RESEARCH ARTICLE

Effects of thinning paper birch on conifer productivity and understory plant diversity

Karen E. Baleshta*, Suzanne W. Simard and W. Jean Roach

*Forest Research Consultant, 135 Battle Street, Kamloops, BC V2C2L1, Canada; Department of Forest Sciences, Faculty of Forestry, University of British Columbia, 3601-2424 Main Mall, Vancouver, BC, V6T 1Z4 Canada; *Skyline Forestry Consultants Ltd., 843 Arlington Court, Kamloops, BC, V2B 8T5 Canada

(Received 6 September 2014; accepted 2 May 2015)

Naturally regenerated paper birch (Betula papyrifera Marsh.) is commonly removed from juvenile interior Douglas-fir (Pseudotsuga menziesii var. glauca [Beissn.] Franco) plantations in southern interior British Columbia, Canada, to increase conifer productivity and create a free-growing stand; however, this practice is expensive and contentious because of possible negative ecological impacts. One solution is to retain an optimal density of birch where growth gains of understory Douglas-fir are balanced against losses to Armillaria ostoyae (Romagn.) Herink and understory plant species diversity. We sought to find this optimal density by comparing four evenly applied birch density reduction treatments (0, 400, 1111, and 4444 retained birch stems ha\(^{-1}\)) and an unthinned control (>7300 retained birch stems ha\(^{-1}\)). The mortality rate of Douglas-fir due to Armillaria root disease increased non-significantly with thinning intensity. Mean diameter increment of surviving Douglas-fir improved the most where birch was completely removed, with little variation among intermediate thinning treatments. Height growth was unaffected by the thinning treatments. Diversity of cryptogams was significantly greater in the control than where all birch was removed. We suggest that the treatment with 4444 retained birch stems ha\(^{-1}\) provides the best balance for improving Douglas-fir growth while minimizing risk of increased Armillaria root disease and reduced understory plant diversity in young mixed stands.

Keywords: Douglas-fir; paper birch; competition; productivity; Armillaria; thinning

Introduction

Mixed stands of conifers and broadleaves comprise 35% of the productive forest land base in British Columbia (Comeau et al. 1996) and are a natural and common part of the landscape in the highly productive cedar-hemlock and Douglas-fir interior wet-belt forests (Meidinger & Pojar 1991). Paper birch (Betula papyrifera Marsh.) is the most widespread broadleaf species, and its pioneer silvical characteristics, including prolific seeding, juvenile height growth that exceeds that of all associated conifers except western larch (Larix occidentalis Nutt.), and nutrient acquisition strategies, enable it to dominate seral stands at densities as high as 20,000 stems ha\(^{-1}\) (Simard & Vyse 1992, 2006), resulting in mixed stands with variable vertical and spatial structure (Peterson et al. 1997). During the early successional phase, broadleaves interact with conifers with a complexity of competitive and facilitative behaviors, but their ability to pre-empt light can reduce juvenile conifer growth rates (Comeau et al. 2003; Simard & Vyse 2006).

There is an opportunity to influence productivity of commercially valuable conifers such as Douglas-fir by adjusting community composition, or the ecosystem’s stable state, through tending of juvenile stands (Holling 1973; Young et al. 2001). With this objective, paper birch and other broadleaf trees are commonly removed from mixed conifer/broadleaf stands 5–15 years after establishment (Comeau et al. 2000; Fahlvik et al. 2005; Wallrup et al. 2006; Härkönen et al. 2008; Fahlvik et al. 2011). This practice is promoted by forest policy in British Columbia, where “free-to-grow” standards require that select conifer species are competition-free, healthy and growing at a minimum density before the forest companies are relieved of their reforestation obligations to the Province (British Columbia Ministry of Forests 2000).

Complete rather than partial removal of broadleaves from mixed conifer plantations has become a standard practice for meeting free-to-grow requirements in British Columbia because it minimizes risk to forest companies of failure, thus reducing long-term costs (Newsome et al. 2012; Coates & Lilles 2013). Studies in British Columbia have reported on responses of various conifer species to complete paper birch removal (Simard & Heineman 1996; Simard et al. 2001), and spruce responses to partial removal of paper birch (Simard & Hannam 2000; Hawkins et al. 2012), but the effects of partial removal of paper birch on Douglas-fir in southern interior British Columbia have not been addressed.
Although high densities of paper birch can negatively impact conifer growth (Simard & Hannam 2000; Comeau et al. 2003), retrospective neighborhood studies show that low to moderate densities have small and variable effects (Simard et al. 2004). In retrospective studies of 10–15-year-old stands, neighborhood densities of up to 2500 stems ha\(^{-1}\) paper birch appeared to have little negative effect on growth of Douglas-fir (Simard 1990; Simard et al. 2001). Recent research suggests yields may be even greater in mixed species stands than in pure stands (Man & Lieffers 1999a; Kelty 2006; Hawkins et al. 2012). Numerous studies have found facilitative effects of broadleaf trees in mixed stands, including reduced frost damage to understory conifers (Man & Lieffers 1999b; Comeau et al. 2009; Filipescu & Comeau 2011), improved soil productivity through inputs of nutrient rich litter (Brockley & Sanborn 2003), provision of habitat for ungulates and birds (Bunnell & Kremsater 1990; Aitken et al. 2002), and reduced insect damage to conifers (Su et al. 1996; Griess & Knoke 2011). In addition, plant community diversity differs among broadleaf, conifer and mixed stands, with consequences for species interactions and ecosystem processes (Legare et al. 2002; Hart & Chen 2008; Chavez & MacDonald 2012). Intensive forest management has been described as a major contributor to the loss of species diversity (Mosquin et al. 1995; May 1998).

Along with their other benefits, broadleaf trees restrict spread of diseases such as Armillaria root disease (Morrison et al. 1988; Woods 1994; Gerlach et al. 1997). Armillaria root disease is pervasive in forest soils and associated with a wide range of tree species worldwide (Baumgartner et al. 2011). It is common and damaging to conifers across Canada, with growth losses of up to 58% measured at mid-rotation (Cruickshank 2011). In wet-belt forests in interior British Columbia, Douglas-fir is highly susceptible to infection by Armillaria ostoyae (Romagn.) Herink and can suffer significant mortality (Morrison & Pellow 1994). Removal of paper birch may increase A. ostoyae incidence in conifer plantations either because of increased inoculum provided in new stumps on the site or reduced beneficial effects of birch; however, the amount of birch that needs to be retained to reduce conifer mortality losses is unknown.

The negative consequences of broadleaf tree removal have the potential to destabilize ecosystems, especially when applied at a large scale and under increasing climate stress. Signs of destabilization have already been reported in recent studies showing substantial conifer mortality losses to insect and disease infestations (Woods & Bergerud 2008; Heineman et al. 2010), with even greater losses projected as climate changes, rendering weeded “free-to-grow” mixed stands below acceptable stocking level. In response to this, we hypothesize that the health, diversity, productivity, and stability of these young stands could be conserved with modest reductions in birch density that still achieve the goal of releasing conifers such as interior Douglas-fir from deleterious competition. As such, there is a need to identify threshold densities of paper birch at which positive and negative interactions with conifers are hopefully balanced and the stability of the forest is conserved.

Our study takes an experimental approach toward identifying broadleaf density thresholds by manipulating mixed conifer/broadleaf stands to create a range of paper birch densities, and examining responses to the treatments. The primary objectives were to determine the effects of various levels of paper birch density reduction on (1) understory Douglas-fir growth and mortality caused by A. ostoyae and (2) plant community diversity. We also measured birch re-sprouting and the percentage transmittance of light to the understory following treatment.

Materials and methods

Study sites

This study was conducted in four 10- to 15-year-old interior Douglas-fir plantations in the ICHmw3 (Thompson Moist Warm Interior Cedar-Hemlock) and IDFmw2 (Thompson Moist Warm Interior Douglas-fir) biogeoclimatic variants in the Adams River drainage of southern interior British Columbia (Lloyd et al. 1990). The ICHmw3 variant has a continental climate with cool, wet winters, and warm, moderately dry summers. Mean annual precipitation range between 431 and 874 mm and mean annual temperature between 3.7\(^{\circ}\)C and 6.9\(^{\circ}\)C (Lloyd et al. 1990). The IDFmw2 variant is situated below the ICHmw3 and is warmer and drier with cool winters, moderate snowfall, and warm, dry summers. Mean annual precipitation range between 487 and 551 mm and mean annual temperature between 4.2\(^{\circ}\)C and 7.6\(^{\circ}\)C (Lloyd et al. 1990). The study sites range between 550 and 940 m in elevation, slope gradients are 30–40%, soil textures are silt loam, moisture regimes are mesic, and physiography is uniform (Table 1).

The four sites were clear-cut, mechanically site prepared, and planted with one-year-old interior Douglas-fir seedlings between the years 1985 and 1988. Birch thinning treatments were applied in 1999, when all sites were dominated by mixed stands of Douglas-fir and naturally regenerated paper birch. The Douglas-fir averaged about 4 m in height with average diameters of 4 cm. Pre-treatment birch densities ranged between 7300 and 19,400 stems ha\(^{-1}\) across the four sites.

In addition to the planted Douglas-fir, there were minor amounts of naturally regenerated western redcedar (Thuja plicata Donn ex (Raf.),) western white pine (Pinus monticola Dougl. ex D. Don in Lamb), hybrid spruce (Picea engelmannii Parry ex Engelm. × Picea glauca (Moench) Voss), western hemlock (Tsuga
Table 1. Site characteristics.

| Characteristics               | Gold creek 1 | Gold creek 2 | Momich river | Burton creek |
|-------------------------------|--------------|--------------|--------------|--------------|
| Latitude                       | 51:00 N      | 51:00 N      | 51:20 N      | 51:31 N      |
| Longitude                      | 119:35 W     | 119:35 W     | 119:15 W     | 119:35 W     |
| Site history\(^a\)              | L 1985       | L 1985       | L 1985       | L 1982       |
|                               | M/B 1987     | M/B 1987     | B 1987       | B 1983       |
|                               | P 1988       | P 1988       | P 1988       | P 1985       |
| BEC\(^b\) variant              | IDFmw2       | IDFmw2       | ICHmw3       | ICHmw3       |
| Douglas-fir density (stems ha\(^{-1}\)) | 1387         | 1538         | 1109         | 724          |
| Initial paper birch density (stems ha\(^{-1}\)) | 10,976       | 19,407       | 14,327       | 7311         |
| Site index (m)\(^c\)           | 29           | 31           | 27           | 22           |
| Elevation (m)                  | 940          | 890          | 550          | 900          |
| Slope (%)                      | 30           | 30           | 40           | 35           |
| Aspect                         | W            | W            | N            | NE           |
| Soil texture                   | SiL          | SiL          | SiL          | SiL          |

\(^a\) (year) = year logged; M/B (year) = year mechanically site prepared and broadcast burned; P (year) = year planted.
\(^b\) BEC = biogeoclimatic ecosystem classification; hierarchical ecological classification system used by the British Columbia Ministry of Forests, Lands and Natural Resource Operations as a method to classify and manage forest and range land sites on an ecosystem-specific basis subdivided first by zone, second by subzone and third by variant. The BEC system incorporates the synthesis of climate, vegetation and soils data and was developed from the biogeoclimatic system studies of Dr V.J. Krajina and his students at the University of British Columbia (Krajina 1969; Watts 1983; Pajar et al. 1987). For further information, see also: https://www.for.gov.bc.ca/hre/becweb/system/how/index.html.
\(^c\) Site index (SI): potential tree height (m) at 50 years breast height age (Thrower and Goudie 1992).

**Experimental design and treatments**

Five birch density thinning treatments were replicated four times in a randomized block design, where site location was used as the blocking factor. The five treatments represented a gradient in paper birch density, decreasing from the control (>7300 stems ha\(^{-1}\)) to 4444 (light thinning), 1111 (moderate thinning), 400 (heavy thinning), and 0 (complete removal) stems ha\(^{-1}\) paper birch. Douglas-fir density was not manipulated and averaged 1190 stems ha\(^{-1}\). Treatment plots were 0.25 ha (50 × 50 m) in size, and included a central 0.09 ha (30 × 30 m) measurement plot with a 10-m surrounding buffer. Paper birch trees were selected for retention based on four criteria: (1) dominant or co-dominant crown class; (2) uniform spacing relative to other paper birch; (3) single, straight, healthy stem; and (4) seed-origin. The paper birch thinning treatments were applied in early-July 1999 using chainsaws to cut the birch stems as close to the ground as safely possible.

**Douglas-fir survival and growth measurements**

In June 1999, prior to treatment, stem diameter (measured at a height of 1.3 m; DBH) and height were measured for all Douglas-fir trees within the measurement plots. In late-summer/early-fall of 1999, 2001, and 2004, each Douglas-fir tree was evaluated for survival, and live trees were measured for DBH (cm), height (m), crown diameter (m), and height to base of live crown (m). Based on these measurements, height:diameter ratio (HDR), stem volume (m\(^3\)), canopy volume (m\(^3\)), five-year diameter increment (cm), and five-year height increment (m) were calculated. Data from the 1999 and 2001 re-measurements are presented in Baleshta et al. (2005). Stem volume was calculated using the formula for a cone (representing stem volume from top height to 1.3 m from the base) plus the formula for a cylinder (representing the stem volume from 0.3 to 1.3 m above the base). Canopy volume was calculated using the crown diameter and crown length (tree height minus height to base of live crown) applied to the formula for a cone (Mawson et al. 1976). Incidence of *A. ostoyae* on individual Douglas-fir was recorded where they were either dead or symptomatic (i.e. with chlorotic or red
foliage; stunted or sparse foliage; basal resinosis on the bark surface; *A. ostoyae* fruiting bodies on or near the sapling stem; and/or creamy-white mycelial fans in the bark of the lower stem; Morrison et al. 1991). Although aboveground symptoms underestimate belowground infection rates (Morrison et al. 2000), we could not excavate root systems to quantify this because it would compromise the long-term viability of the experiment.

**Paper birch sprouting and ingress**

Paper birch sprouts were assessed in summer 2005 (five growing seasons after birch reduction treatments). The five birch thinning treatment plots at each of the four sites were divided into nine 10 × 10 m grid cells. From these, three cells were randomly selected, and within each cell the paper birch stump closest to the center of the cell was used as the center of a circular 1.78 m radius (10 m²) measurement plot. In the control treatment, the closest live birch to the middle of the cells indicated the cell plot center. The average sprout length, the average number of sprouts per cut stump, and the proportion of sprouts in each vigor class were calculated for each treatment. Birch stems that established after the thinning treatments were evaluated for density (stems ha⁻¹), length (cm) and vigor (dead, moribund, poor, moderate, or good).

**Plant community assessments**

Plant community assessments were carried out in the summer of 2005 in the cells selected for the birch sprouting assessments. A total of 60 plant community plots were assessed (4 sites × 5 treatments per site × 3 plots per treatment). In each measurement plot, each plant species was identified and assigned to one of the following layers: (1) trees (conifer and broadleaf), (2) shrubs, (3) herbs (including forbs and grasses), and (4) cryptogams (forest floor mosses and lichens). Percent cover (between 0% and 100%) was estimated visually for each plant species, with the same observer making all estimates. Species richness was calculated as the number of species in each treatment. Species diversity was evaluated using [1] Shannon’s index (Shannon & Weaver 1949) and [2] Simpson’s index (Simpson 1949) as follows:

\[
H' = 1 - \sum [p_i \ln (p_i)]
\]

where \(H'\) is Shannon's index and \(p_i\) is the proportion of total density of species \(i\).

\[
D = 1 - \sum (p_i)^2
\]

where \(D\) is Simpson’s index and \(p_i\) is the proportion of total density of species \(i\).

**Light response**

Transmittance, the percentage of photosynthetic photon flux density (PPFD; 400–700 nm) reaching the understory, was measured using fisheye (hemispherical) photographs. One hemispherical canopy photograph was taken at each plot center under overcast skies in July 2005. The photographs were taken with a tripod-mounted Nikon 4500 equipped with a FC E-8 fisheye lens, mounted at a height of 1.3 m above the ground and facing north. Percent light transmittance was calculated using the Gap Light Analyzer imaging software (Frazer et al. 1999).

**Statistical analysis**

To examine differences among density treatments, data were analyzed using SAS for Windows (Version 8.2, SAS Institute Inc., Cary, NC, USA), based on a randomized block design. Descriptive statistics, histograms, and probability plots were examined to determine normality, and data transformations were used where data points were not normally distributed (Tabachnick & Fidell 1989). One-way analysis of variance was used to test for pre- and post-treatment differences. Vegetation data from the three subplots per treatment plot were pooled to produce a single value for each treatment plot. Means were considered different at \(\alpha = 0.05\). Where differences were found, treatment means for the Douglas-fir variables were separated using Waller and Duncan Bayes least significant difference (LSD) procedure (Duncan 1975), and for the vegetation variables treatment means were separated using the Bonferroni multiple comparison method. Variation among block means was also tested to ensure that the precision of the experiment was increased by use of a randomized block design versus completely random design. For most variables, we found that at least one block mean differed from the others at \(\alpha = 0.05\), justifying the use of blocking. Planned contrasts were used to compare Douglas-fir growth variables among different treatment combinations. Regression analysis was used to evaluate Douglas-fir *Armillaria*-caused mortality response to changes in paper birch density following thinning.

**Results**

**Douglas-fir survival and growth**

Five years post-treatment, Douglas-fir survival was high (97%) and did not differ significantly among treatments \((P > 0.05)\). Douglas-fir mortality due to *A. ostoyae* increased as thinning intensity increased; this trend was significant two years after treatment (Baleshta et al. 2005) but weakened by year five (Table E-1, Supplementary data). The annual mortality rate (based on a five-year period) was 0.22% yr⁻¹ where 4444 birch stems ha⁻¹ were retained and 0.86% yr⁻¹ in the
complete removal treatment. There was no indication of frost damage.

Any level of thinning improved the five-year mean diameter increment of Douglas-fir. Complete paper birch removal produced the largest mean diameter increment and the heavy (400 stems ha\(^{-1}\) birch retained) and light (4444 stems ha\(^{-1}\) birch retained) thinning surpassed the moderate (1111 stems ha\(^{-1}\) birch retained) thinning and the control \((P = 0.0046; \text{ Figure 1})\). There were no significant differences among thinning treatments in mean stem diameter, mean height increment or mean height five years post-treatment \((P > 0.05; \text{ Table 2})\). Planned contrasts were more sensitive at distinguishing Douglas-fir growth differences than the LSD procedure \((P = 0.0001; \text{ Table E-4, Supplementary data})\). This analysis showed that (1) complete broadleaf removal resulted in 15% higher diameter increment than the 400, 1111, and 4444 stems ha\(^{-1}\) birch retention treatments combined, and (2) no thinning (control) resulted in a 31% lower diameter increment than all thinning treatments combined. There were no significant differences in Douglas-fir crown length, crown width, crown volume, or individual stem volume among the five treatments \((P > 0.05; \text{ Table E-2, Supplementary data})\).

Height:diameter ratio (HDR) declined pre-treatment to Year 5 in all thinning treatments: from 117 to 105 in the control, from 94–99 to 85–90 in the partial removal treatments (light, moderate, and heavy thinning), and from 104 to 84 in the complete removal treatment. Five years post-treatment, Douglas-fir HDR was significantly higher in the control than any of the other four thinning treatments \((P = 0.0001; \text{ Table E-4, Supplementary data})\). Complete paper birch removal and heavy thinning produced significantly lower HDR than the moderate or light thinning treatments.

**Birch sprouting and ingress response**

Five years after thinning, the average number of live sprouts per stump was significantly greater in the complete removal (2.5) and heavy thinning (2.1) treatments than the light thinning (0.6). The moderate thinning treatment had intermediate sprout density and was not significantly different from the other removal treatments. There were no sprouts in the control. Average sprout height differed significantly between the broadcast treatment (171 cm) and the heavy thinning (128 cm), with the light and moderate thinning having intermediate heights that did not differ significantly from any of the other treatments. In comparison, the Douglas-fir average height ranged between 5.9 m (moderate thinning) and 6.8 m (light thinning) in 2004 \((\text{Table 2})\). Five years after thinning, the proportion of live sprouts that were of moderate to good vigor varied from 50% to 79%, with the highest proportion in the complete removal and heavy thinning treatments and the lowest proportion in the light thinning treatment. Over the five-year measurement period, 57% of sprouts survived in the complete removal and heavy thinning treatments, 46% survived in the moderate thinning treatment, and 20% survived in the light thinning treatment.

There was more birch ingress where all birch stems had been removed than the other thinning treatments (average 1800 versus 700 stems ha\(^{-1}\), respectively) and no ingress in the control. Over the measurement period, 5% of the newly established birch died in the complete removal treatment and 12% died in the other removal treatments. The new stems were tallest in the complete removal treatment (average 229 cm) and shortest in heavy thinning treatment (average 176 cm). In Year 5, the proportion of new birch that was of moderate or good vigor declined from 90% in the complete removal treatment, to 71% in the heavy and moderate thinning treatments, and 38% in the light thinning treatment.

**Plant community response**

A total of 85 species of vascular plants were identified at the study sites, including 5 species of conifers, 3 species of broadleaves, 27 species of shrubs, and 50 species of herbs. Diversity of cryptogams (ground mosses and lichens) differed significantly among treatments \((P = 0.0067\) for Shannon's index; \(P = 0.0124\) for Simpson's index; \(\text{Table 3}\)) with the highest diversity in the control (mean Shannon's index 0.473) and the lowest diversity in the complete broadleaf removal treatment (mean Shannon's index 0.177). Diversity, species richness, and mean percent cover of shrubs or herbs did not differ among treatments \((P > 0.05)\). Cover of broadleaf trees decreased from 73% in the control to 14% in the complete removal treatment.

![Figure 1. Douglas-fir mean diameter increment (cm) in the birch thinning density treatments in 2000 and 2004. Means with different letters are significantly different in 2004 (\(P = 0.0046\)). The standard error of the treatment mean is ±square root MSE/square root "n", where \(n = 4\) and MSE is the mean square error.](image-url)
Understory light availability
Light transmittance did not differ significantly among treatments ($P > 0.05$), but light tended to increase with thinning intensity. Transmittance values ranged from approximately 15% to 25% (Figure E-1, Supplementary data).

Discussion
Optimal paper birch density
The optimal paper birch density at which conifer productivity, mortality losses due to *A. ostoyae* and vegetation biodiversity changes were balanced on mesic IDFmw2 and ICHmw3 sites was 4444 stems ha$^{-1}$ (Figure 2). At that threshold density, Douglas-fir diameter growth rate and sturdiness were improved, losses to *A. ostoyae* were minimized, and understory plant diversity was not reduced. Reducing birch density below 4444 stems ha$^{-1}$ did not further improve Douglas-fir diameter growth until all birch was removed, and even then, additional growth improvements were small and total diameter, height growth, total height, and stem volume still were no greater than in the control. As emphasized in other studies, competition thresholds are site- and age-specific (Simard & Sachs 2004; Newsome et al. 2010). We stress that results may vary in other situations, including ecosystems where the competitive ability of birch, the height differential between birch and Douglas-fir, the stand age, or the inoculum potential of *Armillaria* differs.

Survival response of Douglas-fir
Excellent survival rates (97%) of Douglas-fir at five years regardless of paper birch thinning indicates complete removal of paper birch, as dictated by current “free-to-grow” policy in British Columbia, is not justified for improving conifer survival on our sites, even though pre-treatment birch densities were substantial (7300–19,400 stems ha$^{-1}$). These results agree with Simard et al. (2001), who found no difference in five-year survival of juvenile Douglas-fir where it was growing in mixture with untreated birch compared to where all birch was removed. Competition from paper birch did not directly cause any mortality among the Douglas-fir trees in our study or in other similarly aged Douglas-fir-paper birch mixtures (Simard & Heineman 1996; Simard et al. 2001).

Table 2. Comparison of means, standard error of the treatment means (SE) and $P$ values of Douglas-fir growth variables among treatments. Treatment means are significantly different at $\alpha = 0.05$.

| Growth variable      | Treatment (no. of birch stems ha$^{-1}$ retained) | 0   | 400  | 1111 | 4444 | Control$^b$ | SE$^a$ | $P$ value |
|----------------------|-----------------------------------------------|-----|------|------|------|-------------|-------|----------|
| Stem diameter (cm)   | 1999                                         | 3.7 | 4.1  | 3.6  | 4.5  | 3.6         | 0.39  | 0.4831   |
|                      | 2004                                         | 7.5 | 7.5  | 6.6  | 7.7  | 6.2         | 0.52  | 0.2553   |
| Height (m)           | 1999                                         | 3.7 | 3.9  | 3.7  | 4.3  | 3.7         | 0.25  | 0.4000   |
|                      | 2004                                         | 6.1 | 6.2  | 5.9  | 6.8  | 6.0         | 0.42  | 0.5554   |
| Mean height increment (m) | Year 1 | 0.42 | 0.44 | 0.39 | 0.50 | 0.50        | 0.05  | 0.3799   |
|                      | Year 5                                        | 2.39 | 2.34 | 2.18 | 2.54 | 2.25        | 0.18  | 0.6861   |

$^a$Standard error of the treatment mean is ±(square root MSE/square root $n$), where $n = 4$ and MSE is mean square error.

$^b$>7300 stems ha$^{-1}$.

Table 3. Comparison of means, standard error of the treatment means (SE) and $P$ values of species diversity using percent cover among treatments in 2005.

| Broadleaves | Shrubs | Herbs | Cryptogams |
|-------------|--------|-------|------------|
| Shannon’s index | 0.302  | 1.561 | 2.037 | 0.177b | 0.174 | 0.693 | 0.984 | 0.084b |
| 400         | 0.031  | 1.703 | 2.211 | 0.429a | 0.013 | 0.717 | 1.134 | 0.261ab |
| 1111        | 0.103  | 1.574 | 2.220 | 0.441a | 0.061 | 0.725 | 1.115 | 0.275a |
| 4444        | 0.249  | 1.569 | 2.084 | 0.337ab | 0.149 | 0.709 | 1.058 | 0.194ab |
| Control (>7300) | 0.198  | 1.337 | 1.906 | 0.473a | 0.135 | 0.597 | 1.030 | 0.297a |

| Broadleaves | Shrubs | Herbs | Cryptogams |
|-------------|--------|-------|------------|
| Simpson’s index |     |       |       |         |       |       |       |       |
| Treatment: (no. birch stems ha$^{-1}$ retained) | 0.097  | 0.147 | 0.197 | 0.049 | 0.061 | 0.044 | 0.087 | 0.038 |
| ANOVA results | 0.3325 | 0.5424 | 0.7793 | **0.0067** | 0.3655 | 0.2886 | 0.7395 | **0.0124** |

Note: $P$ values considered to be significant ($\alpha = 0.05$) are shown in bold. Means with different letters are significantly different.

$^a$Standard error of the treatment mean is ±(square root MSE/square root $n$), where $n = 4$ and MSE is mean square error.
The dominant mortality agent in our experiment was *A. ostoyae*, as found elsewhere in Douglas-fir plantations of southern interior British Columbia. Average mortality rates due to *Armillaria* were low on our sites (3% over a five-year period) compared with Simard et al. (2001) (11% over a five-year period) and Simard and Heineman (1996) (20% over a nine-year period). Incidence of *A. ostoyae* was significantly higher in the thinned treatments than the control after two years (Baleshta et al. 2005), but these differences decreased after five years. Other studies have also shown higher *A. ostoyae* mortality rates among Douglas-fir where paper birch was manually removed than where it was left untreated (Woods 1994; Simard & Heineman 1996; Simard et al. 2001), but as with our study, mortality rates due to the pathogen have eventually merged and slowed. Possible mechanisms explaining the initial increase in *A. ostoyae* following thinning of paper birch on our sites described by Baleshta et al. (2005) include: (1) thinning the broadleaf trees and leaving the cut stumps and root systems in the soil increase the potential of *A. ostoyae* to infect surrounding conifers; (2) root systems of paper birch are more resistant to *A. ostoyae* and may act like a barrier to the spread of *Armillaria* between neighboring conifers; (3) larger, faster growing susceptible conifers in the heavily thinned paper birch treatments may have more extensive root systems and are more likely to come into contact with adjacent infected roots; (4) reductions in paper birch density may have negatively affected the below ground microbial community (populations of *Pseudomonas flourescens*, a plant-growth promoting rhizobacterium with strains antagonistic to *A. ostoyae* in vitro, has been found to be four times as high in mixed stands of paper birch and Douglas-fir than pure Douglas-fir stands (Delong et al. 2002).

That mortality rates due to *A. ostoyae* were low in our study and were subsiding five years after treatment may be explained by the fact the Douglas-fir crop trees were close to the age when mortality rates typically start to decrease. Mortality usually begins at age 5–7 years, reaches its maximum at about age 12, then declines because of increased resistance by host trees and decomposition of inoculated stumps (Cleary et al. 2008).

Topography of the treatment sites may have played a role in the noticeable absence of frost damage to the Douglas-fir, as the experimental sites were located on hillsides, as opposed to valley bottoms where cold air can stagnate (Oke 1987).

**Growth response of Douglas-fir**

Further evidence that thinning paper birch was unnecessary on our sites was the lack of difference in Douglas-fir diameter, height or volume among the treatments five years after they were applied. Moreover, the 1 cm increase in five-year diameter increment with complete birch removal is likely of little practical significance. Although growth improvements sometimes have occurred later than five years post-treatment (Simard & Heineman 1996; Simard et al. 2001), these modest increases come at great financial cost. Economic analysis of silviculture treatments in mixedwood forests clearly shows that removal of broadleaves is a losing investment with such low growth responses (Hawkins et al. 2013).

Our finding that Douglas-fir height did not respond to reductions in overstory birch density supports numerous studies showing poor or slow height response to brushing (Lanner 1985; Wagner & Radosievich 1991; Simard & Heineman 1996; Simard et al. 2001). Height is only affected when competition levels are extreme (Bell et al. 2000; Simard & Hannam 2000; Wagner 2000; Newsome et al. 2008). Although the insensitivity of height to density is well established in the literature, free-to-grow standards are still designed on the expectation that height growth and hence productivity of conifers will improve with reduced broadleaf competition. These results emphasize that expectations of improved forest productivity through growth increases without survival improvements are not justified (Boateng et al. 2009).

When this study was initiated in 1999, the HDR of Douglas-fir in all treatments was >100, which Cremer et al. (1982) describes as high, i.e. the trees were “spindly”, likely reflecting low light availability to the Douglas-fir (Williams et al. 1999). A desirable HDR for Douglas-fir is 50–70 because of increased wind firmness and resistance to snow damage (Jull 2001). HDR values above 55 are commonly indicative of competitive stress (Opio et al. 2000), but ratios that are too low may reduce lumber recovery and wood quality due to strongly tapered stems. In our study, the reduction in HDR was likely beneficial for reducing susceptibility to breakage, abrasion, and snowpress. That HDR naturally decreased over time, including in the control, suggests that the trees are improving with time, but ratios were still high.
(HDR 84-105). Any level of thinning significantly improved HDR compared to the control, but there were small differences among the four thinning levels, indicating that the lightest removal treatment increased sturdiness almost as much as the heavier treatments.

Douglas-fir crowns did not expand in the first five years after the thinning treatments, which agrees with research in older Douglas-fir stands showing that in the first few growing seasons following thinning, release does not accelerate crown expansion, and can reduce crown growth (Reukema 1964). Tree species with low shade tolerance such as paper birch and lodgepole pine (Klinka et al. 2000) are more likely to expand in crown volume as space and light levels increase, compared to Douglas-fir which is moderately shade tolerant (Chen et al. 1996; Williams et al. 1999; Simard & Zimonic 2005).

Birch sprouting and ingress response
Density, height, and vigor of birch sprouts and ingress were maximized with complete removal of birch, which reflects the very low shade tolerance of paper birch. Others have found a similar trend of increasing size of paper birch sprouts with decreasing density of overstory paper birch (Comeau et al. 1999; Simard & Zimonic 2005). New sprouts and ingress provide forage for ungulates such as moose, which are common in our study areas, replacing the uncut birch growing out of their reach. However, moose have high requirements for hiding and thermal cover (Keystone Wildlife Research Ltd 2006), which are likely better provided in the unthinned and lightly thinned areas than more intensively thinned areas. As well, broadleaf or mixed forest stands have been identified as favored moose habitat (Vehviläinen & Koricheva 2006; Milligan & Koricheva 2013).

Plant community response
Five years after birch was thinned, the cryptogam layer (understory mosses and lichens) was the only functional vegetation group that differed among treatments. Cryptogam diversity was highest in the control, lowest where all birch was removed, and intermediate in the partial thinning treatments. The cryptogam diversity in the control may be considered a natural or baseline level, and its substantial reduction with the complete removal of paper birch likely indicates a change in structure and function of this functional group. Mosses and lichens are ecologically valuable for their roles in reducing soil erosion, nitrogen fixation, maintaining soil moisture, reducing soil temperature fluctuations, providing shelter for microfauna and nurseries for regenerating seedlings, and providing food for moose, deer, snails, slugs, moth caterpillars, mites, and termites (Quinby 1997; De Luna et al. 2003).

The lack of response in cover, diversity, and richness of herb and shrub functional groups may have been due to the similarity in understory light environments among treatments or an insufficient time period for plant community differences to develop. Understory vegetation is influenced by overstory composition and structure through modifications of light, water, soil and air temperature, and soil nutrients (Barbier et al. 2008). Results from across Canada show that plant species diversity tends to be higher under broadleaf stands than coniferous or mixed stands, and in some cases mixed stands have the highest diversity (Cavard et al. 2011). Conifer stands tend to be associated with bryophytes in the understory, broadleaf stands with vascular understory species, and mixed stands intermediate between pure conifer and pure broadleaf stands (Hart & Chen 2006).

In mixed stands similar to those in our study, however, complete removal of paper birch has rarely resulted in changes in cover, richness, or diversity of understory vascular plant communities (Simard & Heineman 1996; Simard et al. 2001), probably because resources are not limiting in the understory. The majority of studies from boreal and sub-boreal stands in British Columbia and Alberta, by contrast, have measured increases in understory vegetation cover after partial or complete removal of overstory broadleaves, likely because severe resource limitation in these climatically harsher environments was relieved (Powell & Bork 2006; Man et al. 2008; Kabzems et al. 2011).

In conclusion, our findings support our hypothesis that modest reductions in birch density can conserve health, diversity and productivity of young stands and still release Douglas-fir from competition. Retention of 4444 birch stems ha$^{-1}$ achieved these goals but, in British Columbia, will result in failure of these stands to meet current free-growing requirements, even though their productivity and survival rates are practically the same as open stands (0 or 400 birch stems ha$^{-1}$). Based on previous studies showing that disease risk is expected to increase with climate change (Sturrock et al. 2011), we suggest that free-to-grow standards be adjusted to focus more on the health, diversity, and stability of forests at larger scales rather than fast individual conifer growth for saw log production. With this broader-scale approach, the pressure to completely remove paper birch to meet coniferous free-to-grow administrative goals will decline and practitioners can then focus on selective treatments that ensure forest productivity while conserving the health and diversity of the whole forest ecosystem. This approach will also reduce the risk of adding stress to young forests already struggling to adapt to climate change, thus avoiding shifts toward less productive, diverse, and resilient stable states (Holling 1973; Hawkins & Dhar 2011).
Acknowledgments
We thank the British Columbia Ministry of Forests and Range, Forest Renewal British Columbia, Forest Investment Account, International Forest Products Limited – Adams Lake Lumber Division, and Science Council of British Columbia for supporting this project. We are grateful to Doug Baleshta, Clyde Fuoco, Bernie Warren, Barbara Zimonick, and Loyll Zimonick for assisting with the fieldwork.

Disclosure statement
No potential conflict of interest was reported by the authors.

Funding
We greatly appreciate the support and funding provided by Michael Murray, George Harper and Louise de Montigny of the BC Ministry of Forests, Lands and Natural Resources Operations during the final stages of writing the paper. This work was supported by the British Columbia Ministry of Forests and Range, Forest Renewal British Columbia, Forest Investment Account, International Forest Products Limited – Adams Lake Lumber Division, and Science Council of British Columbia. Funding for this research project does not imply endorsement of any statements or information contained herein.

Supplemental data
Supplemental data for this article can be accessed here.

References
Aitken KEH, Wiebe KL, Martin K. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. The Auk. 119:391–402.
Baleshta KE, Simard SW, Guy RD, Chanway CP. 2005. Reducing paper birch density increases Douglas-fir growth rate and Armillaria root disease incidence in southern interior British Columbia. For Ecol Manage. 208:1–13.
Barbier S, Bossolin F, Balandier P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. For Ecol Manage. 254:1–15.
Baumgartner K, Coetzee MPA, Hoffmeister D. 2011. Secrets of the subterranean pathosystem of Armillaria. Mol Plant Pathol. 12:515–534.
Bell FW, Ter-Mikaelian MT, Wagner RG. 2000. Relative competitiveness of nine early-successional boreal forest species associated with planted jack pine and black spruce seedlings. Can J For Res. 30:790–800.
Boateng JO, Heneman JL, Bedford L, Harper GJ, Linnell Nemec AF. 2009. Long-term effects of site preparation and postplanting vegetation control on Picea glauca survival, growth and predicted yield in boreal British Columbia. Scand J For Res. 24:111–129.
British Columbia Ministry of Forests. 2000. Establishment to free growing guidebook. Kamloops Forest Region, Rev. ed., Version 2.2. For. Prac. Br., B.C. Min. For. Victoria, BC: Forest Practices Code of British Columbia Guidebook.
Brockley RP, Sanborn P. 2003. Effects of Sitka alder on the growth and foliar nutrition of young lodgepole pine in the central interior of British Columbia. Can J For Res. 33:1761–1771.
Bunnell FL, Kremsater LL. 1990. Sustaining wildlife in managed forests. Northw Environ J. 6:243–269.
Cavard X, Macdonald SE, Bergeron Y, Chen HYH. 2011. Importance of mixedwoods for biodiversity conservation: evidence for understory plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. Environ Rev. 19:142–161.
Chavez V, Macdonald SE. 2012. Partitioning vascular understory diversity in mixedwood boreal forests: the importance of mixed canopies for diversity conservation. For Ecol Manage. 271:19–26.
Chen HYH, Klinka K, Kayahara GJ. 1996. Effects of light on growth, crown architecture, and specific leaf area for naturally established Pinus contorta var. latifolia and Pseudotsuga menziesii var. glauca saplings. Can J For Res. 26:1149–1157.
Cleary M, van der Kamp B, Morrison D. 2008. British Columbia’s interior forests: Armillaria root disease stand establishment decision aid. BC J Ecosyst Manage. 9:60–65.
Coates D, Lilles E. 2013. An evaluation of the main factors affecting yield differences between single- and mixed-species stands. BC J Ecosyst Manage. 14:122–130.
Comeau P, Wang J, Letchford T, Coopersmith D. 1999. Effects of spacing paper birch-mixedwood stands in central British Columbia FRBC Project HQ96423-RE (MOF EP 1193): Extent Note 29. Victoria (Canada). B.C. Min. For. Available from: https://www.for.gov.bc.ca/hfd/pubs/docs/en/en29.pdf
Comeau PG, Birig BS, Harper GJ. 2000. Conifer responses to brushing treatments: a summary of British Columbia data. Extent Note 41. Victoria (Canada). B.C. Min. For. Available from: http://www.for.gov.bc.ca/hfd/pubs/Docs/En/En41.pdf
Comeau PG, Filipescu CN, Kabzems R, DeLong C. 2009. Corrigendum to: growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern B.C. – 10 year results. For Ecol Manage. 257:1629–1636.
Comeau PG, Harper GJ, Blache ME, Boateng JO, Thomas KD. 1996. Ecology and management of B.C. hardwoods. In: Workshop Proceedings; 1993 Dec 1–2; Richmond, BC. FRDA Rep 255.
Comeau PG, Wang JR, Letchford T. 2003. Influences of paper birch competition on growth of understory white spruce and subalpine fir following spacing. Can J For Res. 33:1962–1973.
Cremer KW, Borough CJ, McKinnell FH, Carter PR. 1982. Effects of stacking and thinning on wind damage in plantations. NZ J For Sci. 12:244–268.
Cruickshank MG. 2011. Yield reductions in spruce infected with Armillaria solidipes in the southern interior of British Columbia. Forest Pathol. 41:425–428.
De Luna E, Newton AE, Mishler BD. 2003. Bryophyta. Mosses. Version 25, March 2003. Available from: http://tolweb.org/Bryophyta/20599/2003.03.25
Delong R, Lewis KJ, Simard SW, Gibson S. 2002. Fluorescent pseudomonad population sizes beated from soils under pure birch, pure Douglas-fir and mixed forest stands and their antagonism toward Armillaria ostoyae in vitro. Can J For Res. 32:2146–2159.
Duncan DB. 1975. T-tests and intervals for comparisons suggested by the data. Biometrics 31:339–359.
Fahlvik N, Ageestam E, Ekkö PM, Lindén M. 2011. Development of single-storied mixtures of Norway spruce and birch in Southern Sweden. Scand J For Res. 26:36–45.
Fahlvik N, Ageestam E, Nilsson U, Nyström K. 2005. Simulating the influence of initial stand structure on the development of young mixtures of Norway spruce and birch. For Ecol Manage. 213:297–311.
Filipescu CN, Comeau PG. 2011. Influence of Populus tremuloides density on air and soil temperatures. Scand J For Res. 26:421–428.

Scandinavian Journal of Forest Research 707
Frazier GW, Canham CD, Lertzman KP. 1999. Gap light analyzer (GLA): imaging software to extract canopy structure and gap light transmittance indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999. Burnaby, BC/Millbrook, NY: Simon Fraser University/The Institute of Ecosystem Studies.

Gerlach J, Reich PB, Puettman K, Baker T. 1997. Species, diversity, and density affect tree seedling mortality from root rot fungi (Armillaria spp.), Can J For Res. 27:1509–1512.

Griess VC, Knolle T. 2011. Growth performance, windthrow, and insects: meta-analyses of parameters influencing mixed-species stands in boreal and northern temperate biomes. Can J For Res. 41:1141–1159.

Härkönen S, Miina J, Saksan T. 2008. Effect of cleaning methods in mixed pine-deciduous stands on moose damage to Scots pines in southern Finland. Scand J For Res. 23:491–500.

Hart SA, Chen HYH. 2006. Understory vegetation dynamics of North American boreal forests. Crit Rev Plant Sci. 25:381–397.

Hart SA, Chen HYH. 2008. Fire, logging and overstory composition affect understory abundance, diversity, and composition in boreal forest. Ecol Monogr. 78:123–140.

Hawkins CDB, Dhar A. 2011. Mixtures of broadleaves and conifers are ecologically and economically desired in an uncertain future changing climate. In: Muyss B, editor. Proceedings of the Conservation and Management of Forests for Sustainable Development: Where Science Meets Policy; 2011 Nov 23–24; Leuven (Belgium): Katholieke University Leuven, 20.

Hawkins CDB, Dhar A, Lange J. 2013. Vegetation management with glyphosate has little impact on understory species diversity or tree growth in a sub boreal spruce plantation – A case study. Plant Biosyst. 47:104–114.

Hawkins CDB, Dhar A, Rogers BJ. 2012. How much birch (Betula papyrifera) is too much for maximizing spruce (Picea glauca) growth; a case study in boreal plantation forests. J For Sci. 58:314–317.

Heineman JL, Sachs DL, Mather WJ, Simard SW. 2010. Investigating the influence of climate, site, location, and treatment factors on damage to young lodgepole pine in southern British Columbia. Can J For Res. 40:1109–1127.

Holling CS. 1973. Resilience and stability of ecological systems. Ann Rev Ecol Syst. 4:1–23.

Jull M. 2001. Wind damage and related risk factors for interior Douglas-fir leave trees in central BC. Available from: http://www.for.gov.bc.ca/HFD/library/documents/woodthrow.pdf

Kabzems RD, Harper G, Fielder P. 2011. Growing space management in boreal mixedwood forests: 11 year results. West J Appl For. 26:82–89.

Kelty MJ. 2006. The role of species mixtures in plantation forestry. For Ecol Manage. 233:195–204.

Keystone Wildlife Research Ltd. 2006. Identification and management of moose winter habitat in the Cariboo Region: literature review and mapping pilot study. Prepared for: B.C. Min. Environ., Williams Lake, B.C. Available from: http://www.env.gov.bc.ca/cariboo/env_stewardship/ecosystems/reports/id_mgmnt_moose_winter_habitat_car_reg.pdf

Klinka K, Worrall J, Skoda L, Varga, P. 2000. The distribution and synopsis of ecological and silvicultural characteristics of tree species in British Columbia’s forests. Coquitlam (BC): Canadian Cartographics Ltd.

Krajina VJ. 1969. Ecology of forest trees in British Columbia. Ecol West North Am. 2:1–146.

Lanner RL. 1985. On the sensitivity of height growth to spacing. For Ecol Manage. 13:143–148.

Legare S, Bergeron Y, Pare D. 2002. Influences of forest composition on understory cover of boreal mixedwood forests of western Quebec. Silva Fenn. 36:353–366.

Lloyd D, Angove K, Hope G, Thompson C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region: Land Manage. Handb. No. 23. Victoria (Canada): Res. Br., B.C. Min. For. Available from: https://www.for.gov.bc.ca/hfd/pubs/docs/Lmh/Lmh23.pdf.

Man CD, Comeau PG, Pitt DG. 2008. Competitive effects of woody and herbaceous vegetation in a young boreal mixedwood stand. Can J For Res. 38:1817–1828.

Man R, Liefers VJ. 1999a. Are mixtures of aspen and white spruce more productive than single species stands? For Chron. 75:505–513.

Man R, Liefers VJ. 1999b. Effects of shelterwood and site preparation on microclimate and establishment of white spruce seedlings in a boreal mixedwood forest. For Chron. 75:837–844.

Mawson JC, Thomas JW, DeGraaf RM. 1976. PROGRAM HTVOL - the determination of tree crown volume by layers. Res. Pap. NE-354. Upper Darby (PA): U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 9p. Available from: www.fs.fed.us/ne/newtown_squares/pubs/research_papers/ pdfs/scanned/OCR/ne_rp354.pdf.

May E. 1998. At the cutting edge: the crisis in Canada’s forests. Toronto (ON): Key Porter Books.

Meidinger D, Pajar J. 1991. Ecosystems of British Columbia: Special Report Series 6. Victoria (Canada): Res. Br., B.C. Min. For. Available from: https://www.for.gov.bc.ca/hfd/pubs/Docs/Srs/Srs06.pdf.

Milligan HT, Koricheva J. 2013. Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. J Anim Ecol. 82:739–748.

Morrison D, Merler H, Norris D. 1991. Detection, recognition and management of Armillaria and Phellinus root diseases in the southern interior of British Columbia: FRDA Report No. 179. Victoria (Canada): For. Can. and B.C. Min. For. Available from: https://www.for.gov.bc.ca/hfd/pubs/Docs/Frr/Frr179.pdf.

Morrison DJ, Pellow KW. 1994. Development of Armillaria root disease in a 25-year-old Douglas-fir plantation. In: Johansson M, Stenlid J, editors. Proceedings of the 8th International Conference on Root and Butt Rots; 1993 Aug; Wik, Sweden and Haikko, Finland: Swedish University of Agricultural Sciences, Uppsala; p. 560–571.

Morrison DJ, Pellow KW, Norris DJ, Limnell Nemec AF. 2000. Visible versus actual incidence of Armillaria root disease in juvenile coniferous stands in the southern interior of British Columbia. Can J For Res. 30:405–414.

Morrison DJ, Wallis GS, Weir LC. 1988. Control of Armillaria and Phellinus root diseases: 20-year results from the Skimikin stump removal experiment. Can. For. Serv. Pac. For. Cent., Inf. Rep. BC-X-302.

Mosquín T, Whitney PG, McAllister DE. 1995. Canada’s Biodiversity. Ottawa (ON): Canadian Museum of Nature.

Newsome TA, Heineman JL, Limnell Nemec AF. 2010. A comparison of lodgepole pine responses to varying levels of trembling aspen removal in two dry south-central British Columbia ecosystems. For Ecol Manage. 259:1170–1180.

Newsome TA, Heineman JL, Limnell Nemec AF. 2012. Identifying and characterizing important trembling aspen competitors with juvenile lodgepole pine in three south-central
Scandinavian Journal of Forest Research 709

Simard SW, Vyse A. 1992. Ecology and management of paper birch and black cottonwood in southern British Columbia: Land Manage. Report No. 75. Victoria (Canada): B.C. Min. For. Available from: https://www.for.gov.bc.ca/hfd/pubs/Docs/Mr/Lmr/Lmrr075.pdf.

Simard SW, Vyse A. 2006. Trade-offs between competition and facilitation: a case study of vegetation management in the Interior Cedar-Hemlock forests of southern British Columbia. Can J For Res. 36:2486–2496.

Simard SW, Zimonick BJ. 2005. Neighborhood size effects on mortality, growth and crown morphology of paper birch. For Ecol Manage. 214:251–269.

Simpson EH. 1949. Measurement of diversity. Nature. 163: 688.

Sturrock RN, Frankel SJ, Brown AV, Hennon PE, Kliejunas JT, Lewis KL, Worrall JJ, Woods AJ. 2011. Climate change and forest diseases. Plant Pathol. 60:133–149.

Su Q, MacLean DA, Needham TD. 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. Can J For Res. 26:1620–1628.

Tabachnick BG, Fidell LS. 1989. Using Multivariate Statistics. 2nd ed. New York (NY): Harper and Row.

Thrower JS, Goudie JW. 1992. Development of height-age and site-index functions for even-aged interior Douglas-fir in British Columbia: Res. Note No. 109. Victoria (Canada): For. Sci. Res. Br., B.C. Min. For. For. 22 p. ISSN 0226-9368.

Vehviläinen H, Koricheva J. 1996. Moose and vole browsing patterns in experimentally assembled pure and mixed forests stands. Ecography. 29:497–506.

Wagner RG. 2000. Competition and critical-period thresholds for vegetation management decisions in young conifer stands. For Chron. 76:961–968.

Wagner RG, Radosевич SR. 1991. Neighborhood predictions of interspecific competition in young Douglas-fir plantations. Can J For Res. 21:821–828.

Wallrup E, Saetre P, Rydin H. 2006. Deciduous trees affect small-scale floristic diversity and tree regeneration in conifer forests. Scand J For Res. 21:399–404.

Watts SB, editor. 1983. Forestry handbook for British Columbia. 4th ed. Vancouver (Canada): The Forestry Undergraduate Society, Faculty of Forestry, University of British Columbia.

Williams H, Messier C, Kneeshaw DD. 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. Can J For Res. 29:222–231.

Woods A, Bergerud W. 2008. Are free-growing stands meeting timber productivity expectations in the Lakes Timber Supply Area? FREP Series #013. Victoria (Canada): For. Prac. Br., B.C. Min. For. Ran. Available from: https://www.for.gov.bc.ca/ftp/hfd/external/publish/frep/reports/FREP_Report_13.pdf.

Woods AJ. 1994. The behavior and impact of Armillaria ostoyae in mature stands and plantations in the Shuswap region of British Columbia [dissertation]. Vancouver (BC): University of British Columbia.

Young TP, Chase JM, Huddleston RT. 2001. Community succession and assembly comparing, contrasting and combining paradigms in the context of EcolNeal respiration. Ecological Res. 19:5–18.