

Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest III. Growth of crop trees and coniferous stand structure

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Abstract

Enhanced growth of crop trees and development of late-seral structural characteristics in second-growth stands in temperate and boreal forest zones could be achieved by silvicultural practices such as pre-commercial thinning (PCT). This study was designed to test the hypotheses that large-scale stand thinning, at a 15-year period after PCT, would enhance: (i) productivity and structural features (crown volume, diameter, height, and volume growth of lodgepole pine (*Pinus contorta*) crop trees); and (ii) coniferous stand structure (abundance, species diversity, and structural diversity of coniferous tree layers). Replicate study areas were located near Penticton, Kamloops, and Prince George in south-central British Columbia, Canada. Each study area had three stands thinned to densities of ~500 stems/ha (low), ~1000 stems/ha (medium), and ~2000 stems/ha (high), with an unthinned young pine and old-growth pine stand for comparison.

An overall analysis of tree growth in thinned stands, across these regional replicates, indicated that lodgepole pine grew significantly faster in mean diameter in the low- than either of the medium- or high-density stands. There was no difference in mean height growth among stand densities over the 15-year period since PCT. Mean tree volume increment was significantly higher in the low-density than in the high-density stands. Mean stand volume increment (m^3/ha) was similar in the medium-density (108.53) and high-density (132.51) stands, both of which were significantly higher than the low-density stands (72.88). Mean crown volume of crop trees was significantly greater in the low-density (52.8 m^3) and medium-density (42.9 m^3) stands than in the high-density (27.8 m^3), unthinned (11.7 m^3), or old-growth stands (30.9 m^3 pine only). This measure of crown size was similar among pine trees in the low-density, medium-density, and all conifers (43.2 m^3) in the old-growth stands. Other measurements of crown architecture followed this same pattern. Mean densities of understory trees were similar among stands for height classes up to 3 m. Mean species diversity and structural diversity of coniferous tree layers were highest in the low- and medium-density stands than in other treatment stands. Our results support the hypotheses that PCT enhances productivity (diameter and volume growth, but not height growth) and structural features (crown architecture) of young lodgepole pine, as well as diversity of coniferous tree layers in thinned stands. Accelerated development of some structural features of late-seral forest appeared in our young managed stands.

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1. Introduction

A major objective of enlightened forest management in temperate and boreal ecological zones is acceleration of forest succession to develop late-seral structural characteristics in second-growth stands (McComb et al., 1993; Carey and Curtis,

1996; Hayes et al., 1997; Carey, 2000; Sullivan et al., 2001). Old-growth structural attributes include large dominant trees with substantial crowns, a diverse tree community with smaller shade-tolerant trees, multilayered canopies, snags, an abundance of coarse woody debris, canopy gaps, and understory patchiness with some herb and shrub development (Franklin et al., 1981; Franklin and Spies, 1991; Kneeshaw and Burton, 1998; Wells et al., 1998). This approach is designed to meet the biodiversity goals of a range of successional stages and wildlife diversities across forest landscapes dominated by young

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regenerating stands that have developed after clearcut harvesting and wildfire. Such stands are structurally simple, usually with a single canopy layer, few tree species, sparse understory vegetation, and a variable abundance of standing or fallen dead trees (Carey and Johnson, 1995; Hayes et al., 1997).

As discussed by Koch (1996a) and Sullivan et al. (2001), early seral (1–30 years old) lodgepole pine (*Pinus contorta*) is the dominant coniferous tree species ranging across a vast area (several million hectares) of the inland Pacific Northwest of North America. Lodgepole pine has perhaps the greatest potential to respond to various silvicultural practices designed to diversify structural heterogeneity and growth rates of crop trees within stands (Johnstone, 1985; McComb et al., 1993; Koch, 1996b; Hayes et al., 1997; Cochran and Dahms, 1998). Innovative silvicultural strategies in lodgepole pine and other coniferous tree species include conventional pre-commercial thinning (PCT), sometimes over a range of stand densities (Schmidt and Seidel, 1988; Sullivan et al., 2001; Homyack et al., 2004) and variable-density thinning (Carey and Johnson, 1995; Carey et al., 1999; Sullivan et al., 2002). The goal of these silvicultural interventions in young stands is the development of biocomplexity and late-seral structural features over relatively short time periods (Carey and Wilson, 2001). A critical caveat of this approach is that the affinity of those wildlife species occurring in late-seral forests is more likely attributable to structural (ecological) characteristics than to age of the forest (Thomas et al., 1990; Hayes et al., 1997).

The influence of PCT on the development of habitat attributes such as understory composition, abundance, and structural diversity has tended to dominate in much of the forest-wildlife and biodiversity literature. However, it is the responses of crop trees to PCT, in terms of diameter and height growth, as well as crown architecture that are driving these habitat attributes. PCT increases stem diameters (Harrington and Reukema, 1983; Cochran and Barrett, 1993; Cochran and Dahms, 1998; Brisette et al., 1999; Ffolliott et al., 2000; Sullivan et al., 2001; Pothier, 2002; Homyack et al., 2004). PCT alone, or in combination with vegetation management treatments, increases crown volume or size (McCormack and Lemin, 1998; Schmidt and Seidel, 1988; Brisette et al., 1999; Lindgren and Sullivan, 2001; Sullivan et al., 2001; Homyack et al., 2004). Crowns are the production factory of a tree, and hence they reflect the degree of vigor and growth (Schmidt and Seidel, 1988). The structural attributes of crown architecture have considerable relevance to the nesting, foraging, and cover (both hiding and thermal) requirements of a wide variety of wildlife species (Hayes et al., 1997; Spies, 1998; Suzuki and Hayes, 2003).

A range of thinning densities or regimes is conducive to producing a range of wood products (Koch, 1996b; Barbour et al., 1997; Lippke and Fretwell, 1997; Sullivan et al., 2001). Appropriately managed coniferous stands, particularly lodgepole pine and Douglas-fir (*Pseudotsuga menziesii*), could be managed for both structural diversity and a range of wood products. For example, heavily thinned stands may have reduced total wood volume, but can produce large-diameter timber and quality products (Jozsa and Middleton, 1994;

Barbour et al., 1997). Higher density stands will produce much wood volume for the construction lumber market (Jozsa and Middleton, 1994).

A major question is: at what point in time, or successional development, do younger managed stands provide sufficient “structural complexity” and the consequent ecological functions of late-seral forests? Few, if any, studies have investigated the growth responses of crop trees and coniferous stand structure to PCT in young lodgepole pine forests at a spatial scale relevant to wildlife and over a relatively long-term (15 years since treatment) temporal scale. Thus, this study was designed to test the hypotheses that large-scale stand thinning to a wide range of densities, at a 15-year period after PCT, would enhance: (i) productivity and structural features (crown volume and dimensions, diameter, and height growth of crop trees (those dominant trees destined for harvest)); and (ii) coniferous stand structure (abundance, species diversity, and structural diversity of coniferous tree layers). This paper is one of several periodic publications reporting on long-term responses of understory vegetation (Lindgren et al., 2006), northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*) (Ransome et al., 2004), forest floor small mammals (Sullivan et al., 2005), and large mammalian herbivores (Sullivan et al., 2006) to these treatments.

2. Materials and methods

2.1. Study areas

There were five lodgepole pine stands located at each of three replicate study areas in south-central British Columbia, Canada: Penticton Creek, Kamloops, and Prince George. These areas were selected on the basis of having several thousand hectares of young lodgepole pine forest. Stands within these tracts of young forest had relatively uniform tree cover and comparable diameter, height, and density of lodgepole pine trees prior to PCT. Each replicate had four second-growth lodgepole pine stands (age range of 17–27 years); three of which were PCT to low (~500 stems/ha), medium (~1000 stems/ha) or high (~2000 stems/ha) density. The fourth stand was left unthinned. The second-growth stands had very few remnant trees and snags remaining from previous stands. There was also an old-growth lodgepole pine stand (age range 160–250 years) as part of the set of treatment stands at each study area.

The Penticton Creek study area was located 15 km northeast of Penticton (49°34'N; 119°27'W). All stands were located in the Interior Douglas-fir (IDF_{dk}) biogeoclimatic zone (Meidinger and Pojar, 1991). Elevation of stands ranged from 1340 to 1500 m. Topography in the area is hilly with sandy loam soil, southeast aspect, and an average slope of 10%. This area (several thousand ha) was burned by wildfire in 1970, salvage logged in 1971, and planted with lodgepole pine in 1972. Density of pine from natural regeneration ranged from 18,500 to 30,000 stems/ha. Dominant coniferous species in these stands included lodgepole pine with a minor component of Douglas-fir, Engelmann spruce (*Picea engelmannii*), and

Table 1
Characteristics of lodgepole pine stands at the Pentiction, Kamloops, and Prince George study areas, British Columbia

Study area and stand	Density ^a (no./ha)	Area (ha)	Mean age (year)	dbh (cm)				Height (m)	
				1988 ^b		2003		1988 ^b	2003
				$\bar{x} \pm 1\text{S.E.}$	<i>n</i>	$\bar{x} \pm 1\text{S.E.}$	<i>n</i>	$\bar{x} \pm 1\text{S.E.}$	$\bar{x} \pm 1\text{S.E.}$
Pentiction									
A	495	20	17	8.0 ± 0.2	194	17.4 ± 0.3	194	5.1 ± 0.1	10.5 ± 0.1
B	1065	20	17	8.5 ± 0.1	190	15.6 ± 0.2	189	5.6 ± 0.1	11.7 ± 0.1
C	1555	20	17	7.7 ± 0.1	196	14.1 ± 0.2	196	5.3 ± 0.1	11.4 ± 0.1
D	5730	100+	17	–	–	8.7 ± 0.5	100	–	7.8 ± 0.2
Kamloops									
A	465	22	24	11.5 ± 0.2	195	19.3 ± 0.2	194	8.2 ± 0.1	14.3 ± 0.4
B	835	15	23	11.7 ± 0.2	199	16.9 ± 0.2	198	8.6 ± 0.1	14.0 ± 0.2
C	1575	19	27	8.7 ± 0.1	187	14.0 ± 0.2	187	8.4 ± 0.1	12.5 ± 0.1
D	6620	100+	27	–	–	10.3 ± 0.3	100	–	12.7 ± 0.2
Prince George									
A	440	39	20	11.3 ± 0.3	171	20.9 ± 0.3	171	8.7 ± 0.2	14.1 ± 0.2
B	850	32	19	11.0 ± 0.3	189	18.4 ± 0.3	186	8.6 ± 0.2	14.8 ± 0.2
C	1615	30	15–20	8.8 ± 0.3	188	15.4 ± 0.3	183	7.0 ± 0.2	13.2 ± 0.2
D	4065	41	20	–	–	11.6 ± 0.4	100	–	13.4 ± 0.2

^a Lodgepole pine crop trees in 2003.

^b 1989 for the Kamloops study area.

western larch (*Larix occidentalis*). Dominant ground cover included willow (*Salix* spp.), Sitka alder (*Alnus sinuata*), grouseberry (*Vaccinium scoparium*), fireweed (*Epilobium angustifolium*), grasses, and Arctic lupine (*Lupinus arcticus*).

Stands initially underwent PCT in 1978 to ca. 1000–2000 stems/ha. Density of pine, 10 years post-thinning, exceeded 4000 stems/ha from additional ingress of pine. Three treatment stands were PCT again in 1988 to low, medium, and high densities. At time of treatment, mean stand diameter (dbh, diameter at breast height, 1.3 m above the soil surface) ranged from 7.7 ± 0.1 cm (mean ± 1S.E.) to 8.5 ± 0.1 cm. Stand height ranged from 5.1 ± 0.1 to 5.6 ± 0.1 m (Table 1). In 2003, mean stand dbh ranged from 14.1 ± 0.2 to 17.4 ± 0.3 cm and mean stand height ranged from 10.5 ± 0.1 to 11.7 ± 0.1 m (Table 1). All stands were 0.2–2.3 km apart and ranged in area from 20 ha (each of the thinned stands) to 100+ ha (unthinned stand).

The Kamloops study area was located 30 km south of Kamloops (50°28'N; 120°32'W). All stands were located in the Montane Spruce (MS_{dm}) biogeoclimatic zone (Meidinger and Pojar, 1991) and ranged in elevation from 1400 to 1500 m. Topography is hilly with a northerly aspect. This area (ca. 15,000 ha) was burned by wildfire in 1960 and regenerated naturally to lodgepole pine to a density of ca. 20,000 stems/ha. Dominant coniferous species in these stands included lodgepole pine with a minor component of subalpine fir (*Abies lasiocarpa*) and hybrid spruce (*P. engelmannii* × *P. glauca*). Dominant ground cover included Sitka alder, twinflower (*Linnaea borealis*), willow, fireweed, grasses, and Arctic lupine.

Two hundred hectares were PCT from 1975 to 1978 to ca. 1100–1600 stems/ha. Density of pine, 10 years post-thinning, exceeded 7000 stems/ha from additional ingress of pine. Three treatment stands were PCT again in 1989 to low, medium, and

high densities. At time of treatment, mean stand diameter of pine ranged from 8.7 ± 0.1 cm (mean ± 1S.E.) to 11.7 ± 0.2 cm and stand height ranged from 8.2 ± 0.1 to 8.6 ± 0.1 m (Table 1). In 2003, mean stand dbh and height ranged from 14.0 ± 0.2 to 19.3 ± 0.2 cm and 12.5 ± 0.1 to 14.3 ± 0.4 m, respectively (Table 1). All stands were 0.5–5.0 km apart and ranged in area from 15–22 ha (thinned stands) to 100+ ha (unthinned stand).

The Prince George study area was located 60 km west of Prince George (53°52'N; 123°32'W). All stands were located in the Sub-boreal Spruce (SBS_{dw}) biogeoclimatic zone (Meidinger and Pojar, 1991). General topography is gently rolling, at 800 m elevation with variable aspects. This area (ca. 1000 ha) was harvested from 1966 to 1972 and regenerated naturally to lodgepole pine at a density of 2700–4700 stems/ha. Dominant coniferous species in these stands included lodgepole pine with a minor component of subalpine fir and hybrid spruce. Dominant ground cover included willow, Sitka alder, fireweed, grasses, and Arctic lupine.

Three treatment stands were PCT in 1988 to low, medium, and high densities. At time of treatment, mean stand dbh ranged from 8.8 ± 0.3 cm (mean ± 1S.E.) to 11.3 ± 0.3 cm and stand height ranged from 7.0 ± 0.2 to 8.7 ± 0.2 m (Table 1). In 2003, mean stand dbh ranged from 15.4 ± 0.3 to 20.9 ± 0.3 cm and mean stand height ranged from 13.2 ± 0.2 to 14.8 ± 0.2 m (Table 1). All stands were 0.5–1.7 km apart and ranged in area from 30–39 ha (thinned stands) to 41 ha (unthinned stand).

The Pentiction old-growth stand was dominated by lodgepole pine with a relative abundance of 44% followed by spruce (39%) and subalpine fir (17%) for overstory trees (Table 2). The Kamloops stand was dominated by subalpine fir (64%) with lesser proportions of somewhat larger diameter pine and hybrid spruce. The Prince George old-growth stand had similar abundance of lodgepole pine (59%) and hybrid spruce (41%).

Table 2
Characteristics of the old-growth stands at the Pentiction, Kamloops, and Prince George study areas in 2003

Study area	Relative abundance (%), # sample trees	dbh (cm)		Height (m)	Density (stems/ha)		Snags (ha)
		Understory (dbh ≤ 15 cm)	Overstory (dbh > 15 cm)		Understory (≤ 3 m height)	Overstory (> 3 m height)	
Pentiction							310
L. pine	44	12.5 ± 1.3	20.5 ± 0.5	22.3 ± 0.3	0	730	
Spruce	39	12.7 ± 1.1	25.7 ± 1.6	22.2 ± 0.7	120	520	
S. fir	17	12.7 ± 0.5	27.2 ± 1.5	21.1 ± 1.2	3390	390	
Kamloops							290
L. pine	22	10.2	28.0 ± 1.1	21.5 ± 0.9	0	230	
Spruce	14	0.0	27.0 ± 3.1	22.9 ± 1.2	240	140	
S. fir	64	14.1 ± 0.5	22.0 ± 0.8	18.5 ± 0.6	18120	1000	
Prince George							350
L. pine	59	15.0 ± 0.0	27.8 ± 0.8	23.6 ± 0.4	200	510	
Spruce	41	12.1 ± 0.5	23.6 ± 3.5	17.7 ± 0.8	1210	1360	
S. fir	0.0						

Values for dbh and height are mean ± 1S.E. L. pine, lodgepole pine; S. fir, subalpine fir.

Heights of overstory trees ranged from 17.7 to 23.6 m and were similar in all stands. Overall stand density (>3 m height) in stems/ha was 1640 (Pentiction), 1370 (Kamloops), and 1870 (Prince George) (Table 2). Snag densities ranged from 290 to 350 ha⁻¹.

2.2. Experimental design

We investigated a low, medium, and high density of young lodgepole pine forest in our experimental design. In addition, unthinned young and old-growth lodgepole pine stands were included at each study area in the following design: Stand A is low density, target 500 stems/ha; Stand B is medium density, target 1000 stems/ha; Stand C is high density, target 2000 stems/ha; Stand D is unthinned >4000 stems/ha; Stand E is old-growth (Figs. 1 and 2). This range of stand densities, after PCT, was considered large enough to allow detection of 15-year changes in productivity of crop trees and coniferous stand structure. In addition, this broad range of densities was considered sufficient to cause measurable changes in the tree growth attributes of diameter, height, and volume. Treatments were assigned to stands in a randomized block design. Each of the three study areas was considered a regional replicate (block).

Operational thinning was conducted after the growing season in fall of 1988 at the Pentiction and Prince George study areas, and in fall of 1989 at the Kamloops study area. Trees in low-density stands were pruned to a 2.8-m lift (above ground level) at Pentiction (October 1992), Kamloops (September 1992), and Prince George (November 1991). Densities of pine (stems/ha) in unthinned stands were 5000 at Pentiction, 6000 at Kamloops, and 4700 at Prince George in 1988. These densities were 5730, 6620, and 4065, respectively, in 2003 (Table 1).

2.3. Tree growth and stand structure

All sampling of lodgepole pine crop trees was done with 20 variable-radius plots, systematically located in each stand, to

accommodate variations in stand density. For the thinned stands, the 10 crop trees closest to each plot center were permanently tagged. Measurement of the total height (cm) and dbh (cm) at a permanent reference point was done at the initial sampling period in October and November 1988 (Pentiction and Prince George) and November 1989 (Kamloops). Diameter and height re-measurements were conducted in November 2003 to

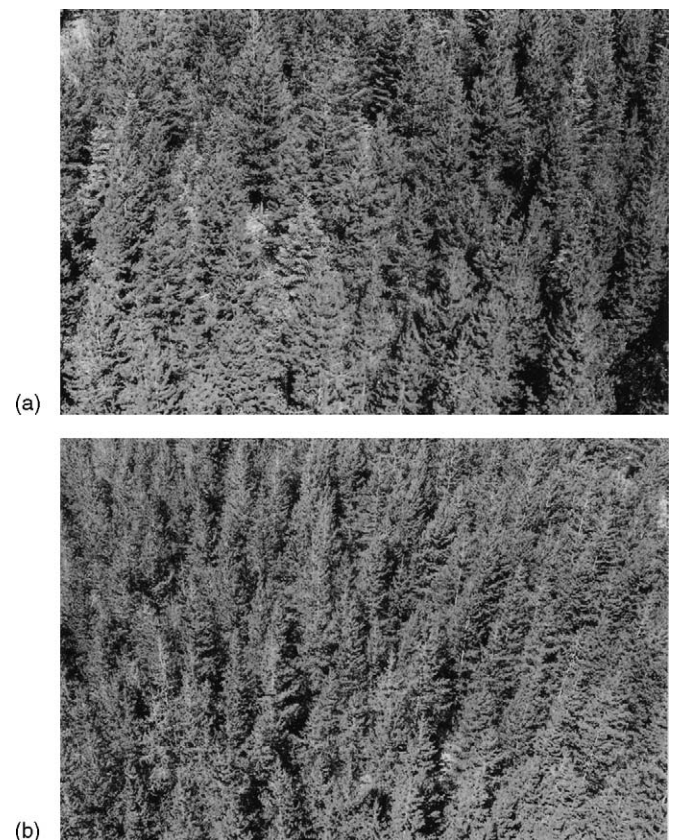


Fig. 1. Aerial photographs of the (a) low-density stand and (b) high-density stand, at Pentiction Creek in July 2003. Note the larger crowns on trees in the low-density stand.

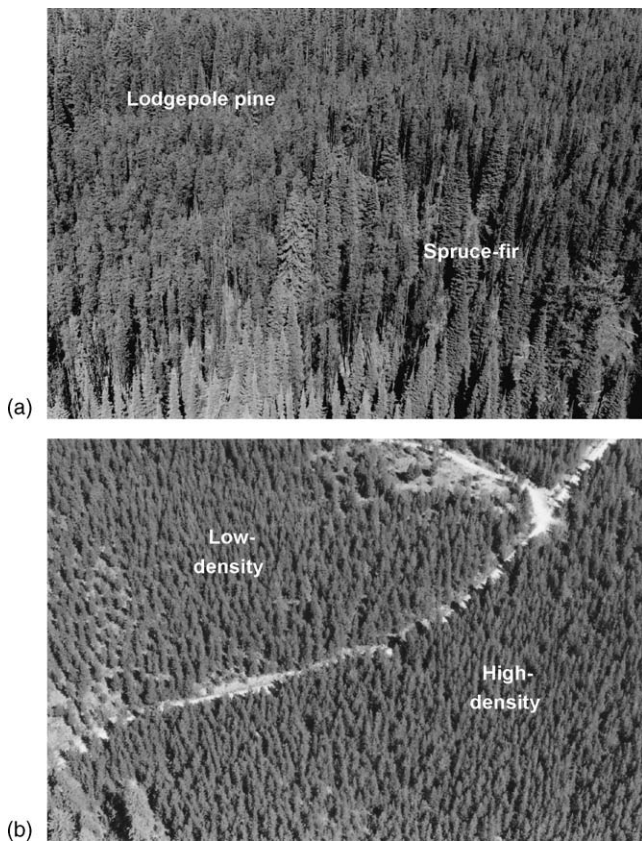


Fig. 2. Aerial photographs of the (a) old-growth stand with lodgepole pine and spruce-fir trees and their respective crown architectures, and (b) the low- and high-density stands, at Pentiction Creek in July 2003.

provide 15-year growth increments at Pentiction and Prince George, and 14-year growth increments at Kamloops. Height (cm) and width (cm) of tree crowns were measured for all sample crop trees in every other plot in the three thinned stands at each study area (after Schmidt and Seidel, 1988).

Permanent sample plots were not installed in the unthinned stand at each study area because the greater diameter and height growth of trees in thinned than unthinned stands was well established in previous studies (Johnstone, 1985; Sullivan et al., 1993). However, 10 temporary plots were located every 50 or 100 m in a grid pattern throughout each of the unthinned stands in 2003 to provide measurements of mean dbh and representative heights for descriptive comparisons with the thinned stands. The 10 potential crop trees closest to each plot center were sampled. Crop trees (dominant or co-dominant stems of good form) were chosen on the basis that those trees would be left as the future crop if the stand was thinned. Height and width of tree crowns of sample trees in all plots were also measured for comparison with trees in the thinned stands. Analyses of diameter, height, and volume growth of trees in the unthinned stands were not done since we did not have initial measurements from trees in permanent plots. In addition, our subjective choice of sample trees in the unthinned stands did not provide for accurate estimates of stand means, but rather likely overestimated measures of dbh, height, and crown dimensions. For this reason, statistical comparisons of tree growth (diameter, height, and volume increments) did not

include the unthinned stands. While our sampling design likely overestimated the mean crown size of trees in the unthinned stands, crown size was consistently smallest in the unthinned stands. Therefore, a sampling regime focusing on the largest trees in each stand would not have changed the interpretation of our results.

Sampling of coniferous tree species in layers in 0–1, 1–2, 2–3, and >3 m height classes was done in a 5.64-m radius circular plot (100 m²) located in the center of each crop tree plot. To complete the tree inventory, the minor species trembling aspen (*Populus tremuloides*) and black cottonwood (*Populus trichocarpa*) were also included. This sampling was conducted in the three thinned stands, one unthinned stand, and one old-growth stand at each study area. To provide a descriptive summary of the old-growth stands, 10 temporary plots of 10 trees each were established in a grid pattern throughout each stand in 2003 as described above. All trees in a given plot were recorded as alive or dead with species and dbh tallied. Tree heights and crown measurements were taken for the ten trees in each plot.

2.4. Statistical analysis

For the tree measurements, data from the three thinned stands were summarized according to initial diameter, height, and volume classes, and this format was maintained throughout the analyses. Because growth rates are dependent on these initial measurements, an analysis of covariance (ANCOVA) was used to determine the effect of stand density on 15-year diameter, height, and volume increments at each study area. Regressions were established for the dependence of: diameter growth increment on initial tree dbh, height growth increment on initial tree height, and tree volume and stand volume increments on initial tree and stand volumes, respectively.

Tree volume (inside bark) was calculated using one of three equations that had been developed by Brockley and Simpson (2004) for similar-aged and similar-sized lodgepole pine trees at research installations close to our study areas. Specific volume equations were chosen on the basis of the range of dbh and tree height observed within a given sample period, as well as the study area. Tree volume was calculated for each sample tree separately. The mean tree volume (averaged across all sample trees within a stand) was then scaled to a per hectare basis by multiplying by an estimate of tree density for a given stand.

In addition, within each study area, an ANCOVA tested for a common slope (homogeneity of regression coefficients) of the regressions that were estimated for the three stands. Where a significant covariate \times stand interaction occurred, separate regression equations were generated for each stand (independent factor regressed on the covariate) and used to adjust growth rates for each individual tree.

A randomized block two-way ANOVA-Model III (Zar, 1999) with factor stand treatment (three stand densities) as a fixed effect and factor block as a random effect was used to evaluate differences in adjusted mean values of diameter, height, and volume growth increments, derived from the ANCOVA. This same analysis with factor stand treatment

(three stand densities, unthinned, and old-growth) as a fixed effect and factor block as a random effect was used to evaluate differences in the following parameters: crown volume, diameter of crown at widest point, crown height, and crown ratio (crown length/total height) of crop trees, and abundance, species diversity, and structural diversity of coniferous tree layers.

Species diversity was represented by the Shannon–Wiener index which is based on information theory and the degree of difficulty in correctly predicting the next species sampled. This diversity index is sensitive to changes in rare species, has good discriminant ability, and is well represented in the ecological literature (Burton et al., 1992; Magurran, 2004). Structural diversity utilized the same index with coniferous tree species represented by height classes and relative abundance represented by density of trees.

Duncan's multiple range test (DMRT) was used to compare mean values. In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. Growth of crop trees

Analysis of the regression relationships indicated that diameter increment regressed on initial dbh, height increment regressed on initial height, and increments of tree volume and stand volume regressed on initial volume measurements all had common slopes ($P > 0.05$) at each of the three study areas. Mean 15-year diameter increments of trees in the low-density stands were significantly higher than those in the medium- and high-density stands at all study areas (Table 3). At the low

density, 15-year diameter increments were 9.35 cm at Penticton and 9.58 cm at Prince George; the 14-year diameter increment for this low-density stand at Kamloops was 7.70 cm. There was no significant difference in diameter increment between the medium- and high-density stands at Penticton nor at Kamloops. However, trees grew significantly faster in diameter in the medium-density (mean of 7.44 cm) than high-density (mean of 6.57 cm) stand at Prince George (Table 3). Mean height increment of trees was similar in the medium- and high-density stands and significantly higher than that in the low-density stands at Penticton and Prince George (Table 3). However, mean 14-year height increment was similar in the low-density (6.08 m) and medium-density (5.50 m) stands at Kamloops, but significantly higher than that (4.16 m) in the high-density stand.

Mean 15-year volume increments of trees in the low-density stands were significantly higher than those in the medium-density stands, and volume of trees in both these stands were higher than those in the high-density stands at all study areas (Table 3). Mean 15-year stand volume increments (m^3/ha) were similar in the medium-density (103.44) and high-density (107.03) stands and these measurements were significantly higher than that in the low-density (49.95) stand at Penticton (Table 3). The mean 14-year stand volume increments at Kamloops were significantly different with the high-density stand (116.60) highest, followed by the medium-density (101.48) and low-density (74.70) stands. At Prince George, the pattern was similar with the highest stand volume increment in the high-density stand followed by the medium- and low-density stands (Table 3).

In an overall analysis of tree growth across the three regional replicates, lodgepole pine grew significantly ($F_{2,4} = 68.42$;

Table 3
Summary of analysis of covariance determining the effect of stand density (low, medium, and high) on mean 15-year diameter (cm), height (m), tree volume (m^3), and stand volume (m^3/ha) of lodgepole pine at each study area

Stand density	Penticton			Kamloops			Prince George		
	Low	Medium	High	Low	Medium	High	Low	Medium	High
Mean initial diameter	8.02	8.52	7.70	11.51	11.65	8.68	11.33	10.97	8.84
Mean diameter increment	9.35 a	6.97 b	6.52 b ^a	7.70 d	5.16 e	5.47 e ^b	9.58 g	7.44 h	6.57 i ^c
Mean initial height	5.13	5.62	5.35	8.18	8.55	8.37	8.68	8.60	6.99
Mean height increment	5.40 a	6.05 b	6.03 b ^d	6.08 d	5.50 d	4.16 e ^c	5.42 g	6.26 h	6.14 h ^f
Mean initial tree volume	0.017	0.019	0.017	0.048	0.052	0.028	0.053	0.052	0.031
Mean tree volume increment	0.105 a	0.088 b	0.072 c ^e	0.164 d	0.113 e	0.075 f ^h	0.196 g	0.158 h	0.106 i ⁱ
Mean initial stand volume/ha	8.24	22.72	24.86	21.83	46.39	43.94	25.55	39.42	51.28
Mean stand volume increment/ha	49.95 b	103.44 a	107.03 a ^j	74.70 c	101.48 d	116.60 e ^k	93.99 h	120.67 g	173.90 f ^l
Sample size	194	189	196	194	198	187	171	186	183

Within a study area, mean values followed by different letters are significantly different according to Duncan's multiple range test.

^a $F_{2,575} = 153.9$; $P < 0.01$.

^b $F_{2,575} = 107.2$; $P < 0.01$.

^c $F_{2,536} = 96.6$; $P < 0.01$.

^d $F_{2,575} = 29.3$; $P < 0.01$.

^e $F_{2,575} = 16.7$; $P < 0.01$.

^f $F_{2,536} = 35.7$; $P < 0.01$.

^g $F_{2,575} = 48.19$; $P < 0.01$.

^h $F_{2,575} = 255.48$; $P < 0.01$.

ⁱ $F_{2,536} = 110.55$; $P < 0.01$.

^j $F_{2,575} = 198.63$; $P < 0.01$.

^k $F_{2,575} = 67.51$; $P < 0.01$.

^l $F_{2,536} = 102.80$; $P < 0.01$.

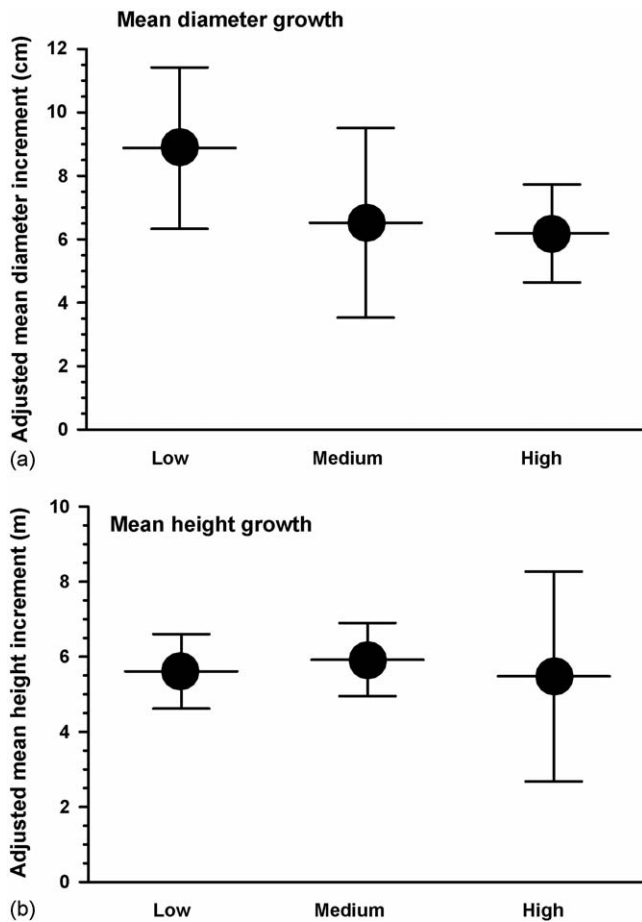


Fig. 3. Adjusted mean ($n = 3$; $\pm 95\%$ confidence intervals) 15-year: (a) diameter and (b) height growth increments of crop trees in low-, medium-, and high-density stands of lodgepole pine.

$P < 0.01$) faster in mean diameter in the low-density (DMRT; $P = 0.05$) than in either of the medium- or high-density stands (Fig. 3a). However, there was no difference ($F_{2,4} = 0.27$; $P = 0.78$) in mean height growth among stand densities over the 15-year period since PCT (Fig. 3b). The pattern of faster diameter growth in the low-density stands was also reflected in the significantly ($F_{2,4} = 13.31$; $P = 0.02$) higher tree volume increment (DMRT; $P = 0.05$) for lodgepole pine in the low- than high-density stands across the regional replicates (Fig. 4a). Mean tree volume increments were similar (DMRT; $P = 0.05$) between the low- and medium-density stands and between the medium- and high-density stands. Mean 15-year stand volume increments were significantly ($F_{2,4} = 12.66$; $P = 0.02$) different among stands with similar volumes in the medium- and high-density stands that were higher (DMRT; $P = 0.05$) than those in the low-density stands (Fig. 4b).

3.2. Architecture of tree crowns

Mean crown volume of lodgepole pine crop trees was significantly ($F_{4,8} = 11.16$; $P < 0.01$) different among the five treatment stands (Fig. 5). Trees in the low-density (52.8 m^3) stands had a similar crown volume to the medium-density

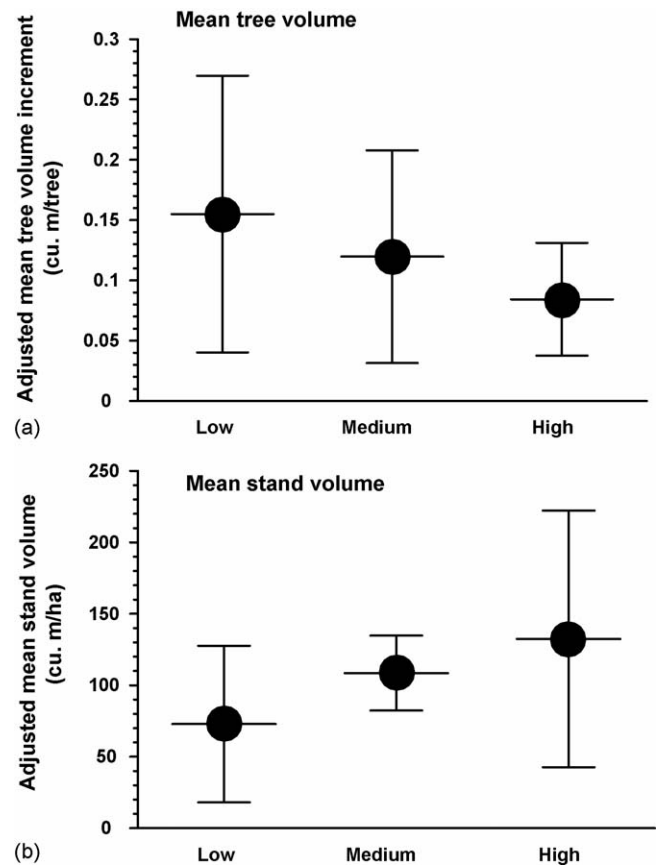


Fig. 4. Adjusted mean ($n = 3$; $\pm 95\%$ confidence intervals) 15-year: (a) tree volume (m^3/tree) and (b) stand volume (m^3/ha) growth increments of crop trees in low-, medium-, and high-density stands of lodgepole pine.

(42.9 m^3) stands, but a greater (DMRT; $P = 0.05$) volume than those in the high-density (27.8 m^3), unthinned (11.7 m^3), or pine component (30.9 m^3) in the old-growth stands. Mean crown volume was also significantly (DMRT; $P = 0.05$) lower in the unthinned than in each of the medium-density, old-growth, and high-density stands. This same analysis was conducted with crown volumes of all conifer species included as an overall mean value for the old-growth stands. Again, mean crown volume was significantly ($F_{4,8} = 14.68$; $P < 0.01$) different among stands, with the low-density, medium-density, and old-growth stands all having greater (DMRT; $P = 0.05$) crown volumes than those in the unthinned and high-density stands.

Mean crown diameter at the widest point was also significantly ($F_{4,8} = 14.49$; $P < 0.01$) different for lodgepole pine in these stands (Table 4). The pattern of differences among stands essentially followed that of crown volume. Measurement of mean crown height indicated that there was a significant ($F_{4,8} = 12.96$; $P < 0.01$) difference among stands with the low-density, medium-density, and old-growth stands having the greatest (DMRT; $P = 0.05$) crown heights among stands. When total conifers were considered in the analysis, trees in the old-growth stands had the highest crown heights of all stands (Table 4).

Mean crown ratio (crown length/total height) of trees was also significantly ($F_{4,8} = 13.84$; $P < 0.01$) different among

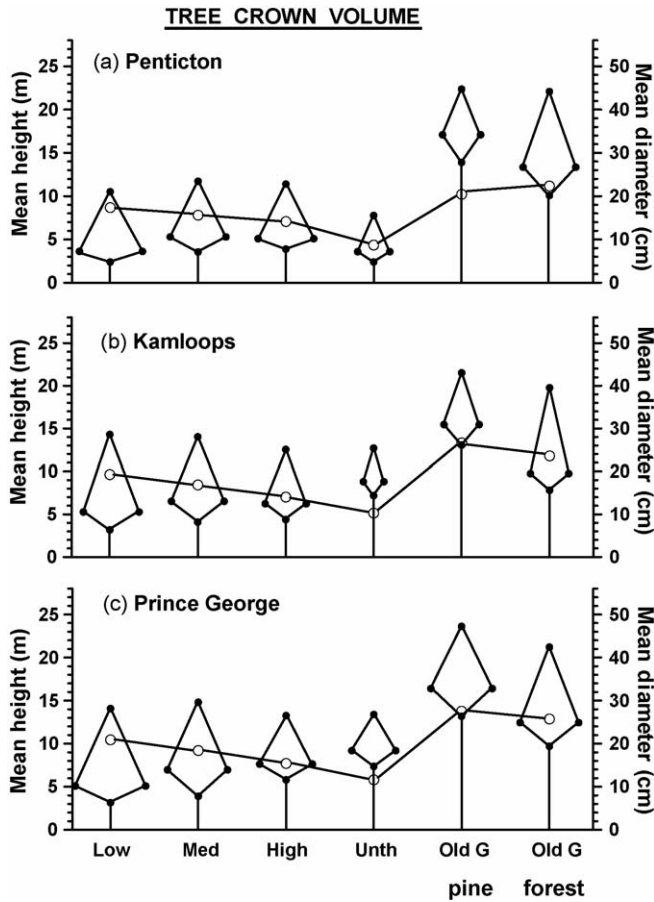


Fig. 5. Mean crown architecture of crop trees in 2003 for the three thinned stands, unthinned stand, and two old-growth forest components at each study area. Mean height (m) is represented by the top of each tree depiction, and mean tree diameter (cm) is represented by the connected data points. Low = low density, Med = medium density, High = high density, Unth = unthinned, and Old G = old-growth.

treatment stands (Table 4). Crown ratios were similar in the low-density (0.77), medium-density (0.72), and high-density (0.62) stands, and both the low- and medium-density stands had higher (DMRT; $P = 0.05$) mean crown ratios than those in the unthinned (0.52) and pine component of the old-growth (0.40) stands. The mean crown ratio for overall conifers in the old-growth stands (0.57) was similar to the high-density and unthinned stands, but was lower (DMRT; $P = 0.05$) than those in the low- and medium-density stands (Table 4).

Table 4
Summary of analysis of variance and mean ($n = 3$) measurements of crown architecture (crown diameter at the widest point, total crown height, and crown ratio) of lodgepole pine crop trees in the four young stands, lodgepole pine by itself and together with the other coniferous species in the old-growth stands

Crown attribute	Low	Medium	High	Unthinned	Old-growth pine	$F_{4,8}$	P	Old-growth conifers	$F_{4,8}$	P
Diameter at widest (m)	4.30 a \pm 0.24	3.85 ab \pm 0.22	3.44 bc \pm 0.28	2.22 d \pm 0.50	3.05 c \pm 0.58	14.49	<0.01	3.27 c \pm 0.38	25.42	<0.01
Total crown height (m)	9.86 a \pm 0.91	9.79 a \pm 0.86	7.83 b \pm 0.27	5.64 c \pm 0.20	9.13 a \pm 0.66	12.96	<0.01	11.82 ^a \pm 0.15	21.12	<0.01
Crown ratio	0.77 a \pm 0.003	0.72 ab \pm 0.02	0.62 bc \pm 0.03	0.52 cd \pm 0.08	0.40 d \pm 0.02	13.84	<0.01	0.57 cd \pm 0.02	6.92	0.01

Mean values followed by different letters are significantly different according to DMRT.

^a This mean value significantly greater than any of the others by DMRT.

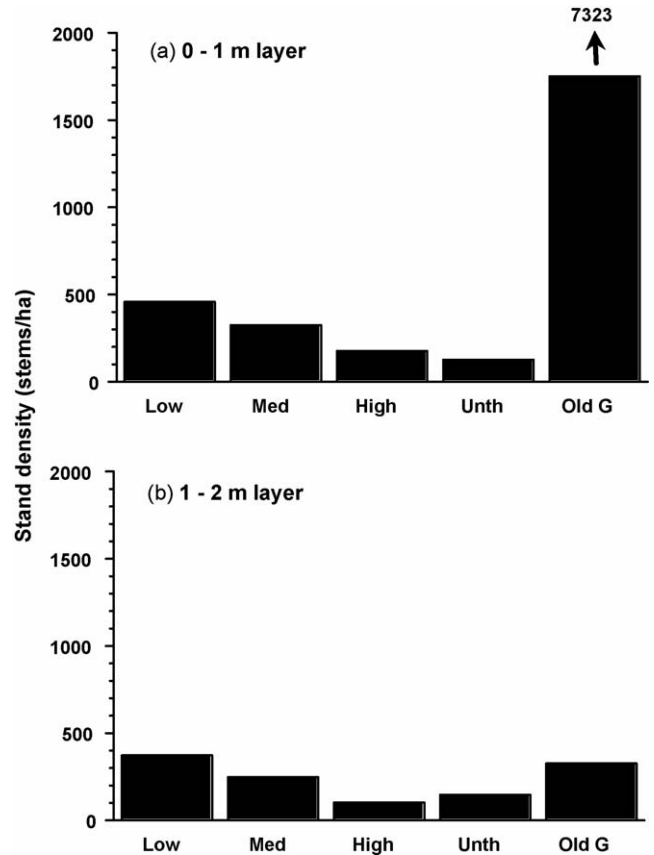


Fig. 6. Mean ($n = 3$) density (stems/ha) of the (a) 0–1 m layer and (b) 1–2 m layer of total coniferous trees in the five treatment stands in 2003. Low = low density, Med = medium density, High = high density, Unth = unthinned, and Old G = old-growth.

3.3. Coniferous stand structure

The tree layer in these stands was dominated by coniferous species with a minor incidence of trembling aspen and black cottonwood. The mean densities of trees were similar ($P > 0.05$) among treatment stands in the 0–1, 1–2, and 2–3 m height classes (Figs. 6a and b and 7a). The 0–1 m layer of the old-growth stands appeared to have a much higher density of trees than any of the younger stands (Fig. 6a), but this was owing to the very high density of subalpine fir seedlings ($17,600 \text{ ha}^{-1}$) at Kamloops. Mean tree density in the $>3 \text{ m}$ height class was significantly ($F_{4,8} = 28.93$; $P < 0.01$) different

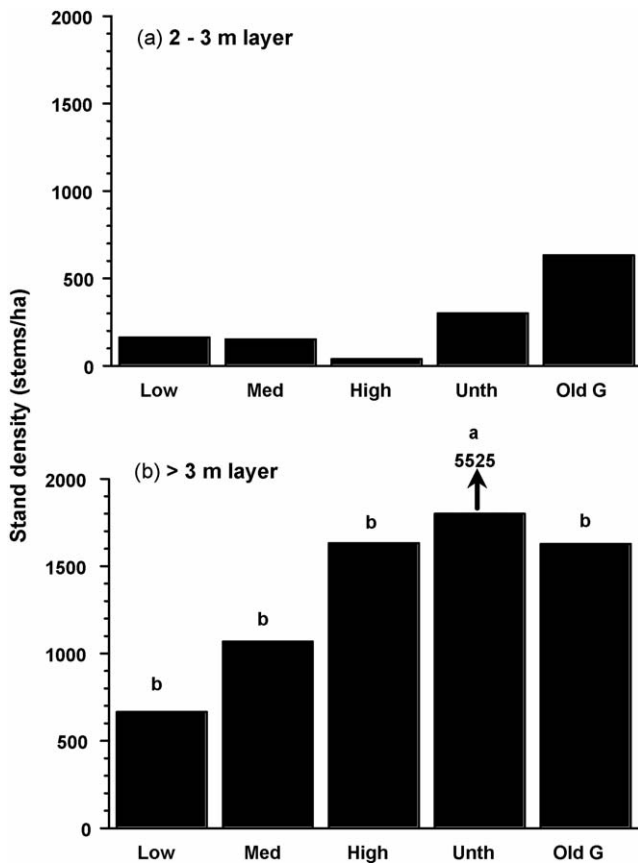


Fig. 7. Mean ($n = 3$) density (stems/ha) of the (a) 2–3 m layer and (b) >3 m layer of total coniferous trees in the five treatment stands in 2003. Mean values represented by histograms with different letters are significantly different according to Duncan's multiple range test. Low = low density, Med = medium density, High = high density, Unth = unthinned, and Old G = old-growth.

among treatment stands with the unthinned stands having the highest (DMRT; $P = 0.05$) numbers (Fig. 7b).

Mean species diversity of coniferous trees at 15 years after PCT was significantly ($F_{4,8} = 13.89$; $P < 0.01$) different among treatment stands (Fig. 8a). The low- and medium-density stands had a similarly diverse assemblage of tree species, which was higher (DMRT; $P = 0.05$) than those of the high-density, unthinned, or old-growth stands. A similar pattern was also recorded for structural diversity of conifers where significantly ($F_{4,8} = 8.68$; $P < 0.01$) higher levels of stand structure occurred in the low- and medium-density stands than in the high-density and unthinned stands (DMRT; $P = 0.05$; Fig. 8b). In addition, the layers of coniferous trees were more diverse in the low-density than in the old-growth stands, at least at 15 years post-thinning (DMRT; $P = 0.05$).

4. Discussion

4.1. Growth of crop trees

To avoid confusion about “thinning lift” with “tree growth”, our ANCOVA took into account the mean size of trees prior to PCT treatments, thereby removing the effect of larger mean tree sizes within low-density stands. And most

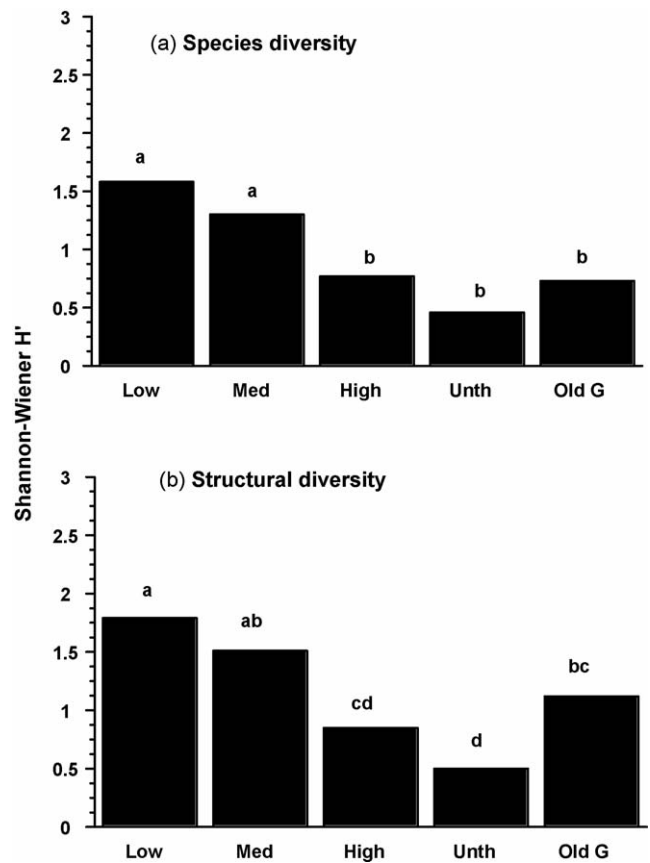


Fig. 8. Mean ($n = 3$): (a) species diversity and (b) structural diversity for coniferous trees in the five treatment stands in 2003. Mean values represented by histograms with different letters are significantly different according to Duncan's multiple range test. Low = low density, Med = medium density, High = high density, Unth = unthinned, and Old G = old-growth.

importantly, comparisons of tree growth increments were conducted among thinned stands only. Comparisons of the largest 100 or 500 trees/ha would have provided a useful comparison of thinning effect on tree growth and would also have factored out any impact of thinning lift. However, this sort of analysis would do little to inform a reader of the actual growth or productivity that could be expected following PCT treatments. Basing an analysis on the largest trees would have overestimated any measures of tree growth, whereas our analysis provided numbers that accurately reflected the stand means (except for the unthinned stands which were not included in the formal statistical comparisons).

The diameter and height growth responses of lodgepole pine to PCT at 15 years after treatment followed the same trajectory reported at 5-year (Sullivan et al., 1996) and 10-year (Sullivan et al., 2001) measurements in these same stands. Heavy thinning to 500 stems/ha (low-density) has consistently maintained faster diameter growth than in the medium- and high-density stands. Height growth continued to be variable but was reasonably uniform at 5.5–6 m when the adjusted mean height increments were analyzed across the regional replicates (Fig. 3b). PCT concentrates the growth potential of the site on selected crop trees because it reduces inter-tree competition and increases the amount of growing space per tree. However, the

less dramatic effects of thinning on height than diameter growth support the contention that a limited degree of crowding is required to maximize the height growth of lodgepole pine (Johnstone, 1985). These growth patterns match those reported earlier from much smaller (<1 ha) research-scale installations (Cole, 1975; Johnstone, 1985; Johnstone and Cole, 1988; Cochran and Dahms, 1998; Johnstone and van Thienen, 2004), and from operational-scale installations (Sullivan et al., 2002).

PCT of lodgepole pine stands has been controversial because the treatment apparently does not necessarily achieve the intended yield objectives and negatively affects wood quality (Johnstone and van Thienen, 2004). These concerns are related to heavy thinning which reduces the total volume of wood (O'Hara, 1988) and the ratio of juvenile to mature wood, thereby affecting the structural integrity (load-bearing) of the final lumber products (Jozsa and Middleton, 1994). However, at least in our study, at 15 years post-thinning in stands 32–42 years of age, mean stand volume (ranging from 108.53 to 132.51 m³/ha) was similar in the medium and high thinning densities, albeit higher than that (72.88) in the low-density thinning. As discussed by Long (1985), density management regimes typically represent a compromise between maximization of volume production (m³/ha for a specified time interval) and maximization of individual tree growth and size. If the management objective is large trees with wide diameters and prominent crown dimensions (i.e. old-growth structural features), then the level of growing stock will be sacrificed in favor of individual tree growth versus stand volume. This pattern was evident in the growth attributes of our stands at 15 years after PCT. This silvicultural trade-off, discussed by Long (1985) in terms of stand density index (SDI), can be used to translate growing stock objectives into density management prescriptions.

The trade-off in stand yield in terms of wood volume versus wood quality has traditionally overlooked the importance of stand structural features to wildlife habitat and biodiversity (McComb et al., 1993; Hayes et al., 1997). Our study is the first detailed evaluation of stand productivity and structural features conducted at operational real-world scales and over a relatively long-term post-treatment (15 years after PCT) period. At least in our study areas in south-central British Columbia, stand volume growth was comparable in the medium- and high-density stands, while concurrently providing structural features of large-diameter trees with large crowns and diverse understory layers of coniferous trees in the low- and medium-density stands. Presumably the increased space for trees to grow at these lower densities produced high-vigor trees with deep crowns and relatively rapid individual tree growth. This increased growth is a likely explanation for the comparable levels of mean stand volume in the medium- and high-density stands. Thus, it would seem that both stand volume output and development of old-growth structural features may be integrated at certain stand densities of lodgepole pine.

In addition, heavy thinning of lodgepole pine has been suggested as a potential means to “beetle-proof” stands from attack by the mountain pine beetle (*Dendroctonus ponderosae*) (Mitchell et al., 1983; Cole and Koch, 1995). This beetle is

endemic in lodgepole pine stands throughout western North America and at epidemic outbreaks becomes the most destructive insect pest of mature pine forests (Shore et al., 2000). There is some evidence that vigorous trees in low-density stands (<750 stems/ha) may be able to withstand attack by mountain pine beetles. Trees with higher vigor produce more resin and may successfully “pitch out” attacking beetles (Whitehead and Russo, 2005). A reduction in the rotation age by growing larger timber faster may also reduce the chance of attack as stands >80 years of age tend to attract beetles. The additional coniferous species observed in these managed pine stands may also help reduce susceptibility to beetle attack.

4.2. Architecture of tree crowns

The dramatic response of tree diameter to PCT was likely related to the size and persistence of crowns, which clearly increased in volume in accordance with the available growing space. This relationship of crown size to stand density at 15 years after PCT was also recorded at the 10-year measurement (Sullivan et al., 2001). A similar relationship was reported for western larch (Schmidt and Seidel, 1988) and for dominant and codominant trees in thinned 20–50-year-old stands (Long et al., 1983; Bailey, 1996). Perhaps the most striking comparison was the higher mean crown volume of pine trees in the low-density than old-growth stands. This pattern was also recorded for diameter at the widest point and crown ratio, but not for total crown height. In addition, mean crown volume was similar in the two heavily thinned stands and the overall conifer crown volume in the old-growth stands. Thus, even at an age of 32–42 years, these young stands have comparable crown volumes to those in the old-growth. However, these young stands clearly lack the height of the old-growth stands and will likely never be as tall before they are harvested. Large trees and crowns provide nesting, roosting, and foraging sites for several species of birds (Hamer and Nelson, 1995), arboreal sciurids (Rothwell, 1979; Carey, 2000), and forest mustelids (Thompson and Harestad, 1994). These structures also provide snow interception and foraging opportunities for ungulates (Armleder et al., 1989).

Although lodgepole pine has a relatively consistent crown shape, some variability is associated with stand density and site quality (Koch, 1996a). Crown form can range from sparsely tufted foliage in the highest density classes to that which is distinctly triangular with greater crown width in relation to length in the very low-density classes of this species (Koch, 1996a). In general, lodgepole pine has a long tapered cone shape in the upper portion of the tree and there sometimes is an inverted and short tapered cone in the lower portion of the tree.

As was seen in this study, unthinned forest conditions produced the smallest crowns and configurations that were quite different from crop trees observed in the managed stands (Fig. 5). Low-vigor lodgepole pine trees have shallow flat-topped crowns with little leaf area, and tufts of needles at branch ends (Kaufmann and Watkins, 1990). High-vigor trees with deep crowns have nearly conical tops and branches with extensive needles. High stand vigor is associated with deep full crowns and rapid individual tree growth, as in our heavily thinned stands.

However, high stand growth efficiency (high ratio of stemwood to total tree biomass) is associated with modest individual tree growth, and hence compact crowns (Smith and Long, 1989). It is perhaps not surprising that conventional wisdom demands relatively high-density stands of trees with narrow crowns to enhance stand productivity, at least in terms of wood volume. Again, however, volume of wood per ha in our stands was similar across the medium- and high-density thinnings.

Thus, our hypothesis (i), that large-scale stand thinning to a wide range of densities would enhance productivity and structural features (tree diameter, height, and volume growth and crown volume) of lodgepole pine crop trees, appears to be supported for diameter and volume growth and crown volume of trees, but not for height growth.

4.3. Coniferous stand structure

Abundance of conifers in the understory classes (<3 m height) was similar across stands. However, the increased species diversity and structural diversity of coniferous tree layers (with minor deciduous trees) in the heavily thinned stands reflect an enhanced array of habitats and microhabitats in the understory of these stands. These results were supported by the increased abundance of herbs and shrubs and structural diversity of the overall plant community in the heavily thinned stands (Lindgren et al., 2006). Thus, with respect to hypothesis (ii), which was partly supported, thinning did enhance coniferous stand structure in terms of species diversity and structural diversity but not conifer abundance.

5. Conclusions

The rapid growth of individual trees in our heavily thinned stands suggests that thinning could move stands out of the closed-canopy stage and accelerate development of conditions found in late-seral forests (McComb et al., 1993; Carey and Curtis, 1996; Hayes et al., 1997). Such successional development may be temporary but this temporal scale would depend on the range of thinning intensities. Clearly, heavy thinning to ≤ 500 stems/ha may prolong “open” stand conditions for extended periods.

Old-growth forests of the Pacific Northwest of North America are characterized by multilayered canopies, a range of tree sizes, the presence of abundant woody debris, canopy gaps with patches of herbs and shrubs, and numerous snags (Franklin et al., 1981). These attributes originally described coastal Douglas-fir-western hemlock (*Tsuga heterophylla*) forests, but they are equally relevant to inland forests as well (Kneeshaw and Burton, 1998). Our heavily thinned (≤ 1000 stems/ha) stands seem to be on a trajectory of developing at least some features of late successional forests. These stands have relatively large trees (at least for young lodgepole pine) and crowns (similar or larger than those in the old-growth stands) as well as the beginning of multi-layered coniferous structure in the understory. Density of trees (≥ 15 cm dbh) in our old-growth stands averaged about 800–1000 stems/ha, with the lodgepole pine component at about 400 stems/ha (Sullivan et al., 2001). These densities correspond well with those

discussed for coastal old-growth forests at <250 trees/ha (Tapeiner et al., 1997). A range of tree sizes will take time to emerge in our stands. Mean volume and composition of woody debris were relatively similar across the five treatment stands (Sullivan et al., 2001). Patches of herbs and shrubs were certainly evident in the understory of the heavily thinned stands (Lindgren et al., 2006). Snags were generally lacking since second-growth stands, arising after clearcutting or intensive wildfire, typically have few, if any, standing dead trees.

Perhaps the best way to answer the question of when our thinned stands start to develop old forest structural features and ecological functions is to measure use by wildlife species. To date, at least for mammals, both the southern red-backed vole (*Clethrionomys gapperi*) and the northern flying squirrel seem to use these managed stands at levels recorded in the old-growth stands (Ransome et al., 2004; Sullivan et al., 2005). Continued monitoring of these mammals, as well as other wildlife groups, over several decades will enhance our understanding of when structural features in managed stands converge with those in old-growth stands.

Acknowledgements

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