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Long-term responses of tree and stand growth of young lodgepole pine to pre-commercial thinning and repeated fertilization



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ABSTRACT

This study was designed to test the hypothesis that application of a range of pre-commercial thinning (PCT) intensities and repeated fertilization would enhance 15-year growth increments of lodgepole pine (Pinus contorta var. latifolia) crop trees at both tree and stand levels. Study areas were located near Summerland and Kelowna in south-central British Columbia, Canada. Each study area had nine treatments: four pairs of stands thinned to densities of ~250 (very low), ~500 (low), ~1000 (medium), and ~2000 (high) stems/ha with one stand of each pair fertilized five times at 2-year intervals, and an unthinned stand. Neither density nor fertilization treatments had any significant effect on 15-year increments of height growth. Mean diameter at breast height (17% increase), basal area (BA) (28% increase), and volume (27% increase) growth increments per tree were significantly enhanced by fertilization, but were not affected by density. Repeated fertilization enhanced both BA (20% increase) and volume (18% increase)/ha at the stand level. Despite the significant decrease in crop tree stand density resulting from PCT, 15-year BA and volume increments were statistically similar across density treatments. Contributions of non-crop trees to total stand productivity appeared to be substantial, particularly within the heavily thinned stands. Because trees provide the majority of all aboveground terrestrial carbon, they are an important sink for atmospheric CO₂. Enhancing stand productivity may provide adaptive advantages for carbon sequestration to help limit greenhouse gases as well as resiliency of forests subjected to changing growing conditions due to climate change.

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1. Introduction

With very few exceptions, Canada's forest industry has been based on extensive silviculture practices that have been able to take advantage of large tracts of unmanaged, old forests, often with little or no investment in silviculture treatments beyond stand establishment. Intensive silviculture has been clearly demonstrated as an economically beneficial strategy within pine (Pinus spp.) plantations throughout the southern United States (US) with growth rates more than doubled and rotation lengths cut by more than 50% (Fox et al., 2007). However, the benefits of intensive silviculture remain largely unrealized throughout northern latitudes, and within boreal and sub-boreal forests in particular (Lautenschlager, 2000; Park and Wilson, 2007). There is an ever-increasing global demand for timber production and forest cover to produce conventional wood products, biofuels production, and sequester carbon in response to climate change (Sedjo, 1999; Raunikar et al., 2010). This demand is concurrent with conservation strategies that endeavor to increase the size of protected areas and conserve biodiversity (Hunter and Schmiegelow, 2011), while

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balancing the unpredictable large-scale loss of existing timber to natural disturbances (e.g., losses to wildfire and insect epidemics; Agee, 1993; Walton et al., 2009). Clearly, enhanced wood production will become increasingly necessary to mitigate current and future wood supply shortfalls (Brooks, 1997; Sutton, 1999).

Intensive silvicultural practices such as pre-commercial thinning (PCT), commercial thinning (CT), and fertilization have the potential to sustain wood and biomass production while creating a diversity of forest habitat conditions to meet the goals of biodiversity conservation (Moore and Allen, 1999; Hartley, 2002; Sullivan et al., 2009). These silvicultural treatments have been used successfully around the world to increase biomass production in existing even-aged forests (Allen et al., 1990; Oliver and Larson, 1996), across northern Europe (Nabuurs et al., 2007; Bergh et al., 2008), the southeastern US (Albaugh et al., 2004; Jokela et al., 2004), and inland lodgepolepine (*Pinus contorta* var. *latifolia*) forests of the Pacific Northwest (PNW) of North America (NA) (Sullivan et al., 2006; Lindgren et al., 2007).

Early- to mid-seral (1–40 years old) lodgepole pine is the dominant coniferous tree species across a vast area of the inland PNW of NA (Koch, 1996; Sullivan et al., 2001). This species likely has the greatest potential to respond favorably to silvicultural treatments designed to enhance the growth of crop trees within stands







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(Johnstone, 1985; Brockley, 2005). Lodgepole pine often regenerates over-abundantly, after wildfire or clearcut harvesting, with excessive stand densities that reduce tree growth and stand productivity. PCT and CT concentrate growth on a smaller number of stems and provide some control over the rotation, yield, and value of the future crop (Johnstone, 1985; Cole and Koch, 1996). Because they originated from repeated fire disturbance, lodgepole pine forests usually occupy sites of low-N status (Brockley et al., 1992), and hence respond well to conventional, single applications of nitrogen, as well as in combination with other elements (Weetman, 1988; Brockley, 1996). Sustained growth responses to fertilization with optimum nutrition formulations have been demonstrated in field experiments with lodgepole pine (Brockley, 2005; Lindgren et al., 2007) and other *Pinus* species (Malkonen and Kukkola, 1991; Tamm et al., 1999; Fox et al., 2007).

Operational scale nutrition experiments apply nutrients infrequently, usually in a larger amount. Thinning and repeated fertilization treatments are applied over an entire ecosystem, and hence they have the potential to significantly increase stand-level wood production and structural diversity. Small-scale studies have demonstrated the concept of "steady-state" nutrition, whereby small, balanced supplies of nutrients are provided at optimum rates consistent with estimated demand (Linder, 1987; Raison and Myers, 1992; Brockley, 2005). Stand production and structural diversity may be enhanced by maintaining steady state nutrition with repeated optimum nutrient applications. With respect to stand structure and biodiversity, we have barely begun to explore the possibilities (Sullivan et al., in press).

This study was designed to test the hypothesis that, among managed stands, application of a range of PCT intensities and repeated fertilization with optimum nutrition formulations would enhance the 15-year growth increments of lodgepole pine crop trees at both tree and stand levels.

2. Methods

2.1. Study areas

Three study areas each containing several lodgepole pine stands were originally established in 1993. The Summerland study area is located in the Bald Range, 25 km west of Summerland in south-central British Columbia (BC), Canada (49°40'N; 119°53'W). The Kelowna study area is located 37 km northwest of Kelowna, BC (50°04'N; 119°34'W). Both areas are in the Montane Spruce (MS_{dm};

d,m = dry precipitation regime, mild temperature regime) biogeoclimatic zone (Meidinger and Pojar, 1991). A third study area near Williams Lake, BC, reported in Lindgren et al. (2007), was decimated by mountain pine beetle (MPB) (*Dendroctonus ponderosae*) in 2005, and therefore excluded from this analysis. Descriptions of these study areas are provided in Lindgren et al. (2007).

At the start of the study (1993), mean DBH (diameter at breast height, 1.3 m above the forest floor) at Summerland ranged from 2.2 \pm 0.1 cm (mean \pm S.E.) to 4.1 \pm 0.1 cm with a mean age of 12–14 years. Tree height ranged from 2.3 \pm 0.1 m to 3.4 \pm 0.1 m (Fig. 1). Stand areas ranged from 4.4 to 11.3 ha (Table 1). In 1993 at Kelowna, the mean tree diameter and height ranged from 3.1 \pm 0.1 cm to 4.7 \pm 0.1 cm and 3.0 \pm 0.1 m to 4.1 \pm 0.1 m, respectively (Fig. 2), with a mean stand age of 12–13 years. Stand areas ranged from 9.5 to 12.6 ha (Table 1).

2.2. Experimental design

The two study areas were replicates (blocks). Within each replicate, there were five experimental lodgepole pine stands PCT in the following randomized block design: very low density (target 250 stems/ha), low density (target 500 stems/ha), medium density (target 1000 stems/ha), high density (target 2000 stems/ha), and unthinned (at least 4000 stems/ha). Fertilization treatments were applied to one half of each of the thinned units, resulting in a total of nine stands per study area: (1) 250 stems/ha, (2) 250 stems/ha with fertilization, (3) 500 stems/ha, (4) 500 stems/ ha with fertilization, (5) 1000 stems/ha, (6) 1000 stems/ha with fertilization, (7) 2000 stems/ha, (8) 2000 stems/ha with fertilization, and (9) unthinned (Table 1). The restriction on randomization for the allocation of fertilizer treatment (i.e., applied to one-half of each density treatment) resulted in an overall splitplot design, with density as the main-plot effect and fertilization as the split-plot effect. A fertilized unthinned experimental unit was not included as this treatment combination would not be part of any management prescription. Pruning (3-m lift) was carried out within all stands with densities <2000 stems/ha in 1998, 5 years after PCT.

2.3. Density and fertilization treatments

The initial treatment was PCT of pine in autumn of 1993. Fertilization treatments were designed as large-scale "optimum nutrition" applications initiated in November 1994 using a blended



Fig. 1. Mean DBH (cm) and top height (m) of 12- to 14-year old lodgepole pine crop trees immediately post-thinning (fall of 1993) at the Summerland study area. Numbers along the *x*-axis represent target thinning densities (stems/ha) for each of the treatment stands. The unthinned stand had a density of ca. 10,700 stems/ha. The F identifies stands selected for repeated fertilization treatments. Error bars indicate SE.

Table 1

Area (ha) and estimate of stand density (stems/ha; measured immediately pre- and post-PCT in 1993) by replicate study area (blocks) and the split-plot allocation of density and fertilizer treatments.

Block	Density treatment (main plot) (target pct density; stems/ha)	Stand area (ha)						
		Fertilizer treatm	nent (split plot)	Stand density ^a (stems/ha)				
		Unfertilized	Fertilized	1993; pre-thinning	1993, post-thinning			
Summerland	250	11.3	11.3	9980-11,150	268			
	500	7.6	7.6	9980-11,150	511			
	1000	4.5	4.5	9980-11,150	936			
	2000	4.4	4.4	9980-11,150	1774			
	Unthinned	5.0	-	10,700	10,700			
Kelowna	250	10.0	10.0	8686	286			
	500	11.0	11.0	8686	619			
	1000	9.5	9.5	8686	1004			
	2000	11.9	11.9	8686	1739			
	Unthinned	12.6	-	4029	4029			

^a Estimates of stand density for a given density treatment apply equally to both the unfertilized and fertilized stands.



Fig. 2. Mean DBH (cm) and top height (m) of 12- to 13-year old lodgepole pine crop trees immediately post-thinning (fall of 1993) at the Kelowna study area. Numbers along the *x*-axis represent target thinning densities (stems/ha) for each of the treatment stands. The unthinned stand had a density of ca. 4000 stems/ha. The F identifies stands selected for repeated fertilization treatments. Error bars indicate SE.

fertilizer formulated to provide 100 kg/ha N (100 N) (urea), 100 kg/ ha Phosphorus (100 P), 100 kg/ha Potassium (100 K), 50 kg/ha Sulfur (50 S), 25 kg/ha Magnesium (25 Mg), and 1.5 kg/ha Boron (1.5 B). The objective was to maintain a foliar N level of 1.3%, with foliar levels of all other nutrients in proportional balance with foliar N concentration. The blended product (11-25-13-5.5S-2.7Mg-0.17B) was applied by helicopter at a rate of 906 kg/ha to each of the four fertilized stands at the two study areas. Foliar sampling was conducted in the year after fertilization to monitor the nutrient status of the crop trees and develop appropriate multi-nutrient formulations for subsequent fertilizer applications (see Lindgren et al., 2007). In May 1997, two growing seasons after study initiation, stands were fertilized with a N + S blended fertilizer (36-0-0-9S) at an application rate of 547 kg/ha (200 N and 50 S). In October 1998, four growing seasons after study initiation, stands were fertilized with a blended product (37-0-0-6.1S-0.7B) at an application rate of 404 kg/ha (150 N, 25 S, and 3 B). In October 2000, six growing seasons after study initiation, stands were fertilized with a blended product (31.1-0-0-11.3S) at an application rate of 439.4 kg/ha (150 N and 50 S). And finally, during May 2003, eight growing seasons after study initiation, stands were fertilized with a blended product (44.6-0-0-0.45B) at an application rate of 336.1 kg/ha (150 N and 1.5 B). Details of these treatments are given in Lindgren et al. (2007).

2.4. Crop tree measurements

In each stand, sampling of lodgepole pine crop trees was done within permanent tree plots with variable-radius to accommodate variations in stand density. The initial sampling measured DBH (cm) and tree height (m) and was conducted after PCT in the fall of 1993. Subsequent samples were carried out at 5-year intervals during the fall of 1998, 2003, and 2008, and included additional measurements of crown width and heights to the base and widest parts of the crown. In 1998, tree measurements were completed immediately prior to pruning. Crown measurements were made within one-half of the tree plots. Initial tree height measurements (1993) were made using a telescopic height pole, which measured top height to the nearest 0.01 m. Re-measurements of tree heights in 1998, 2003, and 2008 were to the nearest 0.1 m using a digital hypsometer (Forestor Vertex).

At the tree-level, growth response of the stem to thinning and fertilizer treatments was described by 15-year increments (1993–2008) of top height, DBH, basal area (BA), and volume.

Five- and 10-year increments are reported in Lindgren et al. (2007). Tree volume was calculated using a variable-exponent taper function developed for lodgepole pine in the central interior of BC (Kozak, 1988):

$$V = a_1 + a_2 D^2 H \tag{1}$$

where *V* is gross total inside bark volume (m³), *D* is DBH (m), and *H* is top height of tree (m). The two constants, a_1 and a_2 , varied depending on the study area and range of DBH and tree heights observed within a given sample period. Pre-treatment stem volumes were estimated using a_1 and a_2 values of 1254 and 0.349, respectively. Stem volumes for trees sampled in 2008 were estimated using a_1 and a_2 values of 3633 and 0.347, respectively.

At the stand-level, BA/ha and volume/ha were estimated by multiplying the mean tree values by an estimate of stand density (stems/ha) for each stand. Initial stand density was determined immediately following PCT in 1993. Stand densities in 2008 were estimated based on the observed percentage of dead or severely snowpressed trees among the permanently tagged crop trees. This estimate of mortality was used to adjust the initial stand density by a percentage assumed to be representative of the mortality experienced throughout a given stand. As a result, stand-level estimates of BA/ha and volume/ha within thinned stands apply only to the residual cohort of dominant and codominant lodgepole pine trees selected during thinning in 1993 and do not account for any ingress that occurred during the 15 years following thinning.

Crown measurements were initially made immediately prior to pruning in 1998. Crown area represented the widest horizontal cross-section of a crown, and was calculated using the widest crown diameter measurement. Crown characteristics following pruning (1998) were estimated based on the assumption that the new base of the live crown created by pruning was equal to the base of the live crown in 2003 (Fig. 7). These estimates of postpruning crown dimensions should be reasonably accurate because lodgepole pines do not regrow lower branches by epicormic branching (Ballard and Long, 1988) and pruned stands had yet to experience any self-pruning as of 2003. To account for the effects that pruning had on crown characteristics, crown development was calculated relative to the 1998 post-pruning estimates rather than the 1998 pre-pruning measurements.

Density of coniferous trees (crop trees and any other trees that were not culled during thinning treatments or established post-thinning) was estimated among four height classes during the final 10 years (1998–2008) using 20 fixed-radius (100 m^2) plots within the permanent crop tree plots. Within each plot, all trees were tallied by species and height class (0-1.0, 1.1-2.0, 2.1-3.0, and >3.0 m). Three separate samples were carried out at 5-year intervals; 1998, 2003, and 2008.

2.5. Statistical analysis

The experimental design restricted the randomness of fertilizer treatment allocation (i.e., applied to one-half of each of the thinned stands), and hence a split-plot analysis of variance (ANOVA) was used to compare treatment means. The density and fertilizer treatments were assigned as the main- and split-plots, respectively. When several years of data were analyzed together, the time factor was assigned as a split-split plot. The two replicates functioned as blocks. Tree growth is correlated with initial tree size (Johnstone, 1985). Therefore, using initial tree size as a covariate, a split-plot analysis of covariance (ANCOVA) was used to evaluate stem growth rate responses to the treatments.

Before the adjusted means could be used, the assumption of homogeneity of regression coefficients had to be tested. Testing this assumption was carried out using the same blocked, split-plot ANCOVA design described above. A significant covariate \times density \times fertilizer interaction indicated that the assumption was violated and precluded any further analyses using ANCOVA. When this occurred, separate regression equations were generated for each stand (independent factor regressed on the covariate) and used to adjust tree growth to the same rate. These adjusted values were then analyzed using a blocked, split-plot ANOVA. Effects of treatments on stand density and crown characteristics were analyzed without a covariate, using a blocked, split-plot ANOVA.

Duncan's multiple range test (DMRT), adjusted for multiple contrasts, was used to compare treatment means (Saville, 1990). In all analyses, the level of significance was at least P = 0.05. *P*-values ranging from 0.06 to 0.10 were also considered of interest and are reported as marginally significant.

The experimental design was unbalanced because there were no unthinned, fertilized stands. To maintain the power and sensitivity of a balanced design, the unthinned level of the density treatment was omitted from all statistical analyses. Data from unthinned stands are presented in graphs to allow for a visual comparison with managed stands.

3. Results

3.1. Stand density

Estimates of post-PCT stand densities among thinned stands after PCT (Table 1) indicated that thinning treatments had a significant ($F_{3,3}$ = 430.19; P < 0.01) effect on crop tree density. While actual post-thinning densities were slightly different than the PCT target densities, each of the four thinning levels resulted in significantly different (DMRT; P = 0.05) crop tree densities. Across all treatments, the post-PCT crop tree density estimated in 1993 changed little during the following 15 years as only a mean of 5.8% of crop trees were lost during this period; primarily due to snowpress.

Because very few understory saplings and/or seedlings existed in stands prior to thinning and the objective of PCT was to remove all trees that could compete with future crop trees, postthinning tree composition was a single stratum of crop trees, which ranged in height from approximately 2.5 to 4.0 m. Therefore, immediately following thinning, this tallest height class (taller than 3.0 m) included only crop trees. However, five to 15 years post-thinning, the density of this tallest height class was significantly affected ($F_{3,3} = 2982.89$; P < 0.01) by PCT (Table 2). As was reported for 1993, in 1998, 2003, and 2008 each of the four density levels had significantly different mean density of this dominant tree stratum (DMRT; P = 0.05) according to PCT intensity (i.e., 2000 > 1000 > 500 > 250 stems/ha; Fig. 3). During this period, mean density of the dominant tree layer was also significantly affected by time ($F_{2,16}$ = 31.76; P < 0.01); increasing as shorter trees grew into this upper height class. A marginally significant time \times density interaction ($F_{6,16}$ = 2.56; P = 0.06) resulted from dominant tree layer densities increasing far more rapidly within the heavily thinned stands compared to those lightly thinned (Fig. 3). From 1998 to 2008, the dominant tree layer density increased by 182%, 134%, 33%, and 9% among the 250, 500, 1000, and 2000 stems/ha stands, respectively (Fig. 3). Fertilizer treatments did not significantly affect the dominant tree layer density.

PCT density treatments did not have an overall significant effect on the densities of any of the understory tree layers (Table 2). However, a significant time × density effect ($F_{6,16}$ = 8.79; P < 0.01) for the tallest understory stratum (2.1–3.0 m) revealed that the density effect, while only marginally significant 5 years post-PCT ($F_{3,3}$ = 5.68; P = 0.09), became significant 10 ($F_{3,3}$ = 11.26; P = 0.04)

Table 2

Summary of split-split plot ANOVA investigating the effects of PCT density (main plot; four levels; target of 250, 500, 1000, and 2000 crop trees/ha), fertilizer (split plot; two levels; unfertilized and repeatedly fertilized), and time (split-split plot; three levels; 1998, 2003, and 2008) on density of all trees among four height classes.

Height class	Density		Fertilizer		$\text{Density} \times \text{fertilizer}$		Time		$\text{Time} \times \text{density}$		$\text{Time} \times \text{fertilizer}$	
	F _{3,3}	Р	F _{1,4}	Р	F _{3,4}	Р	F _{2,16}	Р	F _{6,16}	Р	F _{2,16}	Р
Dominant layer >3.0 m	2982.89	<0.01	0.66	0.46	1.50	0.34	31.76	<0.01	2.56	0.06	0.84	0.45
Understory layers 2.1–3.0 m 1.1–2.0 m 0.0–1.0 m	0.95 2.48 0.87	0.51 0.24 0.55	2.19 9.89 42.60	0.21 0.03 <0.01	0.24 0.03 1.14	0.87 0.99 0.43	84.55 12.74 39.00	<0.01 <0.01 <0.01	8.79 0.89 0.26	<0.01 0.53 0.95	5.17 19.59 4.45	0.02 <0.01 0.03



Fig. 3. Mean total density (stems/ha) of trees within the dominant tree layer (taller than 3 m) among the four density treatments measured at 5-year intervals; 1998, 2003, and 2008. Densities include crop trees, as well as other trees that grew into this upper height class with time. Numbers along the *x*-axis represent target PCT densities (stems/ha). Error bars indicate SE and are based on two replicate study areas (n = 2).

and 15 years post-PCT ($F_{3,3} = 9.29$; P = 0.05). Ten years following PCT, mean density of the 2.1 to 3.0-m tall tree stratum was significantly greater within the three most heavily thinned stands (250, 500, and 1000 stems/ha) compared to the least thinned stands (2000 stems/ha) (DMRT; P = 0.05). By 15 years post-PCT, the significant difference was only evident between the two most heavily thinned stands (250 and 500 stems/ha) compared to both of the lightly thinned stands (DMRT; P = 0.05). A significant time × fertilizer effect for all three understory tree strata (Table 2) resulted from a lack of significantly less density observed within fertilized compared to unfertilized stands for all height classes in 2008.

3.2. Growth of crop trees

Adjusted mean 15-year height increments varied less than 0.75 m among all of the treated stands (from 5.32 ± 0.54 to 6.04 ± 0.52 m; Fig. 4a). Restated, a mean annual increment (MAI) of less than five cm height growth separated the fastest (fertilized 1000 stems/ha) from slowest (fertilized 250 stems/ha) growing stands. Neither density nor fertilizer treatments had a significant effect on 15-year height increment (Table 3).

Adjusted mean 15-year DBH increments among treated stands were positively correlated with PCT intensity and further increased by fertilization (Fig. 4b). Mean DBH increment was $51 \pm 2\%$ greater within stands with the fastest (fertilized 250 stems/ha) compared to the slowest (unfertilized 2000 stems/ha) diameter growth; 14.01 ± 0.14 vs. 9.31 ± 0.07 cm, respectively. While DBH increment



Fig. 4. Adjusted mean 15-year increments (1993–2008) of (a) height and (b) DBH of young lodgepole pine crop trees among nine treatment stands. Treatment stands include four PCT densities, both unfertilized and repeatedly fertilized, and an unthinned stand for comparison. Numbers along the *x*-axis represent target thinning densities (stems/ha). Unthinned stand densities ranged from 4000 to 10,700 stems/ha. Error bars indicate SE and are based on two replicate study areas (n = 2).

increased with decreasing stand density, the density effect was not significant (Table 3). The effect of repeated fertilization on 15-year DBH increment was significant ($F_{1,3} = 134.08$; P < 0.01), with 17 ± 1% greater diameter growth resulting from fertilizer treatments; 12.42 ± 0.08 vs. 10.64 ± 0.08 cm, respectively (Table 3).

Adjusted mean 15-year tree BA increments among treated stands were positively correlated with PCT intensity and further increased by fertilization (Fig. 5a). Tree BA was 88 ± 9% greater within fertilized 250 stems/ha compared to unfertilized 2000 stems/ha stands; 2.43 ± 0.11 vs. 1.29 ± 0.01 m² × 10^{-2} , respectively. While the density effect was not significant, the effect of fertilizer was ($F_{1,3} = 121.51$; P < 0.01), with a mean of $28 \pm 3\%$ greater tree BA growth resulting with fertilizer treatments; 2.05 ± 0.03 vs. 1.60 ± 0.03 m² × 10⁻², respectively (Table 3). Adjusted mean 15-year stand BA increments among treated stands were positively correlated with crop tree density and increased by fertilization (Fig. 5b). Stand BA increment was 151 ± 28% greater within the fertilized 2000 stems/ha compared to the unfertilized 250 stems/ha stands; 20.64 ± 2.26 vs. 8.22 ± 0.17 m²/ha, respectively. Despite the notable effect of PCT treatments on stand BA growth, the density effect was not significant (Table 3). The effect of fertilizer on 15-year stand BA increment was marginally significant ($F_{1,3}$ = 8.35; P = 0.06), with 20 ± 6% greater BA growth

Table 3

Adjusted mean (n = 2 replicate study areas) (SE) 15-year increments (1993–2008) of crop tree attributes for young lodgepole pine among four density and two fertilization treatments. Results of split-plot analysis of covariance (ANCOVA) are also provided. Within a row, mean values with different letters are significantly different by Duncan's multiple range test, adjusted, if necessary, for multiple contrasts.

	Estimated marginal means (adjusted for covariate)					Split-plot ANCOVA						
						Density		Fertilizer		Density \times fertilizer		
					F _{3,2}	Р	F _{1,3}	Р	F _{3,3}	Р		
HT (m)	250 stems/ha 5.52 (0.42) Unfertilized 5.64 (0.56)	500 stems/ha 5.68 (0.92)	1000 stems/ha 5.71 (0.45) Fertilized 5.70 (0.74)	2000 stems/ha 5.77 (0.79)	0.12	0.94	0.20	0.69	2.76	0.21		
DBH (cm)	250 stems/ha 13.25 (0.12) Unfertilized 10.64b (0.08)	500 stems/ha 12.20 (0.82)	1000 stems/ha 10.83 (0.64) Fertilized 12.42a (0.08)	2000 stems/ha 9.83 (0.30)	3.77	0.22	134.08	<0.01	4.10	0.14		
BA/tree (m ² x10 ⁻²)	250 stems/ha 2.24 (0.06) Unfertilized 1.60b (0.03)	500 stems/ha 2.00 (0.24)	1000 stems/ha 1.64 (0.13) Fertilized 2.05a (0.03)	2000 stems/ha 1.42 (0.05)	3.44	0.23	121.51	<0.01	4.33	0.13		
BA/ha (m²)	250 stems/ha 8.30 (0.24) Unfertilized 12.33 (0.25)	500 stems/ha 12.09 (1.70)	1000 stems/ha 14.39 (1.58) Fertilized 14.75 (0.64)	2000 stems/ha 19.38 (1.16)	4.94	0.17	8.35	0.06	0.87	0.54		
Vol./tree (m ³)	250 stems/ha 0.10 (0.01) Unfertilized 0.07b (0.01)	500 stems/ha 0.09 (0.02)	1000 stems/ha 0.07 (0.00) Fertilized 0.09a (0.01)	2000 stems/ha 0.07 (0.00)	1.70	0.39	23.96	0.02	1.75	0.33		
Vol./ha (m ³)	250 stems/ha 48.02 (2.29) Unfertilized 59.72b (4.81)	500 stems/ha 63.06 (12.03)	1000 stems/ha 67.38 (3.27) Fertilized 70.24a (3.33)	2000 stems/ha 81.47 (5.25)	2.24	0.32	10.82	0.05	1.83	0.32		



Fig. 5. Adjusted mean 15-year increments (1993–2008) of (a) tree and (b) stand BA of young lodgepole pine crop trees among nine treatment stands. Treatment stands include four PCT densities, both unfertilized and repeatedly fertilized, and an unthinned stand for comparison. Numbers along the *x*-axis represent target thinning densities (stems/ha). Unthinned stand densities ranged from 4000 to 10,700 stems/ha. Error bars indicate SE and are based on two replicate study areas (n = 2).

resulting from fertilizer treatments; 14.75 ± 0.64 vs. 12.33 ± 0.25 m²/ha, respectively (Table 3).

Adjusted mean 15-year tree volume increments among treated stands were positively correlated with PCT intensity and further increased by fertilization (Fig. 6a) and were 75% greater within fertilized 250 stems/ha compared to unfertilized 2000 stems/ha stands; 10.62 ± 1.36 vs. 6.08 ± 0.46 m³ $\times 10^{-2}$, respectively. While the density effect was not significant, the effect of fertilizer was $(F_{1,3} = 23.96; P = 0.02)$, with 27 ± 17% greater tree volume growth resulting with fertilizer treatments; 9.18 ± 1.00 VS. $7.24 \pm 0.54 \text{ m}^3 \times 10^{-2}$, respectively (Table 3). Adjusted mean 15year stand volume increments among treated stands were positively correlated with crop tree density and increased by fertilization (Fig. 6b). Stand volume was 89% greater within the fertilized 2000 stems/ha compared to the fertilized 250 stems/ha stands; 86.95 ± 1.77 vs. 46.07 ± 3.42 m³/ha, respectively. Despite the notable effect of PCT treatments on stand volume increment, the density effect was not significant (Table 3). The effect of fertilizer on 15-year stand volume increment was significant ($F_{1,3}$ = 10.82; P = 0.05), with 18% greater stand volume growth resulting from fertilizer treatments; 70.24 ± 3.33 vs. 59.72 ± 4.81 m³/ha, respectively (Table 3).

Crop tree crown dimensions (width, length, and live crown ratio) were noticeably affected by thinning and fertilization treatments and, of course, pruning (Fig. 7). In 2008 (15 years after PCT and 5 years after the most recent fertilization application), mean crown area per tree among treated stands was positively correlated with PCT intensity and further increased by fertilization. Tree crown area was 83% greater within fertilized 250 stems/ha compared to unfertilized 2000 stems/ha stands; 11.71 ± 0.86 vs. 6.39 ± 1.13 m², respectively. While the density effect was not significant, the effect of fertilizer was marginally significant ($F_{1,4} = 6.79$; P = 0.06), with a mean of 20% greater tree crown area resulting from fertilizer treatments.



Fig. 6. Adjusted mean 15-year increments (1993–2008) of (a) tree and (b) stand volume of young lodgepole pine crop trees among nine treatment stands. Treatment stands include four PCT densities, both unfertilized and repeatedly fertilized, and an unthinned stand for comparison. Numbers along the x-axis represent target thinning densities (stems/ha). Unthinned stand densities ranged from 4000 to 10,700 stems/ha. Error bars indicate SE and are based on two replicate study areas (n = 2).

4. Discussion

Intensive management is the norm within pine plantations of the southern US where the economic benefits of PCT, fertilization, and vegetative competition control have been clearly demonstrated for loblolly pine plantations (Albaugh et al., 2004; Sword Sayer et al., 2004; Fox et al., 2007). In contrast, management of plantations throughout Canada continues to be extensive rather than intensive, with little or no silviculture intervention beyond stand establishment, despite the clear potential for many benefits (economic, ecological, and social) possible with increased tree culture (Lautenschlager, 2000; Park and Wilson, 2007). Relative to extensive silviculture, intensive silviculture would require a significant increase in long-term investments, which, because of constantly changing economic, ecological, and social constraints, is legitimately viewed as risky (Brown et al., 1999). Therefore, an improved understanding of treatment effects and potential benefits associated with intensive silviculture is needed, particularly for northern ecosystems (Lautenschlager, 2000), before managers are likely to make intensive silviculture a part of standard practices.

Prior to this study, the potential for intensive management within Canadian pine plantations remained largely theoretical, or demonstrated only at a small-scale (<0.1 ha sample plots), as no other studies have reported on long-term tree responses (>10 years) to operational-scale (several hectares) applications of intensive silviculture treatments. Our study represents a large effort that provides 15 years of tree growth response data from the most intensively managed plantations in Canada. Total area of treatment stands (combined over two replicate study areas) was 158 ha, of which 140 ha were thinned, 108 ha were pruned, and 70 ha were repeatedly fertilized. The five applications of fertilizers totaled 750 kg N/ha (as well as smaller amounts of P, K, S, B, and Mg) resulting in more than 52 tonnes of N being applied over an 8-year period. Treatment effects were monitored using a total of 360 variable-radius plots including 3600 permanently tagged crop trees (for quantifying growth of crop trees; sampled four times at 5-year intervals) as well as 360 fixed radius plots (for quantifying total tree densities among height classes; sampled three times at 5-year intervals).

4.1. Height class distribution and ingress

When this study was initiated in 1993, stands were predominantly comprised of a single cohort of densely stocked (more than 4000 and 10,000 stems/ha at the Kelowna and Summerland study areas, respectively), 12- to 14-year old lodgepole pine trees, that were approximately 2.5–4.0 m in height. As intended, the PCT treatments had a dramatic and significant effect on stand density and fertilizer treatments significantly increased foliar N levels



Fig. 7. Mean (n = 2 replicate study areas) crop tree crown dimensions as measured at 5-year intervals (1998, 2003, and 2008) among the nine treatment stands.

without creating any nutrient imbalances or deficiencies (Lindgren et al., 2007). The reduced competition among trees following thinning treatments resulted in low mortality as very few crop trees were lost during the 15-year post-PCT period. However, as tree canopies continue to close with fast growing crop trees and ingress of a new cohort of non-crop trees, increased competition is expected to initiate self-thinning. While density of tall trees among the heavily thinned stands continued to increase 15 years post-PCT, densities have leveled off, or even decreased within stands that received the lightest thinning treatment (2000 stems/ha), indicating that self-thinning is just beginning within these dense stands.

The contribution of ingress to total stand volume was not inferred from the height class distribution data; particularly when the height class which contributed the majority of volume was not finite (i.e., >3.0 m). Intuitively, it would seem that there will be considerable fiber value provided by the non-crop trees, however, without specific data, one is left to speculate as to the significance of this ingress. A pilot study carried out within treatment stands at the Kelowna study area during the fall of 2009 (16 years post-PCT) estimated the stem volume of all trees taller than 1.3 m using 20 fixed-radius plots $(3.99 \text{ m}; 50 \text{ m}^2)$ per treatment stand and distinguished crop- from non-crop trees (unpublished data). This limited study found that thinning increased the proportional contribution of ingress to total stand volume by as much as 47% within the 250 stems/ha unfertilized stand, and that this proportion decreased with increasing crop tree density. This same analysis found the fertilizer effect on total stand volume appeared to be negligible, however, a density effect was evident. When averaged across unfertilized and fertilized stands, the impact of PCT was apparent, with a mean of 39%, 31%, 12%, and 2% of the total stand volume attributed to ingress within the 250, 500, 1000, and 2000 stems/ha stands, respectively. A portion of the stand volume contributed by ingress will undoubtedly be non-merchantable (i.e., too small). However, the stand-level productivity of crop trees should not be interpreted as total productivity, as ingress will clearly mitigate some of the stand volume losses resulting from intensive PCT.

4.2. Crop trees

Height growth of non-repressed lodgepole pine has been recognized by other studies to not benefit from increased resources (Johnstone, 1985; Brockley, 2007), as trees allocate increased photosynthate production into crown and stem radial growth more than height (Tamm et al., 1999). Amponsah et al. (2004) also hypothesized that the higher flow capacity (increased hydraulic conductivity, sapwood permeability, and leaf specific conductivity) observed within lower branches following repeated fertilizations, may cause water stress and reduced growth for the upper portions of the tree, including the terminal leader. Brockley (2007) reported that annual fertilizer applications to lodgepole pine resulted in less height growth than periodic applications. Increased resources (light from thinning and nutrients from fertilization) may also stimulate the growth of non-crop plants, which then increase competition, possibly eliminating much of the desired growth response intended for the crop trees (Powers and Reynolds, 1999). For these reasons, excessive thinning and fertilization may, with time, result in decreased height growth. Our study supported this premise as neither density nor fertilization treatments had any significant effect on 15-year increments of height growth.

The significantly greater DBH and BA per tree increments observed among heavily compared to lightly thinned stands reported for the initial 10-years post-PCT (Lindgren et al., 2007) was not evident when considering the entire 15-year growth increment. The loss of density effect for DBH growth for this longer period resulted from a greater decrease in rates of diameter and BA growth during the final 5 years within the heavily compared to lightly thinned stands. A likely cause was increased competition from non-crop trees as well as well-developed herb and shrub layers. Mean BA per tree growth continued to accelerate during the years 11–15 among all treatments, except for the slowest growing stand (2000 stems/ha), which nearly resulted in a significant density effect. The significantly enhanced DBH and BA growth rate resulting from fertilization reported for the initial 10-year increment (Lindgren et al., 2007) continued for the duration of this 15-year study.

At the tree level, mean 15-year crop tree volume increment followed the same trend as reported for the initial 10-year increment (Lindgren et al., 2007); enhanced by thinning (although not significantly) and significantly increased by fertilization. Most studies evaluated the effectiveness of thinning treatments relative to no thinning and nearly all indicate significantly enhanced tree volume growth rates with thinning (e.g., Valinger et al., 2000; Blevins et al., 2005; Zhang et al., 2006; Jiménez et al., 2011; Soucy et al., 2012). While our experimental design did not allow a comparison of growth rates between thinned and unthinned stands, it is reasonable to expect that tree volume increment was enhanced by thinning as has been consistently reported for other studies.

The hypothesis that 15-year, tree-level growth increments of lodgepole pine crop trees would be enhanced by PCT and repeated fertilization was partially supported by the results. While visual comparison of the density effect on DBH, BA, and volume (Figs. 4b, 5a, and 6a) were in support of this hypothesis, the statistical comparison, which did not include the unthinned control, did not detect a significant density effect among the thinned stands. The fertilizer effect did support the hypothesis in that DBH, BA, and tree volume, were all significantly enhanced by repeated fertilization.

At the stand level, despite the significant impact that PCT had on crop tree density, 15-year BA and volume increments were statistically similar across density treatments. This contrasted with the initial 10-year increment, where higher density stands had greater BA/ha (marginally significant; P = 0.08) and volume/ha increments (P < 0.01) than lower density stands (Lindgren et al., 2007). This pattern indicated that the enhanced growth rates observed at the tree level among heavily thinned stands, while not significant, was enough to compensate for some of the losses of stand level crop tree productivity caused by heavy thinning treatments. If also including the contributions that non-crop trees make to net total stand volume, it became apparent that initial losses associated with thinning, even well below full stocking levels, can decrease substantially over time. While net total stand volume can be significantly greater than merchantable volume, the significance of non-merchantable trees should not be discounted. For several reasons, non-merchantable trees may have considerable value as, for example, future crop trees, advanced regeneration (should anything damage the overstory crop, such as a MPB infestation), carbon sinks, habitat structure, and for visual quality objectives. Alternatively, the development of an understory of nonmerchantable trees may be counter to the objectives of a stand. A manager may prescribe that such ingress be controlled (i.e., thinned), for example, to decrease competition with overstory trees, enhance and prolong suitable range conditions for grazing ungulates, and decrease fire risk by reducing "ladder fuels".

Fertilizer treatments can further mitigate losses associated with heavy thinning. Averaged over 15 years, the fertilizer treatments resulted in an increase to mean annual crop tree volume increment of $0.70 \pm 0.39 \text{ m}^3$ /ha/year. The longevity of this beneficial fertilizer effect is of key interest as the repeated applications had the objective of achieving a sustained rather than temporary increase in tree and stand growth (Tamm et al., 1999; Brockley, 2007). It is encouraging to note that the significantly enhanced rate of growth within

fertilized stands was maintained during the final 5 years (2003-2008); a period that did not include any fertilizer applications. However, future sampling will be required to determine how long this enhanced growth will be sustained. While the current study assessed only a single level of fertilizer application, Brockley (2007) investigated several levels of fertilizers (both different formulations as well as frequencies of application) over a period of 12 years. The response of lodgepole pine crop trees in his study showed clear evidence of diminishing returns with increasing intensity of fertilization. Annual applications of fertilizer provided only slightly increased, or even decreased mean annual stand volume increments relative to various fertilizer formulations applied at 6-year intervals (Brockley, 2007). Interestingly, such negative dose responses have not been reported for southern pines such as loblolly, which respond favourably to large, and frequent, nutrient additions (Albaugh et al., 2004). With only a single level of fertilization, our study is unable to comment on whether or not a negative dose response has occurred. However, the conclusions of Brockley (2007) suggest that even larger gains in wood production may be possible with a less intensive fertilization prescription, and also with the addition of vegetative competition control (Wagner et al. 2006).

The hypothesis that 15-year, stand-level growth increments of lodgepole pine crop trees would be enhanced by PCT and repeated fertilization was partially supported by the results. The density effect on stand BA and volume growth was not significant, while fertilization significantly enhanced both attributes.

4.3. Stand management and climate change

Carbon sequestration is one way to moderate the continuing increase in atmospheric carbon dioxide (CO₂), and therefore is an important process for mitigating climate change. Trees provide 74% of all aboveground terrestrial carbon and are an important sink for atmospheric CO₂ (Birdsey, 1992). The increased stand volume of crop trees and ingress generated by PCT and fertilization should enhance carbon sequestration. Jiménez et al. (2011) noted that intense PCT (more than 90% reduction in density) of denselv stocked. post-fire maritime pine (Pinus pinaster) in northwestern Spain resulted in increased foliar efficiency and growth of residual saplings that compensated for much of the carbon storage lost by thinning, at least in the short-term (5 years post-thinning). Blevins et al. (2005) noted that stand-level volume growth rates returned to control levels just 4 years following thinning within repressed stands of lodgepole pine in BC. Stand-level carbon storage losses resulting from PCT are further mitigated if accounting for the contributions of residues and understory vegetation (Campbell et al., 2009; Jiménez et al., 2011).

Huettl and Zoettl (1992) noted that the potential to increase carbon storage capacity in forests is often limited by poor nutrient availability. In addition, Hoen and Solberg (1994) indicated that fertilization was one of the best methods to increase net CO₂ fixation. Enhanced forest productivity resulting from fertilization can increase carbon storage capacity not only by increasing volume and biomass of trees (as was reported in our study), but also by increasing the carbon input to forest soils (Jandl et al., 2007; Nave et al., 2009). In addition to mitigating the effects of climate change through enhanced carbon sequestration, incremental silviculture treatments may enhance the resiliency of managed stands to the difficult growing conditions predicted as a result of climate change (Millar et al., 2007). For example, the increased intensity of summer droughts associated with climate change would negatively impact the health and survival of young and older forests alike; particularly those growing in areas that historically experience water stress, such as much of the lodgepole pine forests of the PNW. Thinning of densely stocked forest stands has been suggested as an adaptive management strategy to enhance soil water content and reduce water stress for forests growing within dry environments (Papadopol, 2000).

5. Conclusions

Our results indicated a trend of increasing tree-level growth (15-year increments of DBH, BA, and volume) with increasing levels of PCT, however, the density effect among thinned stands was not significant, and resulted in similar stand-level increments of BA and volume. This lack of stand-level density effect 15-years post-PCT was important considering the striking difference in crop tree density following thinning treatments (i.e., each increasing level of thinning intensity corresponded with a decrease in crop tree density of 50%). While stand-level productivity of crop trees was still clearly correlated with crop tree density 15 years post-PCT, the lack of significant difference indicated that more crop tree wood was being produced within the heavily than lightly thinned stands, which mitigated the initial loss of productivity associated with intensive thinning. The five fertilization treatments had a consistent and significant positive effect on 15-year growth increments of DBH (17% increase), BA/tree (28% increase), volume/tree (27% increase), BA/ha (20% increase), and volume/ha (18% increase).

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References

- Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, USA.
- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. For. Ecol. Manage. 192, 3–19.
- Allen, H.L., Dougherty, P.M., Campbell, R.G., 1990. Manipulation of water and nutrients – practice and opportunity in southern US pine forests. For. Ecol. Manage. 30, 437–453.
- Amponsah, I.G., Lieffers, V.J., Comeau, P.G., Brockley, R.P., 2004. Growth response and sapwood hydraulic properties of young lodgepole pine following repeated fertilization. Tree Phys. 24, 1099–1108.
- Ballard, L.A., Long, J.N., 1988. Influence of stand density on log quality of lodgepole pine. Can. J. For. Res. 18, 911–916.
- Bergh, J., Nilsson, U., Grip, H., Hedwall, P.O., Lundmark, T., 2008. Effects of frequency of fertilization on production, foliar chemistry, and nutrient leaching in young Norway spruce stands in Sweden. Silva Fenn. 42, 721–733.
- Birdsey, R.A., 1992. Carbon Storage and Accumulation in United States Forest Ecosystems. USDA Forest Service, General Technical, Report WO-59.
- Blevins, D.P., Prescott, C.E., Allen, H.L., Newsome, T.A., 2005. The effects of nutrition and density on growth, foliage biomass, and growth efficiency of high-density fire-origin lodgepole pine in central British Columbia. Can. J. For. Res. 35, 2851– 2859.
- Brockley, R.P., 1996. Lodgepole Pine Nutrition and Fertilization: A Summary of British Columbia Ministry of Forests Research Results. FRDA Report 266. Forest Resource Development Agreement, Canadian Forestry Service British Columbia Ministry of Forests, Victoria, Canada.
- Brockley, R.P., 2005. Effects of post-thinning density and repeated fertilization on the growth and development of young lodgepole pine. Can. J. For. Res. 35, 1952– 1964.
- Brockley, R.P., 2007. Effects of 12 years of repeated fertilization on the foliar nutrition and growth of young lodgepole pine in the central interior of British Columbia. Can. J. For. Res. 37, 2115–2129.

- Brockley, R.P., Trowbridge, R.L., Ballard, T.M., Macadam, A.M., 1992. Nutrient management in interior forest types. In: Proceedings Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests, University of Washington Institute of Forest Resources Contribution 73, Seattle, WA, pp. 43–64.
- Brooks, D.J., 1997. The outlook for demand and supply of wood: implications for policy and sustainable management. Commonwealth Forest. Rev. 76, 31–36.
- Brown, J.R., Hemck, J., Price, D., 1999. Managing low-output agroecosystems sustainably: the importance of ecological thresholds. Can. J. For. Res. 29, 1112– 1119.
- Campbell, J., Alberti, G., Martin, J., Law, B.E., 2009. Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. For. Ecol. Manage. 257, 453–463.
- Cole, D.M., Koch, P., 1996. Managing Lodgepole Pine to Yield Merchantable Thinning Products and Attain Sawtimber Rotations. USDA Forest Service Intermountain Research Station. Research Paper INT-RP-482.
- Fox, T.R., Jokela, E.A., Allen, H.L., 2007. The development of pine plantation silviculture in the southern United States. J. For. 105, 337–347.
- Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155, 81–95.
- Hoen, H.F., Solberg, B., 1994. Potential and economic efficiency of carbon sequestration in forest biomass through management. For. Sci. 40, 429–451.
- Huettl, R.F., Zoettl, H.W., 1992. Forest fertilization: its potential to increase the CO₂ storage capacity and to alleviate the decline of the global forests. Water, Air, Soil Pollut. 64, 229–249.
- Hunter Jr., M.L., Schmiegelow, F.K.A., 2011. Wildlife, Forests, and Forestry. Principles of Managing Forests for Biological Diversity, second ed. Prentice Hall, New York, NY.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268.
- Jiménez, E., Vega, J.A., Fernández, C., Fonturbel, T., 2011. Is pre-commercial thinning compatible with carbon sequestration? A case study in a maritime pine stand in northwestern Spain. Forestry 84, 149–157.
- Johnstone, W.D., 1985. Thinning lodgepole pine. In: Baumgartner, D.M., Krebill, R.G., Arnott, J.T., Weetman, G.F. (Eds.), Lodgepole Pine: The Species and Its Management. Washington State University Cooperative Extension, Spokane, Washington, USA, and Vancouver, BC, pp. 253–262.
- Jokela, E.J., Dougherty, P.M., Martin, T.A., 2004. Long-term production dynamics of loblolly pine stands in the southern United States: a synthesis of seven longterm experiments. For. Ecol. Manage. 192, 117–130.
- Koch, P., 1996. Lodgepole Pine in North America. For. Prod. Soc, Madison, WI.
- Kozak, A., 1988. A variable exponent taper equation. Can. J. For. Res. 18, 1363–1368. Lautenschlager, R.A., 2000. Can intensive silviculture contribute to sustainable
- forest management in northern ecosystems? For. Chron. 76, 293–295. Linder, S., 1987. Responses to water and nutrients in coniferous systems. Ecol. Stud.
- 61, 180–202.
- Lindgren, P.M.F., Sullivan, T.P., Sullivan, D.S., Brockley, R.P., Winter, R., 2007. Growth response of young lodgepole pine to thinning and repeated fertilization treatments: 10-year results. Forestry 80, 587–611.
- Malkonen, E., Kukkola, M., 1991. Effect of long-term fertilization on the biomass production and nutrient status of Scots pine stands. Fert. Res. 27, 113–127.
- Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia. Research Branch, Ministry of Forests, Victoria, BC. Special Report Series No. 6.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.
- Moore, S.E., Allen, H.L., 1999. Plantation forestry. In: Hunter, M.L., Jr. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, New York, NY, pp. 400–433.
- Nabuurs, G.J., Pussinen, A., van Brusselen, J., Schelhaas, M.J., 2007. Future harvesting pressure on European forests. Eur. J. For. Res. 126, 391–400.

- Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2009. Impacts of elevated N inputs on north temperate forest soil C storage, C/N, and net N-mineralization. Geoderma 153, 231–240.
- Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics, updated edition. Wiley, New York.
- Papadopol, C.S., 2000. Impacts of climate warming on forests in Ontario: options for adaptation and mitigation. For. Chron. 76, 139–149.
- Park, A., Wilson, E.R., 2007. Beautiful plantations: can intensive silviculture help Canada to fulfill ecological and timber production objectives? For. Chron. 83, 825–839.
- Powers, R.F., Reynolds, P.E., 1999. Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. Can. J. For. Res. 29, 1027–1038.
- Raison, R.J., Myers, B.J., 1992. The biology of forest growth experiment: linking water and nitrogen availability to the growth of *Pinus radiata*. For. Ecol. Manage. 52, 279–308.
- Raunikar, R., Buongiornoa, J., Turnerb, J.A., Zhu, S., 2010. Global outlook for wood and forests with the bioenergy demand implied by scenarios of the Intergovernmental Panel on Climate Change. For. Pol. Econ. 12, 48–56.
- Saville, D.J., 1990. Multiple comparison procedures: the practical solution. Am. Stat. 44, 174–180.
- Sedjo, R.A., 1999. The potential of high-yield plantation forestry for meeting timber needs – recent performance, future potentials, and environmental implications. New For. 17, 339–359.
- Soucy, M., Lussier, J., Lavoie, L., 2012. Long-term effects of thinning on growth and yield of an upland black spruce stand. Can. J. For. Res. 42, 1669–1677.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2001. Stand structure and small mammals in young lodgepole pine forest: 10-year results after thinning. Ecol. Appl. 11, 1151–1173.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2006. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest: III. Growth of crop trees and coniferous stand structure. For. Ecol. Manage. 228, 69–81.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2009. Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. For. Ecol. Manage. 258S, S127–S141.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2013. Stand structure and small mammals in intensively managed forests: scale, time, and testing extremes. Forest Ecol. Manage (in press).
- Sutton, W.R.J., 1999. The need for planted forests and the example of radiata pine. New For. 17, 95–109.
- Sword Sayer, M.A., Goelz, J.C.G., Chambers, J.L., Tang, Z., Dean, T.J., Haywood, J.D., Leduc, D.J., 2004. Long-term production dynamics of loblolly pine stands in the southern United States. For. Ecol. Manage. 192, 71–96.
- Tamm, C.O., Aronsson, A., Popovic, B., Flower-Ellis, J., 1999. Optimum nutrition and nitrogen saturation in Scots pine stands. Stud. For. Suec., 206.
- Wagner, R.G., Little, K.M., Richardson, B., McNabb, K., 2006. The role of vegetation management for enhancing productivity of the world's forests. Forestry 79, 57– 79.
- Walton, A., Hughes, J., Eng, M., Fall, A., Shore, T., Riel, B., Hall, P., 2009. Provinciallevel Projection of the Current Mountain Pine Beetle Outbreak. British Columbia Ministry of Forests and Range, Victoria, BC.
- Weetman, G.F., 1988. Nutrition and fertilization of lodgepole pine. In: Proceedings Future Forests of the Mountain West: A Stand Culture Symposium. USDA Forest Service. Gen. Tech. Rep. INT-243, Ogden, Utah.
- Zhang, S.Y., Chauret, G., Swift, D.E., Duchesne, I., 2006. Effects of precommercial thinning on tree growth and lumber quality in a jack pine stand in New Brunswick, Canada. Can. J. For. Res. 36, 945–952.