolerant species such as *A. amabilis* and *T. heterophylla*. However, it is also apparent that further research is needed to find the optimal density and basal area of green trees to provide adequate shade, but not suppress tree growth. Forest Service records of harvests of mature stands indicate that many of the trees harvested in our study area were considered to be cull and were unmerchantable. Therefore, leaving some of these trees standing would not represent a loss of timber revenue.

To have minimum impact on the ecological functions of high-elevation forests, it is important to incorporate management practices appropriate for these forest ecosystems into harvest and post-harvest management.

Advance regeneration is an important component on all unburned sites and should be encouraged at moderate densities, particularly at high elevations where natural regeneration performs better than planted stock (Arnott *et al.* 1995; Koppenaal *et al.* 1995). In this study, DBH and height of advance regeneration were greater than that of planted trees. A study of *A. amabilis* in British Columbia found that approximately 20% of advance regeneration in a stand suffers injury due to logging damage (Herring and Etheridge 1976), suggesting that limiting mechanical site preparation may be beneficial to advance regeneration. Our results suggest that scattering unmerchantable materials instead of burning may provide better establishment and growth conditions for advance regeneration.

In addition to encouraging advance regeneration, natural regeneration should also be encouraged to maintain pre-harvest species composition. In this study, all seedlings apparently originated from adjacent mature stands, which maintained pre-harvest species diversity. In a study of the Vancouver Forest Region in British Columbia in 1992, *A. amabilis* and *T. heterophylla* forests comprised 34% of all forested lands before harvest. Fifteen years after harvest, 22% of all regenerating forests had a similar species composition. Of those forests, only 2% were planted, whereas the remaining forests were a result of natural regeneration (B.C. Ministry of Forests 1992).

Burning high-elevation sites can result in nutrient loss and potential effects on long-term productivity (DeByle 1974; Vogt *et al.* 1989). As demonstrated in this study, broadcast burning kills, or greatly reduces, all advance regeneration on a site, which can lead to slower stand initiation and growth. Furthermore, numbers of *A. amabilis* are greatly reduced on burned sites, indicating that it does not establish as well after a fire.

Competition between desirable tree species and understorey vegetation can affect regeneration and growth. In our study area, *E. angustifolium*, *Vaccinium* spp., and *Rubus* spp. dominate the understorey on all clearcuts. Comparable data on mature stands from the Forest Service show that these species are much less common in mature forests because of the shade provided by canopy cover. Although none of the alternative harvest studies previously cited investigated understorey competition with seedlings, competition may be less of a factor on sites where some of the overstorey is left to provide shade after harvest. Additional data on understorey-overstorey interactions in high-elevation forest ecosystems of the Pacific Northwest would improve our

Our results suggest that scattering unmerchantable materials instead of burning may provide better establishment and growth conditions for advance regeneration.

understanding of the effects of understorey competition on regeneration.

Managing for Late-Successional Conditions

Under the U.S. Northwest Forest Plan, late-successional communities are defined as forests older than 175–200 years of age, which include a multilayered canopy, large living trees, snags, large woody debris, and the presence of species and ecological processes that are unique to “old-growth” conditions (Forest Ecosystem Management Assessment Team 1993). When managing for a late-successional stand, a forest manager can elect to let stand development progress naturally, but must be aware that ecological disturbance affects the development of stands.

Several studies have found that post-fire subalpine sites have a 30–100 year lag time before a substantial recruitment peak, as well as continuous recruitment for up to 200 years (Agee and Smith 1984; Huff and Agee 1991; Little *et al.* 1994). Historical records indicate that before cutting, stands in this study were 250 to over 300 years old, with approximately 16–41 trees per hectare ranging from 56 to 79 cm DBH. If these regenerating stands remain free of severe natural or human-caused disturbances, it is probable that they will reach late-successional status in 250–300 years and have a species composition and structure similar to historical conditions.

Although one can assume “stable conditions” when devising a long-term management plan, addressing the possibility of disturbance may also be important. *Abies amabilis* forests experience infrequent, high-severity fires, which are usually stand replacing because of the thin bark and shallow roots of this species. Fire return intervals can range from 300 to 600 years (Agee 1993) and are a real possibility within a management context of 300+ years. The consequence of such an event would potentially be a return to stand initiation conditions.

In addition to natural disturbances, considering the consequences of climatic change may also be important in a management plan that extends over the next several hundred years. Current models predict a climatic shift in the Pacific Northwest to warmer, wetter winters, and possibly warmer summers (Joint Institute for the Study of Atmosphere and Oceans 1999). The effects of warmer, wetter winters would be a smaller snowpack owing to increased precipitation as rain rather than snow (Joint Institute for the Study of Atmosphere and Oceans 1999). Because high snowpack is one of the primary constraints on seedling establishment in high-elevation forests of the western Cascade Range, a reduction in snowpack could allow higher rates of seedling establishment, and possibly faster establishment of stands and higher rates of tree growth (Peterson 1998; Peterson and Peterson 2001; Peterson *et al.* 2002).

Based on predictions of warmer summers, a further consequence of climatic change could involve an alteration of the fire regime to one of higher frequency (McKenzie *et al.* 2004). Although such a trend could introduce greater instability into the ecosystem, actual effects on these forests are uncertain. Established *A. amabilis* forests do not exhibit a strong response to climatic variability in the absence of disturbance (Joint Institute for the Study of Atmosphere and Oceans 1999). However, an altered fire regime of more frequent, smaller-scale events, as opposed to large, infrequent events, could lead to a shift in species composition that favours more fire-tolerant species such as *P. menziesii*.

To more accurately predict future structure, long-term monitoring over the next several decades would be beneficial to quantify emerging species composition and stand structure as the forests mature. Monitoring may be needed only once every decade or so because of slow tree growth in these high-elevation forests. This low-intensity monitoring would provide valuable insights into post-harvest succession in high-elevation forest ecosystems.

Acknowledgements

Drs. Susan Prichard, Robert Edmonds, and Timothy White reviewed earlier drafts of the manuscript, and Kelly O'Brian assisted with editing. Drs. Dean Billhimer, Don McKenzie, and Dave W. Peterson provided statistical consultations. Ze'ev Gedalof, Hillary Cook, Megan Wilson, Peter Springs, Seth Kirby, Melissa Poe, Jacqueline Klug, Steve Goodman, and Carolyn Menke assisted with fieldwork. Robert Norheim helped with field site reconnaissance, GIS support, and Figure 1.

Funding was provided by the U.S. Geological Survey Global Change Research Program and the USDA Forest Service, Pacific Northwest Research Station. This paper is a contribution of the Western Mountain Initiative.

References

- Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington D.C.
- Agee, J.K. and L. Smith. 1984. Subalpine tree re-establishment after fire in the Olympic Mountains, Washington. *Ecology* 65:810–819.
- Alaback, P.B. and J.C. Tappeiner, II. 1991. Response of western hemlock (*Tsuga heterophylla*) and early huckleberry (*Vaccinium ovalifolium*) seedlings to forest windthrow. *Canadian Journal of Forest Research* 21:534–539.
- Arnott, J.T., R.K. Scagel, R.C. Evans, and F.T. Pendl. 1995. High elevation regeneration strategies for subalpine and montane forests of coastal British Columbia. B.C. Ministry of Forests, Victoria, B.C. FRDA Report No. 229.
- Bell, F.W., M.T. Ter-Mikaelian, and R.G. Wagner. 2000. Relative competitiveness of nine early-successional boreal forest species associated with planted jack pine and black spruce seedlings. *Canadian Journal of Forest Research* 30:790–800.
- British Columbia Ministry of Forests. 1992. British Columbia's forests: Monoculture or mixed forests? Silviculture Interpretations Working Group, Victoria, B.C.
- Boecksteigel, L. 1982. Management experience on Pacific silver fir from the Forest Service–Mt. Baker–Snoqualmie view. In *Proceedings of the symposium on the biology and management of true fir in the Pacific Northwest*. C.D. Oliver and R.M. Kenady (editors). University of Washington, Seattle, Wash. Contribution No. 45, pp. 305–309.
- Coates, K.D., W.H. Emmingham, and S.R. Radosevich. 1991. Conifer-seedling success and microclimate at different levels of herb and shrub cover in a *Rhododendron–Vaccinium–Menziesia* community of south-central British Columbia. *Canadian Journal of Forest Research* 21:858–866.
- Comeau, P. 1988. Light attenuation by thimbleberry-fireweed communities in the ICH zone and its potential effects on conifer growth. In *Vegetation competition and responses*. Proceedings of the Third Annual Vegetation Management Workshop. B.C. Ministry of Forests, Victoria, B.C. FRDA Report No. 026, pp. 5–6.

- DeByle, N.V. 1974. Soil fertility as affected by broadcast burning following clearcutting in northern Rocky Mountain larch/fir forests. *In* Proceedings, Tall Timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, Fla. 14:447-464.
- Dunsworth, B.G. and J.T. Arnott. 1995. Growth limitations of regenerating montane conifers in field environments. *In* Montane alternative silvicultural systems (MASS). Proceedings of a workshop held June 7-8, 1995 in Courtenay, B.C. J.T. Arnott, W.J. Beese, A.K. Mitchell, and J. Peterson (editors). Canadian Forest Service, Victoria, B.C. FRDA Report No. 238, pp. 48-68.
- Feller, M.C. and K. Klinka. 1998. Seedfall, seed germination, and initial survival and growth of seedlings of *Thuja plicata* in southwestern British Columbia. *Northwest Science* 72:157-169.
- Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: An ecological, economic, and social assessment. Report of the Forest Management Assessment Team. U.S. Department of Agriculture and U.S. Department of the Interior, Washington, D.C.
- Franklin, J.F. and A.A. Pechanec. 1968. Comparison of vegetation in adjacent alder, conifer, and mixed alder-conifer communities. I. Understorey vegetation and stand structure. *In* Biology of alder. Proceedings of a symposium held at the Northwest Scientific Association Fortieth Annual Meeting, Pullman, Wash., April 14-15, 1967. U.S. Department of Agriculture Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oreg. pp. 37-43.
- Franklin, J.F. and C.T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oreg.
- Franklin, J.F. and R.T. Forman. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecology* 1:5-18.
- Gray, A.N. and T.A. Spies. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78:2458-2473.
- Haeussler, S., D. Coates, and J. Mather. 1990. Autoecology of common plants in British Columbia: A literature review. B.C. Ministry of Forests, Victoria, B.C. FRDA Report No. 158.
- Harrington, C.A. and M.D. Murray. 1982. Patterns of height growth in western true firs. *In* Proceedings of the symposium on the biology and management of true fir in the Pacific Northwest. C.D. Oliver and R.M. Kenady (editors). University of Washington, Seattle, Wash. Contribution No. 45, pp. 209-214.
- Harris, L.D. 1984. The fragmented forest: Island biogeography theory and the preservation of biotic diversity. The University of Chicago Press, Chicago, Ill.
- Herring, L.J. and D.E. Etheridge. 1976. Advance amabilis fir regeneration in the Vancouver Forest District. B.C. Forest Service, Victoria, B.C. Canadian Forest Service Joint Report No. 5.
- Hetherington, J.C. 1965. The dissemination, germination and survival of seed on the west coast of Vancouver Island from western hemlock and associated species. B.C. Forest Service, Victoria, B.C. Research Note No. 39.
- Huff, M.H. and J.K. Agee. 1991. Subalpine forest dynamics after fire in the Pacific Northwest national parks. National Park Service Coop. Park Studies Unit, College of Forest Resources, University of Washington, Seattle, Wash.
- Joint Institute for the Study of Atmosphere and Oceans. 1999. Impacts of climate variability and change in the Pacific Northwest. Climate Impacts Group, University of Washington, Seattle, Wash. Contribution No. 715.
- Koppenaar, R.S. and A.K. Mitchell. 1992. Regeneration of montane forests in the coastal western hemlock zone of British Columbia: A literature review. Canadian Forest Service, Victoria, B.C. FRDA Report No. 192.
- Koppenaar, R.S., B.J. Hawkins, and A.K. Mitchell. 1995. Acclimation of natural and planted amabilis fir to clearcut and stand edge microclimates on a coastal montane reforestation site. Canadian Forest Service, Victoria, B.C. FRDA Report No. 232.
- Kübner, R., P.E. Reynolds, and F.W. Bell. 2000. Growth response of *Picea mariana* seedlings to competition for radiation. *Scandinavian Journal of Forest Research* 15:334-342.
- Little, R.L., D.L. Peterson, and L.L. Conquest. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: Effects of climate and other factors. *Canadian Journal of Forest Research* 24:934-944.
- McCaughey, W.W., C.E. Fiedler, and W.C. Schmidt. 1991. Twenty-year natural regeneration following five silvicultural prescriptions in spruce-fir forests of the intermountain West. U.S. Department of Agriculture Forest Service, Intermountain Research Station Research Paper INT-439.

- McKenzie, D., Z. Gedalof, D.L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. *Conservation Biology* 18:890–902.
- Messier, C. and J.P. Kimmins. 1991. Above- and below-ground vegetation recovery in recently clearcut and burned sites dominated by *Gaultheria shallon* in coastal British Columbia. *Forest Ecology and Management* 46:275–294.
- Minore, D. 1979. Comparative autoecological characteristics of northwestern tree species: A literature review. U.S. Department of Agriculture Forest Service, Pacific Northwest Forest Range Experiment Station, Portland, Oregon. General Technical Report PNW-87.
- Minore, D. and M.E. Dubrasich. 1981. Regeneration after clearcutting in subalpine stands near Windigo Pass, Oregon. *Journal of Forestry* 79:619–621.
- Mitchell, A.K. 2001. Growth limitations for conifer regeneration under alternative silvicultural systems in a coastal montane forest in British Columbia, Canada. *Forest Ecology and Management* 145:129–136.
- Mitich, L.W. 1999. Fireweed, *Epilobium angustifolium*. *Weed Technology* 13:191–194.
- Oswald, E.T. and B.N. Brown. 1993. Vegetation development on skid trails and burned sites in southeastern British Columbia. *The Forestry Chronicle* 69:75–80.
- Peterson, D.L. 1998. Climate, limiting factors and environmental change in high-altitude forests of western North America. In *The impacts of climate variability on forests*. Springer-Verlag, New York, N.Y. pp. 191–208.
- Peterson, D.W. and D.L. Peterson. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal scales. *Ecology* 82:3330–3345.
- Peterson, D.W., D.L. Peterson, and G.J. Ettl. 2002. Growth responses of subalpine fir (*Abies lasiocarpa*) to climatic variability in the Pacific Northwest. *Canadian Journal of Forest Research* 32:1503–1517.
- Peterson, D.L., E.G. Schreiner, and N.M. Buckingham. 1997. Gradients, vegetation and climate: Spatial and temporal dynamics in the Olympic Mountains, U.S.A. *Global Ecology and Biogeography Letters* 6:7–17.
- Simard, S. and A. Nicholson. 1990. Balancing the positive and negative effects of non-crop plants on conifers: Pinegrass, fireweed, Sitka alder and paper birch—friend and foe. In *Vegetation management: An integrated approach*, Proceedings of the Fourth Annual Vegetation Management Workshop. Canadian Forest Service, Victoria, B.C. FRDA Report No. 109, pp. 45–48.
- Solbreck, C. and D. Andersson. 1987. Vertical distribution of fireweed, *Epilobium angustifolium*, seeds in air. *Canadian Journal of Botany* 65:2177–2178.
- Tappeiner, J.C. and P.B. Alaback. 1989. Early establishment and vegetative growth of understorey species in the western hemlock–Sitka spruce forests of southeast Alaska. *Canadian Journal of Botany* 67:318–326.
- Tappeiner, J., J. Zasada, P.R. Newton, and M. Newton. 1991. Salmonberry clonal and population structure: The basis for a persistent cover. *Ecology* 72:609–618.
- Thevathasan, N.V., P.E. Reynolds, R. Kuessner, and W.F. Bell. 2000. Effects of controlled weed densities and soil types on soil nitrate accumulation, spruce growth and weed growth. *Forest Ecology and Management* 133:135–144.
- Tuchman, E. T. and M.H. Brookes. 1996. The Northwest Forest Plan: A report to the President and Congress. U.S. Department of Agriculture, Office Forest Economics Assistance, Portland, Oregon.
- U.S. Department of Agriculture (USDA) Forest Service 2001. Fire Effects Information System. Rocky Mountain Research Station, Ogden, Utah. URL: www.fs.fed.us/database/feis
- Vogt, K.A., E. Moore, S. Gower, D. Vogt, D. Sprugel, and C. Grier. 1989. Productivity of upper slope forests in the Pacific Northwest. In *Maintaining the long-term productivity of Pacific Northwest ecosystems*. Timber Press, Portland, Oregon. pp. 137–163.
- Zabowski, D., B. Java, G. Scherer, R.L. Everett, and R. Ottmar. 2000. Timber harvesting residue treatments. Part 1. Responses of conifer seedlings, soils and microclimate. *Forest Ecology and Management* 126:25–34.
- Zar, J.H. 1999. Biostatistical analysis. 4th edition. Prentice Hall, Upper Saddle River, N.J.

Test Your Knowledge . . .

Effects of post-harvest treatment on high-elevation forests in the North Cascade Range, Washington

How well can you recall some of the main messages in the preceding research report?

Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. *Epilobium angustifolium* (fireweed) is a very competitive understorey species on high-elevation sites following disturbance. What gives this species this competitive advantage?
 - A) It spreads advantageously through the use of rhizomes
 - B) It spreads through the production of abundant seed
 - C) It is both a rhizomatous and wind-dispersed colonizer

2. *Rubus* species are also early colonizers on high-elevation sites and usually initiate development from buried seeds. How long can these seeds remain viable in these high-elevation seed banks?
 - A) 10 years
 - B) 50 years
 - C) 100 years

3. Because of the prevalence of regeneration problems, the research results from this study appear to indicate that, for timber production, some form of alternative harvesting system (through partial cutting, shelterwood, and green tree retention), which leaves partial tree cover including advanced regeneration, can improve regeneration and growth of shade-tolerant species in these high-elevation forests.
 - A) True
 - B) False

ANSWERS

1. C 2. C 3. A