

# Growth response of young lodgepole pine to thinning and repeated fertilization treatments: 10-year results

P. M. F. LINDGREN<sup>1</sup>, T. P. SULLIVAN<sup>2\*</sup>, D. S. SULLIVAN<sup>1</sup>,  
R. P. BROCKLEY<sup>3</sup> AND R. WINTER<sup>4</sup>

<sup>1</sup>Applied Mammal Research Institute, 11010 Mitchell Avenue, Summerland, British Columbia, Canada V0H 1Z8

<sup>2</sup>Faculty of Forestry, Department of Forest Sciences, 2424 Main Mall, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

<sup>3</sup>Kalamalka Research Station, Ministry of Forests and Range, 3401 Reservoir Road, Vernon, British Columbia, Canada V1B 2C7

<sup>4</sup>Forest Practices Branch, Ministry of Forests and Range, 727 Fisgard Street, Victoria, British Columbia, Canada V8W 9C2

\*Corresponding author. E-mail: tom.sullivan@ubc.ca

## Summary

This study was designed to test the hypothesis that large-scale pre-commercial thinning (PCT) to various stand densities, at ages 12–14 years, combined with repeated fertilization, would, over a 10-year treatment period, enhance productivity of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) crop trees. Study areas were located near Summerland, Kelowna and Williams Lake 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<sup>-1</sup>, with one stand of each pair fertilized five times at 2-year intervals, and an unthinned stand. The very low, low- and medium-density stands were also pruned to a 3-m lift 5 years after thinning. At the tree level, fertilization treatments significantly increased diameter at breast height (DBH), basal area (BA) and volume growth and heavy PCT significantly increased DBH and BA growth. Pruning may mitigate some of the negative stem form and wood quality attributes associated with fast-growing trees without adversely affecting stem growth. At the stand level, PCT to very low and low densities significantly decreased the volume growth compared with high-density stands. The potential beneficial impacts that PCT and repeated fertilization treatments have for mitigating timber supply shortfalls, as well as potentially minimizing crop tree losses due to mountain pine beetle (*Dendroctonus ponderosae* Hopk.), are also discussed.

## Introduction

Conservation of primary/old-growth forests has reached a critical threshold in all forested land-

scapes on earth. In the temperate zones, only Canada and Russia still harbour great tracts of true forest wilderness. Unfortunately, the world human populations' demand for wood products,

and hence harvesting of remaining old-growth forests, continue to increase (Brooks, 1997; Sutton, 1999). Intensively managed forests, in association with appropriate land zonation, could help alleviate the pressure on old-growth forests, as promoted by the enlightened vanguard of the environmental movement (Alverson *et al.*, 1994; Sedjo and Botkin, 1997) and scientists alike (Carey *et al.*, 1999; Hunter, 1999). Intensively managed forest stands may produce three to seven times the usable wood per hectare produced by unmanaged stands (Farnum *et al.*, 1983; Sedjo, 1999; Jokela *et al.*, 2004), but this production potential varies greatly among forest types around the world (Sedjo *et al.*, 1998).

Of all tree species in the inland areas of the Pacific Northwest of North America, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) likely has the greatest potential to respond favourably to silvicultural treatments such as thinning and fertilization. The species often regenerates over-abundantly, resulting in excessive stand densities and reduced stand and tree growth. By concentrating growth on a smaller number of stems, pre-commercial thinning (PCT) offers the forest manager some control over the rotation, yield and value of the future crop (Johnstone, 1985; Cole and Koch, 1996). Extensive lodgepole pine forests are usually perpetuated through repeated fire disturbance, and therefore often occupy sites of low-N status (Brockley *et al.*, 1992). Not surprisingly, this species responds well to conventional, single-application fertilization with nitrogen alone and in combination with other elements (Weetman, 1988; Brockley, 1996). Although a single fertilizer application typically produces only a temporary increase in growth, sustained growth responses to repeated fertilization have been demonstrated in field experiments with lodgepole pine (Kishchuk *et al.*, 2002; Brockley, 2005) and other *Pinus* species (Malkonen and Kukkola, 1991; Tamm *et al.*, 1999; Albaugh *et al.*, 2004; Sword Sayer *et al.*, 2004). Many of these field studies have been designed to approximate the concept of 'steady-state' nutrition, whereby small, balanced supplies of nutrients in solution are provided at rates consistent with estimated demand (Linder, 1987; Raison and Myers, 1992).

The so-called 'optimum nutrition' field experiments, such as the study reported herein, are less

tightly controlled than steady-state studies, with nutrients applied less frequently, usually in solid form and in larger amounts per application. Foliar nutrient levels are monitored so that the rates and frequency of nutrient additions can be adjusted to maintain elevated foliar nutrient levels over a prolonged period. Because thinning and repeated fertilization treatments are applied over the whole ecosystem, they have the potential to significantly increase stand-level wood production.

This study was designed to test the hypothesis that large-scale stand PCT and repeated fertilization would enhance the tree- and stand-level productivity of lodgepole pine crop trees (dominant trees destined for harvest).

## Materials and methods

### Study areas

Three study areas were chosen on the basis of having candidate stands of young lodgepole pine that had relatively uniform tree cover, comparable diameter, height and density of trees prior to stand treatments. Location, proximity (boundaries) and size of candidate stands were determined by a balance between adequate interspersions of experimental units (Hurlbert, 1984) and the logistics and access for conducting the operational-scale treatments of PCT and fertilization.

The Summerland study area was located in the Bald Range 25 km west of Summerland in south-central British Columbia (BC), Canada (49°40'N; 119°53'W). This area is within the Montane Spruce (MS<sub>dm</sub>) biogeoclimatic zone (Meidinger and Pojar, 1991) at an elevation range of 1450–1520 m with gently rolling topography and sandy loam soil. The MS has a cool, continental climate with cold winters and moderately short, warm summers. Mean annual temperature is 0.5–4.7°C and precipitation ranges from 380 to 900 mm. The MS landscape has extensive, young and maturing seral stages of lodgepole pine, which have regenerated after wildfire. Hybrid interior spruce (*Picea engelmannii* × *Picea glauca* (Moench) Voss) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are the dominant shade-tolerant climax trees. Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco. var. *glauca* (Beissn.) Franco) is an

important seral species in the zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen (*Populus tremuloides* Michx.) is a common seral species and black cottonwood (*Populus trichocarpa* T. & G.) occurs on some moist sites (Meidinger and Pojar, 1991).

Clear-cut harvesting of lodgepole pine with some uniform and group seed-tree reserves of Douglas-fir began in this area in 1978 in response to an outbreak of mountain pine beetle. Depending on the original composition of the harvested stands and the degree of windthrow after harvesting, the number of residual Douglas-fir ranged from none to one or two trees per hectare in our candidate stands. Lodgepole pine regenerated naturally after harvesting and was the dominant tree species in these young stands. Three harvested units with pre-thinning stand densities ranging from 9980 to 11 150 stems ha<sup>-1</sup> were divided into eight treatment stands and one control stand, as per the experimental design (Table 1). Minor components of the stands included Douglas-fir, interior spruce, subalpine fir, Ponderosa pine (*Pinus ponderosa* Laws.), willow (*Salix* spp.), Sitka alder (*Alnus sinuata* (Regel) Rydb.) and trembling aspen.

At the start of the study (1993), diameter at breast height (DBH, 1.3 m above the forest floor) ranged from 2.2 ± 0.1 cm (mean ± SE) to 4.1 ± 0.1 cm with a mean age of 12–14 years. Stand height ranged from 2.3 ± 0.1 m to 3.4 ± 0.1 m (Figure 1). Area of stands ranged from 4.4 to 11.3 ha. The unit with stands A and B was 1.2 km from the unit containing stands C and D; this latter unit was 0.6 km from the unit containing E, F, G and H. Stand I was 0.2 km from this last unit. Within units, stands were contiguous on one side only.

The Kelowna study area was located 37 km northwest of Kelowna, BC (50°04'N; 119°34'W) in the MS<sub>dm</sub> biogeoclimatic sub-zone. Topography of this area is also gently rolling to flat with sandy loam soil at 1220- to 1240-m elevation. This area was clear-cut harvested in 1979–1980 and also regenerated naturally to lodgepole pine with the other coniferous species, including western larch (*Larix occidentalis* Nutt.), as minor components. One large unit (84.8 ha) with a pre-thinning density of 8686 stems ha<sup>-1</sup> was shaped in a horseshoe with an unharvested riparian buffer zone separating the two arms. This riparian zone had a steep ravine and varied in width from 75 to 300 m. The overall unit was separated into eight treatment stands as per the experimental design (Table 1). An additional unit (12.6 ha) 0.5 km away was used as the unthinned stand.

In 1993, the mean stand diameter and height ranged from 3.1 ± 0.1 cm to 4.7 ± 0.1 cm and 3.0 ± 0.1 m to 4.1 ± 0.1 m, respectively, with a mean stand age of 12–13 years (Figure 2). Area of stands ranged from 9.5 to 12.6 ha.

The Cariboo study area was located in the Alex Fraser Research Forest (University of British Columbia), 75 km northeast of Williams Lake, BC (52°29'N; 121°45'W) in the sub-boreal spruce (SBS<sub>dm</sub>) biogeoclimatic zone (Meidinger and Pojar, 1991). The general topography is gently rolling to flat at 850–870 m elevation. In mature stands, hybrid interior spruce, subalpine fir and some Douglas-fir are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. This unit covered 80 ha and was clear-cut harvested in 1976 followed by some natural regeneration and some planting of lodgepole pine in 1983. Pre-thinning stand density was 3333 stems ha<sup>-1</sup>. Eight treatment stands were located

Table 1: Allocation of thinning, pruning and fertilization treatments as per the experimental design

	Thinned and pruned to a 3-m lift			Thinned not pruned	Unthinned
Target density (stems ha <sup>-1</sup> )	250	500	1000	2000	>3000
Unfertilized	<b>A</b> (11.3, 10.0, 1.5)	<b>C</b> (7.6, 11.0, 4.5)	<b>E</b> (4.5, 9.5, 3.2)	<b>G</b> (4.4, 11.9, 4.3)	<b>I</b> (5.0, 12.6, 3.3)
Fertilized	<b>B</b> (11.3, 10.0, 1.5)	<b>D</b> (7.6, 11.0, 4.5)	<b>F</b> (4.5, 9.5, 3.2)	<b>H</b> (4.4, 11.9, 4.3)	

Bold letters indicate stand identification and numbers within brackets indicate stand areas (hectares) within the Summerland, Kelowna and Cariboo replicates, respectively.

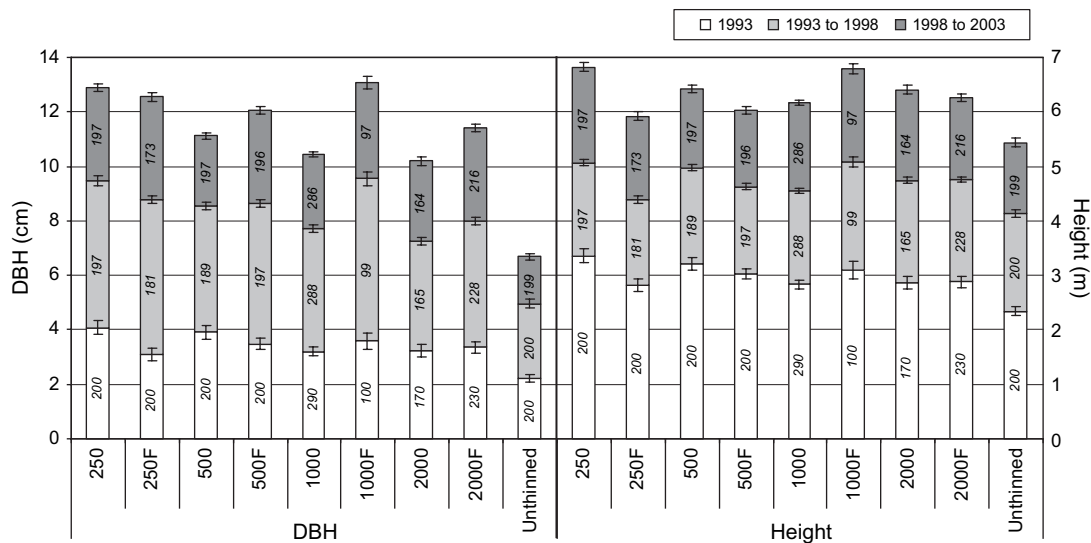


Figure 1. Mean DBH and top height of trees (sample size indicated within columns) within the nine treatment stands at the Summerland study area. Stands were measured at 5-year intervals over 10 years. Numbers along the x-axis represent target stand density (stems ha<sup>-1</sup>) and F = fertilized. Error bars represent 95 per cent confidence intervals.

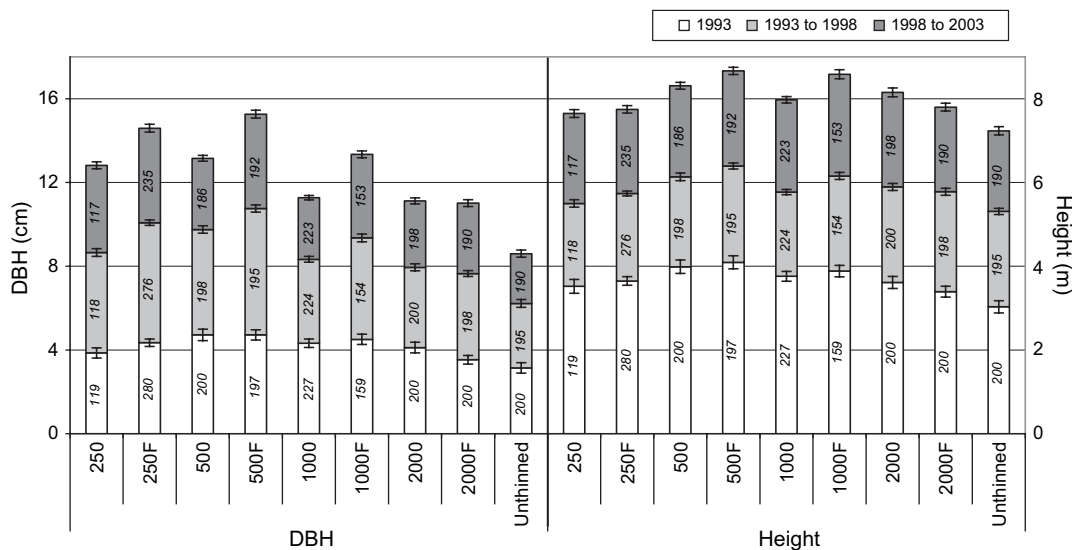


Figure 2. Mean DBH and top height of trees (sample size indicated within columns) within the nine treatment stands at the Kelowna study area. Stands were measured at 5-year intervals over 10 years. Numbers along the x-axis represent target stand density (stems ha<sup>-1</sup>) and F = fertilized. Error bars represent 95 per cent confidence intervals.

on this unit. Paired stands were contiguous on one side only. A ninth treatment stand acted as the unthinned stand, as per the experimental design (Table 1).

In 1993, the mean stand diameter and height ranged from  $4.4 \pm 0.2$  cm to  $7.2 \pm 0.3$  cm and  $3.4 \pm 0.1$  m to  $5.4 \pm 0.2$  m, respectively (Figure 3), with a mean stand age of 13 years. Area of stands ranged from 1.5 to 4.5 ha. These stands were separated by 0.2–0.5 km.

### Experimental design

The three study areas acted as regional replicates (blocks). Within each replicate, there were five experimental sites that had lodgepole pine stands PCT in the following randomized block design: (1) very low density, target 250 stems  $\text{ha}^{-1}$ ; (2) low density, target 500 stems  $\text{ha}^{-1}$ ; (3) medium density, target 1000 stems  $\text{ha}^{-1}$ ; (4) high density, target 2000 stems  $\text{ha}^{-1}$  and (5) unthinned, >3000 stems  $\text{ha}^{-1}$ . Fertilization treatments were applied to one-half of each of the thinned stands, resulting in a total of nine experimental units per replicate as follows: stand A, 250 stems  $\text{ha}^{-1}$ ; stand

B, 250 stems  $\text{ha}^{-1}$  with fertilization; stand C, 500 stems  $\text{ha}^{-1}$ ; stand D, 500 stems  $\text{ha}^{-1}$  with fertilization; stand E, 1000 stems  $\text{ha}^{-1}$ ; stand F, 1000 stems  $\text{ha}^{-1}$  with fertilization; stand G, 2000 stems  $\text{ha}^{-1}$ ; stand H, 2000 stems  $\text{ha}^{-1}$  with fertilization and stand I, unthinned >3000 stems  $\text{ha}^{-1}$  (Table 1). The restriction on randomization for the allocation of fertilizer treatment resulted in an overall split-plot design, with density as the main-plot and fertilization as the split-plot. A fertilized unthinned experimental unit was not included in this design 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  $\text{ha}^{-1}$  in 1998, 5 years after PCT (Table 1).

### Stand density

The initial treatment was PCT of young stands of pine at an appropriate time to maximize growth response potential before they experience severe growth repression. Thinning, using chainsaws, was carried out at all study areas in the late summer–early fall of 1993, at which time stands were

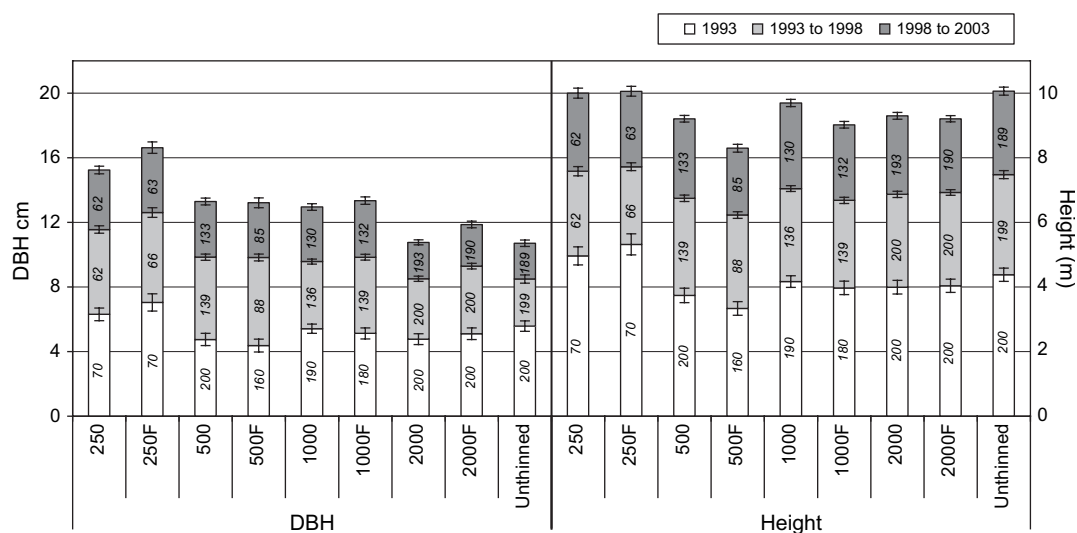


Figure 3. Mean DBH and top height of trees (sample size indicated within columns) within the nine treatment stands at the Cariboo study area. Stands were measured at 5-year intervals over 10 years. Numbers along the x-axis represent target stand density (stems  $\text{ha}^{-1}$ ) and F = fertilized. Error bars represent 95 per cent confidence intervals.

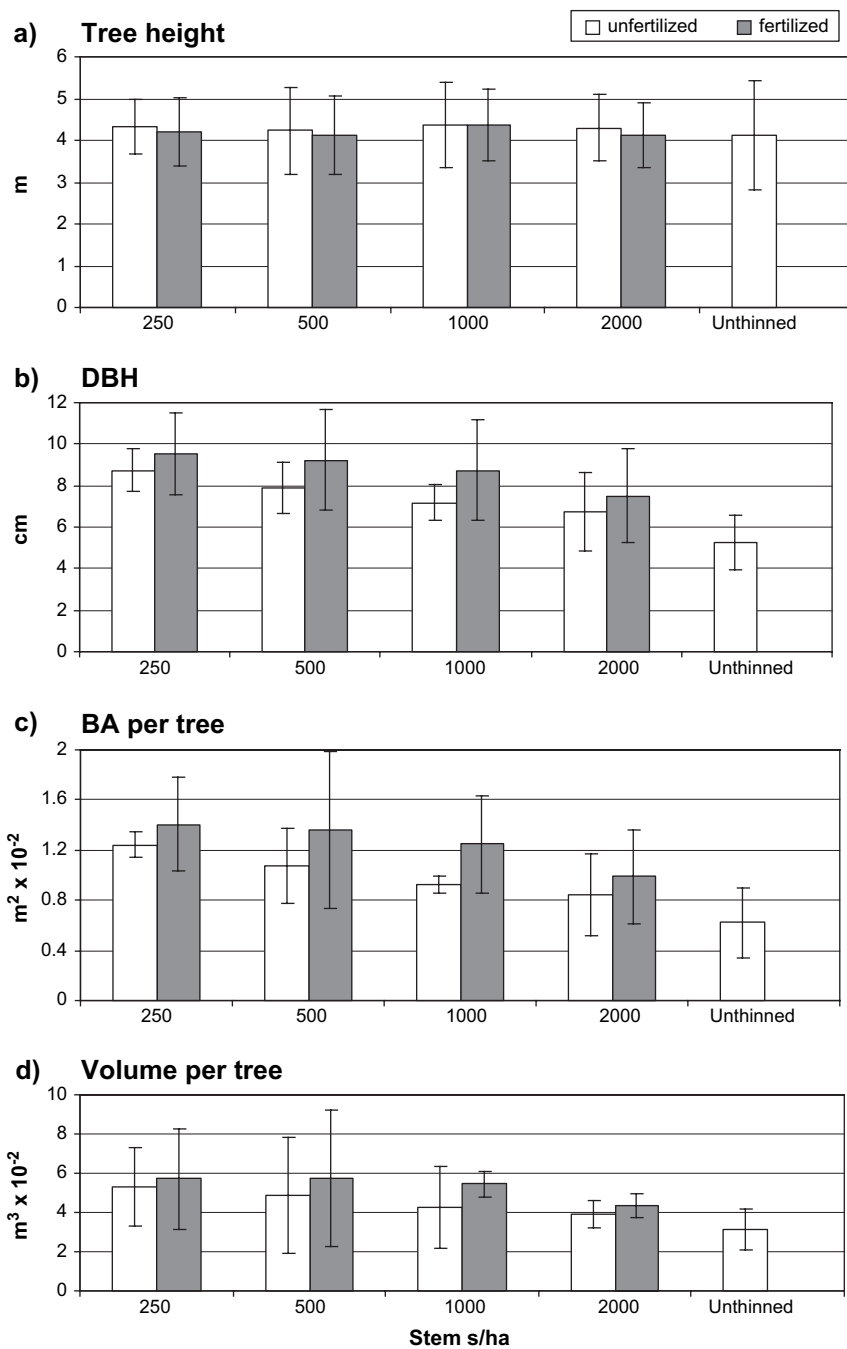


Figure 4. Adjusted mean ( $n=3$  replicate sites) 10-year increment per tree for (a) tree top height, (b) DBH, (c) BA and (d) volume within each of the nine treatment stands. Error bars indicate 95 per cent confidence intervals.

12–14 years old. All thinned material (slash) was maintained on site. To provide reasonably rigorous measurements of the various response variables, treatments were applied at a spatial scale large enough to be comparable to real-world operational installations. The usual prescription (>90 per cent of stands) for PCT of lodgepole pine in BC is 1600–2000 stems  $\text{ha}^{-1}$ , with variations from this range tending to be higher rather than lower density. The broad range of densities applied during this study (250–2000 stems  $\text{ha}^{-1}$ ) was clearly testing extremes beyond standard operational prescriptions and was deemed necessary to cause measurable changes in attributes of crop tree productivity, as well as measures of understorey vegetation, stand structural diversity and wildlife diversity. The effects of PCT and repeated fertilization on these non-timber attributes are the focus of several concurrent studies. The rationale for PCT to densities below full-stocking (e.g. 250 and 500 stems  $\text{ha}^{-1}$ ) may be questioned in terms of stand-level wood production, as heavy thinnings would likely result in reduced timber yields (Farnden, 1996). Regardless of the current value-based objectives for maintaining fully stocked stands, understanding the response of lodgepole pine to heavy thinnings should be viewed as important and relevant to future forest practices for several reasons. For example, the application of heavy thinnings within pine forests is likely to become increasingly common in order to meet both timber (e.g. accelerated growth rates for addressing timber supply shortfalls) and non-timber objectives.

### Fertilization

The fertilization treatments were designed as large-scale applications of the previously established ‘optimum nutrition’ fertilization field experiments in Sweden (Tamm *et al.*, 1999) and BC (Kishchuk *et al.*, 2002; Brockley, 2007). Our aim was to maintain elevated foliar N levels (~1.3 per cent), with levels of all other nutrients in proportional balance with N (Linder, 1995).

Fertilization treatments were initiated in November 1994 using a blended fertilizer formulated to provide 100 kg  $\text{ha}^{-1}$  nitrogen (100 N) (urea), 100 kg  $\text{ha}^{-1}$  phosphorus (100 P), 100 kg  $\text{ha}^{-1}$  potassium (100 K), 50 kg  $\text{ha}^{-1}$  sulphur

(50 S), 25 kg  $\text{ha}^{-1}$  magnesium (25 Mg) and 1.5 kg  $\text{ha}^{-1}$  boron (1.5 B). The blended product (11-25-13-5.5S-2.7Mg-0.17B) was applied at a rate of 906 kg  $\text{ha}^{-1}$  to each of the four treatment stands (B, D, F and H) at all three study areas. Fertilizer was applied by helicopter at the Summerland and Kelowna study areas, whereas the fertilizer at the Cariboo study area was spread by hand because of the relatively small size of the experimental units. Fertilization of the Cariboo site was completed prior to initiation of tree growth in April 1995.

During the fall of 1995 (1 year following initial fertilization), replicated samples of current year’s foliage were collected from all stands. Foliar sampling was carried out to monitor the nutrient status of the crop trees and to develop appropriate multi-nutrient formulations for subsequent fertilizer applications. Foliage was collected from 10 representative healthy dominant or co-dominant trees evenly distributed within each stand. Samples were collected from the lower portion of the top third of the live crown, consistent with standardized foliar sampling guidelines (Brockley, 2001). Foliar sampling was repeated each year, during late September or October, for the duration of the study. Individual foliage samples were frozen following field collection, and then dried in a forced-air oven at 70°C for 20 h before analysis. Two composite samples per stand, each sample consisting of equal amounts of foliage from five of the trees, were prepared for chemical analysis. Dried composite samples were ground in an electric coffee grinder and sent to a commercial laboratory for nutrient analysis.

Composite samples for all years were digested using a variation of the sulphuric acid – hydrogen peroxide procedure described by Parkinson and Allen (1975). The digests were analysed colorimetrically for N on a Technicon Autoanalyzer. A spectrophotometer measured P, using a procedure based on the reduction of the ammonium molybdiphosphate complex by ascorbic acid (Watanabe and Olson, 1965). Total K, Ca, Mg and Mn were determined by atomic absorption spectrophotometry. Total S was determined by combustion using a LECO sulphur analyzer. Separate sub-samples were dry-ashed, and Cu, Zn and Fe concentrations were determined by atomic absorption spectrophotometry. After dry-ashing, B was determined colorimetrically using

the azomethine-H method described by Gaines and Mitchell (1979).

Findings from foliar analyses were used to develop appropriate blends and application rates for subsequent treatments. In May of 1997, two growing seasons after initial application, stands were re-fertilized with a N+S blended fertilizer (36-0-0-9S) at an application rate of 547 kg ha<sup>-1</sup> (200 N and 50 S). In October of 1998, two growing seasons after the second application, stands were re-fertilized with a blended product (37-0-0-6.1S-0.7B) at an application rate of 404 kg ha<sup>-1</sup> (150 N, 25 S and 3 B). During the fall of 2000, two growing seasons after the third application, stands were re-fertilized with a blended product (31.1-0-0-11.3S) at an application rate of 439.4 kg ha<sup>-1</sup> (150 N and 50 S). And finally, during the spring of 2003, two growing seasons after the fourth application, stands were re-fertilized with a blended product (44.6-0-0-0.45B) at an application rate of 336.1 kg ha<sup>-1</sup> (150 N and 1.5 B).

Application methods described for the initial fertilization treatment (i.e. aerial *vs* manual) remained constant for the duration of this study.

### *Pruning*

Pruning of lodgepole pine and Douglas-fir crop trees, to a height of ~3.0 m, in stands thinned to <2000 stems ha<sup>-1</sup> (stands A, B, C, D, E and F) was conducted in September to December 1998, 5 years after PCT. All pruning was carried out using manual pruning saws.

### *Tree measurements*

All sampling of lodgepole pine crop trees was done with variable-radius plots to accommodate variations in stand density. Sampling plots were located every 50 m along compass lines (50 m apart) that systematically covered each stand. Sample plots (range of 11–29) were established in each of the nine stands at a given study area. The 10 crop trees closest to each plot centre were permanently tagged, resulting in a sample of 110–290 trees per stand. This variability in the number of sample plots and trees per stand was the result of changed boundaries between fertilized and unfertilized stands. Changes to the

original stand boundaries were deemed necessary for logistical reasons during the initial aerial application of fertilizer in 1994. The small size of the low-density stands (A and B) at the Cariboo study area (Table 1) resulted in only seven plots (70 trees) being sampled within each of these two stands. Within the unthinned stands, the 10 potential crop trees closest to each plot centre were sampled. Potential crop trees were chosen on the basis that these trees would have been left as the future crop if the stands were to be thinned (i.e. suppressed trees were avoided). The initial sampling was carried out immediately after thinning in the fall of 1993 and top height (m) and DBH (cm) were measured at a permanent reference point. Subsequent samples were carried out 5 and 10 years after thinning during the fall of 1998 and 2003. In addition to top height and DBH, the 1998 and 2003 samples also measured crown attributes including base of live crown height (m), widest crown height (m) and widest crown diameter (m). Diameter of widest crown was determined by standing directly below the widest part of the crown and measuring the horizontal distance from stem to drip-line created by the longest branch (measured to the nearest 0.1 m with a measuring tape) and multiplying this radius by two. The 1998 sample was 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. During the 1998 and 2003 re-measurements, tree heights were measured to the nearest 0.1 m with a digital hypsometer (Forestor Vertex). Trees that were noted as having died, or that had suffered severe snowpress or a broken top at any point during this study, were omitted from any subsequent analyses.

### *Stem growth*

At the tree level, growth response of the stem to thinning and fertilizer treatments was described by 10-year increments (1993–2003) of top height, DBH, basal area (BA) and volume. Tree volume was calculated as

$$V = a_1 + a_2 D^2 H, \quad (1)$$

where  $V$  is gross total inside bark volume ( $\text{m}^3$ ),  $D$  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. All pre-treatment tree volumes were estimated using  $a_1$  and  $a_2$  values of 1254 and 0.349, respectively. Post-treatment volumes for both the Summerland and Kelowna study areas were estimated using  $a_1$  and  $a_2$  values of 4186 and 0.340, respectively. Post-treatment volumes for the Cariboo study area were estimated using  $a_1$  and  $a_2$  values of 5482 and 0.353, respectively. Equations were developed as described by Brockley and Simpson (2004) for similar-aged and similar-sized lodgepole trees at research installations near our study areas (R. Brockley, unpublished data).

At the stand level, BA per hectare and volume per hectare were estimated by multiplying the mean tree values by an estimate of stand density (stems per hectare) for each stand. Initial stand density was determined immediately following PCT in 1993. Subsequent stand densities were

estimated based on the observed percentage of dead or severely snowpressed trees among the permanently tagged crop trees during the 1998 and 2003 samples. This estimate of mortality was used to adjust the initial stand density by a percentage that was assumed to be proportional to the mortality experienced throughout a given stand. As a result, stand-level estimates of BA/hectare and volume/hectare within thinned stands apply only to the residual cohort of dominant and co-dominant lodgepole pine trees selected during thinning and, therefore, do not account for any ingress that had occurred over the course of this 10-year study.

Stand density estimates for the unthinned stands included trees of all sizes; however, only dominant and co-dominant trees were measured for stem growth. As a result, BA/hectare and volume/hectare will be overestimated for unthinned stands and are, therefore, provided for visual comparison only with thinned stands (Figure 5). Statistical comparisons of stem growth do not include the unthinned treatment (see Statistical Analysis section below).

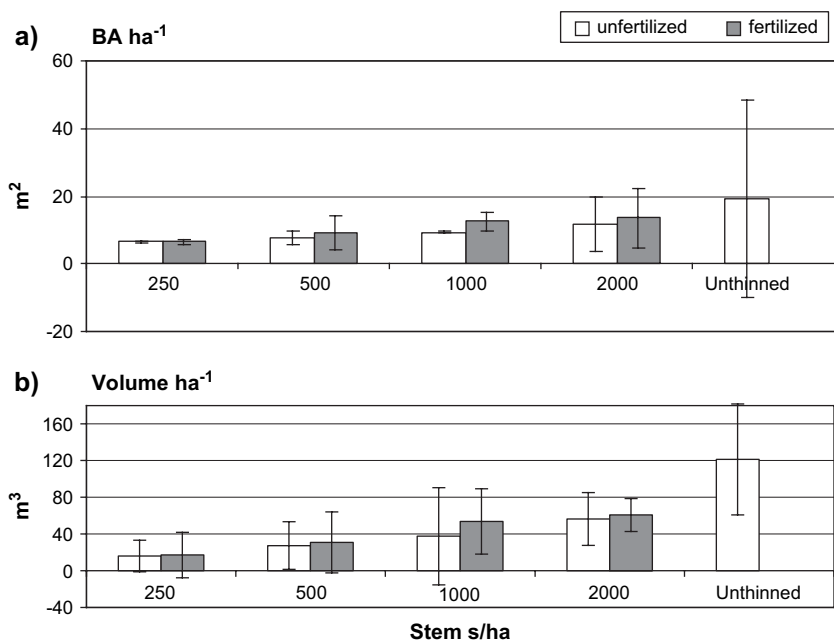


Figure 5. Adjusted mean ( $n=3$  replicate sites) 10-year increment per hectare for (a) BA and (b) volume within each of the nine treatment stands. Error bars indicate 95 per cent confidence intervals.

Changes in growth rate over time were described by comparing the growth observed during the first 5 years with that of the final 5 years. The initial periodic increment (1993–1998) was subtracted from the later periodic increment (1998–2003) such that a positive result would indicate the amount by which the growth rate had accelerated during the final 5 years, whereas a negative result would indicate the amount by which the growth had decreased.

### Crown architecture

The response of crown architecture to thinning and fertilizer treatments was described by measures of crown area, volume, length and live crown ratio (LCR) as well as the changes in these attributes during the last 5 years (1998–2003). Crown area represented the widest horizontal cross-section of a crown, and was calculated using the widest crown diameter measurement. Crown volume was calculated using a simple cone volume equation and was based on the assumption that crown volume of lodgepole pine trees can be represented by two cones; the upper portion above the widest crown (a long upright cone) and the lower portion below the widest crown (a shorter inverted cone) (Sullivan *et al.*,

2001). Crown length was the total vertical length of live crown and was calculated by subtracting the base of live crown height from top height. LCR was the proportion of tree height covered by live crown and was calculated as top height divided by crown length.

Crown measurements were made immediately prior to pruning in 1998. Crown architecture immediately following pruning (1998) was estimated based on the assumption that the new base of live crown height created by pruning was equal to the base of live crown height observed in 2003 (see Figure 6). These estimates of post-pruning crown architecture should be reasonably accurate because lodgepole pine does not regrow lower branches via epicormic branching (Ballard and Long, 1988) and pruned stands had yet to experience any self-pruning as of 2003. Crown development during the final 5 years was calculated by subtracting the 1998 post-pruning estimates from the 2003 measured attributes.

### Statistical analysis

Because the experimental design of this study restricted the randomness of fertilizer treatment allocation (i.e. applied to one-half of each of the thinned stands), a split-plot analysis of

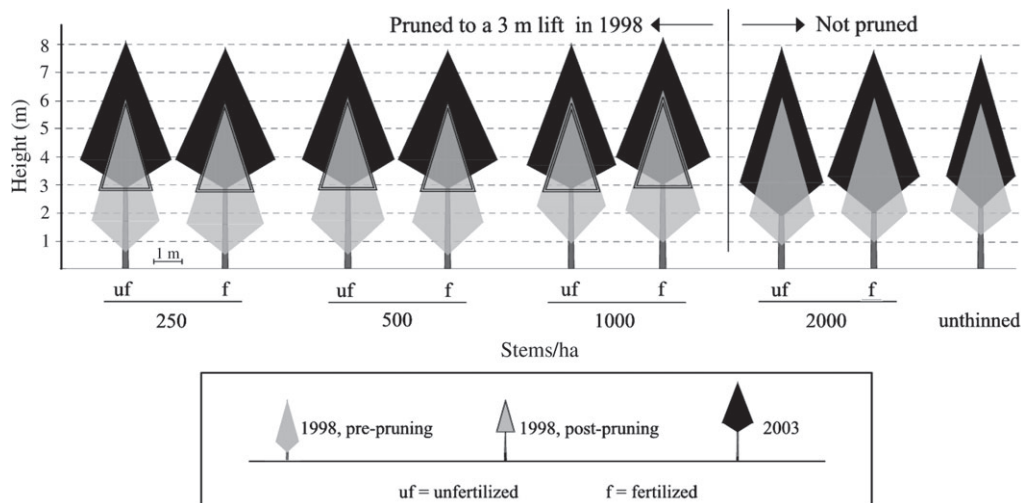


Figure 6. Mean ( $n=3$  replicate sites) crown configuration of trees within each of the nine treatment stands during 1998 (pre- and post-pruning) and 2003.

Table 2: Adjusted mean ( $n = 3$  replicate sites) (SE) 10-year increments per tree observed among density and fertilizer treatments

	Split-plot ANCOVA													
	Density			Fertilizer			Density × fertilizer			P				
	$F_{3,5}$	$P$		$F_{1,7}$	$P$		$F_{3,7}$	$P$		$F_{3,7}$	$P$			
Height (m)	250 stems $ha^{-1}$	4.23 (0.19)	500 stems $ha^{-1}$	4.15 (0.24)	1000 stems $ha^{-1}$	4.34 (0.23)	2000 stems $ha^{-1}$	4.19 (0.20)	2.48	0.18	4.34	0.08	0.51	0.69
	Unfertilized				Fertilized									
	4.28 (0.22)		500 stems $ha^{-1}$	8.59*† (0.39)	1000 stems $ha^{-1}$	7.99** (0.36)	2000 stems $ha^{-1}$	7.15** (0.47)	6.00	0.04	42.45	<0.01	1.39	0.32
DBH (cm)	250 stems $ha^{-1}$	9.18* (0.34)	500 stems $ha^{-1}$	8.59*† (0.39)	1000 stems $ha^{-1}$	7.99** (0.36)	2000 stems $ha^{-1}$	7.15** (0.47)	6.00	0.04	42.45	<0.01	1.39	0.32
	Unfertilized				Fertilized									
	7.66† (0.16)		500 stems $ha^{-1}$	1.22*† (0.10)	1000 stems $ha^{-1}$	1.09** (0.06)	2000 stems $ha^{-1}$	0.93* (0.09)	5.89	0.04	33.20	<0.01	1.42	0.32
BA ( $m^2 \times 10^{-2}$ )	250 stems $ha^{-1}$	1.33* (0.06)	500 stems $ha^{-1}$	1.22*† (0.10)	1000 stems $ha^{-1}$	1.09** (0.06)	2000 stems $ha^{-1}$	0.93* (0.09)	5.89	0.04	33.20	<0.01	1.42	0.32
	Unfertilized				Fertilized									
	1.03† (0.03)		500 stems $ha^{-1}$	5.29 (0.65)	1000 stems $ha^{-1}$	4.88 (0.25)	2000 stems $ha^{-1}$	4.15 (0.14)	3.64	0.10	11.44	0.01	0.78	0.54
Volume ( $m^3 \times 10^{-2}$ )	250 stems $ha^{-1}$	5.49 (0.43)	500 stems $ha^{-1}$	5.29 (0.65)	1000 stems $ha^{-1}$	4.88 (0.25)	2000 stems $ha^{-1}$	4.15 (0.14)	3.64	0.10	11.44	0.01	0.78	0.54
	Unfertilized				Fertilized									
	4.59† (0.37)		500 stems $ha^{-1}$	5.31* (0.38)	1000 stems $ha^{-1}$	5.31* (0.38)	2000 stems $ha^{-1}$	5.31* (0.38)	5.31*	0.38	5.31*	0.38	5.31*	0.38

Split-plot ANCOVA results are also provided. Within a row, mean values with different symbols are significantly different by Duncan's multiple range test, adjusted for multiple comparisons.

Table 3: Adjusted mean ( $n = 3$  replicate sites) (SE) difference in tree growth rates observed between the first and last 5 years of this 10-year study

	Split-plot ANCOVA									
	Density		Fertilizer		Density × fertilizer					
	$F_{3,5}$	$P$	$F_{1,7}$	$P$	$F_{3,7}$	$P$				
Height (m)	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	2.48	0.18	4.34	0.08	0.51	0.69
	-0.14 (0.19) Unfertilized	-0.22 (0.24) Fertilized	-0.03 (0.23) Fertilized	-0.18 (0.20) Fertilized						
DBH (cm)	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	0.90	0.50	2.34	0.17	0.19	0.90
	-1.40 (0.32) Unfertilized	-1.73 (0.14) Fertilized	-1.34 (0.46) Fertilized	-1.21 (0.21) Fertilized						
BA (m <sup>2</sup> × 10 <sup>-3</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	0.75	0.57	4.82	0.06	0.22	0.88
	1.24 (0.54) Unfertilized	0.46 (0.40) Fertilized	0.71 (0.55) Fertilized	0.46 (0.39) Fertilized						
Volume (m <sup>3</sup> × 10 <sup>-3</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	2.19	0.21	5.01	0.06	0.30	0.82
	11.98 (2.55) Unfertilized	8.72 (3.06) Fertilized	9.35 (2.17) Fertilized	5.67 (1.87) Fertilized						
	7.57 (1.82)	10.29 (2.58)								

Positive values indicate the magnitude by which the growth rate increased during the last 5 years compared with the first 5 years, and vice versa. Split-plot ANCOVA results are also provided.

variance (ANOVA) was used to compare treatment means. The density and fertilizer treatments were assigned as the main- and split-plots, respectively. The three regional replicates functioned as blocks and were assigned as a random factor. Because tree growth response increases with initial tree size (Johnstone, 1985), analysis of covariance (ANCOVA) was used to adjust the treatment means by accounting for differences in tree sizes observed at the beginning of the study (i.e. covariate = initial tree size). Therefore, a split-plot ANCOVA was used to compare adjusted treatment means for all stem growth rates.

Before the ANCOVA-adjusted means could be used, the homogeneity of regression coefficients assumption 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 would indicate that the assumption had been violated and would have precluded any further analyses using ANCOVA. When this occurred, separate regression equations were generated for each experimental unit (independent factor regressed on the covariate) and used to adjust growth rates for each individual tree. These adjusted values were then analysed using a blocked, split-plot ANOVA. Treatment effects on crown architecture were also analysed with a blocked, split-plot ANOVA.

The unthinned and fertilized treatment combination was not included within our experimental design due to the well-documented lack of operational feasibility of such a treatment (Groot *et al.*, 1984; Yang, 1998; Valinger *et al.*, 2000). Therefore, unthinned stands are included within figures simply as a visual comparison of managed *vs* unmanaged stand attributes. To maintain the power and sensitivity of a balanced design, the unthinned level of the density factor was omitted from all statistical analyses. Duncan's multiple range test was used to compare mean values based on ANOVA results. In all analyses, the level of significance was at least  $P=0.05$ .

## Results

### *Foliar analysis*

Foliar N was strongly affected by fertilizer N additions at all three study areas. Foliar levels in

fertilized stands remained higher than in unfertilized stands throughout the 10-year study period. Foliar levels peaked in the year following each re-fertilization. Averaged across all sites and years, residual stand density had little effect on foliar N levels and there was no overall density  $\times$  fertilizer interaction.

Periodic S and B additions had a strong positive effect on foliar S and B levels at all study sites. Foliar S and B levels were largely unaffected by residual stand density. Overall, foliar levels of other nutrients were largely unaffected by fertilization or stand density.

Foliar N/S ratios were largely unaffected by repeated fertilization with N and S. Foliar N/S levels were not affected by stand density. Conversely, foliar N/K and N/P ratios were increased by fertilization at all sites. Averaged across all years and sites, foliar N/Mg ratio was affected by both fertilization and stand density. However, the effects of fertilization on foliar N/Mg ratio varied differentially with residual stand density at two study areas.

### *Stem growth*

Mean 10-year height increments appeared to be less in fertilized stands than in unfertilized stands (Figure 4a); however, neither density nor fertilizer treatment had any significant effect on tree height growth (Table 2). Rate of height growth decreased during the last 5 years; however, this decrease was unaffected by treatments (Table 3). Mean 10-year DBH increment was significantly affected by stand density ( $F_{3,5}=6.00$ ;  $P=0.04$ ) and fertilizer treatments ( $F_{1,7}=42.45$ ;  $P<0.01$ ). Crop trees grew significantly faster in diameter in the very low than high-density stands and in the fertilized than unfertilized stands (Table 2 and Figure 4b). Rate of diameter growth was observed to decrease slightly during the last 5 years; however, this decrease was unaffected by treatments (Table 3). Mean 10-year BA/tree increment was significantly affected by both stand density ( $F_{3,5}=5.89$ ;  $P=0.04$ ) and fertilizer treatments ( $F_{1,7}=33.20$ ;  $P<0.01$ ) (Figure 4c). Mean 10-year BA/tree increment was significantly enhanced by fertilization treatments and increased with decreasing stand density with the very low density stands experiencing significantly greater BA growth than both

the medium- and high-density stands (Table 2). Rate of BA/tree increment appeared to increase with time and, although greater within the very low density and fertilized stands, was statistically similar among all stands (Table 3). Mean 10-year tree volume increment appeared to be enhanced by thinning treatments (Figure 4d); however, increments were statistically similar ( $F_{3,5}=3.64$ ;  $P=0.10$ ) among stand densities (Table 2). Tree volume was significantly ( $F_{1,7}=11.44$ ;  $P=0.01$ ) greater in the fertilized stands compared with the unfertilized stands (Table 2). Rate of tree volume increment appeared to increase with time and, while thinning and fertilization tended to accelerate volume growth, rate of increase was statistically similar among all stands (Table 3).

Mean 10-year stand BA (BA/hectare) increment increased with increasing stand density (Figure 5a); however, differences were not statistically significant ( $F_{3,5}=4.26$ ;  $P=0.08$ ) (Table 4). Fertilizer treatments, however, significantly ( $F_{1,7}=30.40$ ;  $P<0.01$ ) increased stand BA increment compared with unfertilized stands (Table 4). Rate of stand BA increment was maintained throughout this 10-year study (Table 5). Mean 10-year stand volume (volume/hectare) increment was significantly ( $F_{3,5}=13.40$ ;  $P<0.01$ ) affected by stand density treatments (Table 4 and Figure 5b). Stand volume increment in high-density stands was significantly greater than in the lower density stands (Table 4). Fertilizer treatments appeared to enhance stand volume increment (Figure 5b); however, differences were not formally significant ( $F_{1,7}=5.18$ ;  $P=0.06$ ) (Table 4). Rate of stand volume increment increased with time and fertilized stands experienced a significantly ( $F_{1,7}=19.76$ ;  $P<0.01$ ) accelerated rate of volume increment compared with the unfertilized stands (Table 5).

#### *Crown architecture*

In 1998, before pruning (5 years after thinning and after two fertilizer applications), crowns tended to be larger in the low- vs high-density stands and fertilized vs unfertilized stands; however, differences were not statistically significant (Table 6). Averaged over the six pruned stands, pruning removed ~41 per cent of the crown length (5.4–3.2 m) and 63 per cent of the crown volume (11.7–4.3 m<sup>3</sup>) and decreased the crown area

by 44 per cent (5.9–3.3 m<sup>2</sup>) and LCR by 43 per cent (0.90–0.51) (Figure 6). Immediately following pruning, trees growing in the pruned densities (250, 500 and 1000 stems ha<sup>-1</sup>) had significantly smaller crown length ( $F_{3,6}=27.21$ ;  $P<0.01$ ), area ( $F_{3,6}=14.92$ ;  $P<0.01$ ), volume ( $F_{3,6}=16.93$ ;  $P<0.01$ ) and LCR ( $F_{3,6}=25.25$ ;  $P<0.01$ ) than trees growing in the 2000 stems ha<sup>-1</sup> stands, which had not been pruned. In 2003 (10 years after thinning, 5 years after pruning and after five fertilizer applications), all but one of the crown architecture attributes were similar among density and fertilizer treatments. Mean crown area was significantly ( $F_{1,8}=12.85$ ;  $P<0.01$ ) greater for trees growing in the fertilized than unfertilized stands (Table 6).

During the post-pruning period of 1998–2003, tree crowns continued to get larger in all stands (Figure 6). However, rate of change for various crown architecture attributes was significantly different among stand density and fertilization treatments. Trees growing with the pruned densities experienced the most rapid increase in crown length, area, volume and LCR compared with the unpruned 2000 stems ha<sup>-1</sup>; however, only crown length and LCR were significantly different ( $F_{3,6}=6.33$ ;  $P=0.03$  and  $F_{3,6}=48.52$ ;  $P<0.01$ , respectively) (Table 7). Rate of change was significantly greater for trees growing in fertilized stands compared with unfertilized stands with regards to both crown area ( $F_{1,8}=17.99$ ;  $P<0.01$ ) and crown volume ( $F_{1,8}=8.12$ ;  $P=0.02$ ) (Table 7).

## Discussion

In the southern US, loblolly pine (*Pinus taeda* L.) is one of the most important commercial species (Jokela *et al.*, 2004). Intensive management of loblolly pine has been well studied and has clearly demonstrated the increased production and economic benefits made possible by manipulating resource availability (e.g. Albaugh *et al.*, 2004; Sword Sayer *et al.*, 2004). As a result, incremental silvicultural practices such as PCT and fertilization have become the norm for management of this species throughout the southeastern US (Albaugh *et al.*, 2004). Our study is the first large-scale evaluation of the influence of the silvicultural practices of PCT and fertilization on growth of lodgepole pine in North America. It

Table 4: Adjusted mean ( $n = 3$  replicate sites) (SE) 10-year increments per hectare observed among density and fertilizer treatments

	Split-plot ANCOVA									
	Density		Fertilizer		Density × fertilizer					
	$F_{3,5}$	$P$	$F_{1,7}$	$P$	$F_{3,7}$	$P$				
BA ( $m^2$ )	250 stems $ha^{-1}$	500 stems $ha^{-1}$	1000 stems $ha^{-1}$	2000 stems $ha^{-1}$	4.26	0.08	30.40	<0.01	3.88	0.06
	5.72 (0.14) Unfertilized 7.81* (0.58)	7.58 (0.80) Fertilized 9.79 (0.53) 9.43* (0.96)	9.79 (0.53) Fertilized 9.43* (0.96)	11.41 (2.04) Fertilized 9.43* (0.96)	11.41 (2.04) Fertilized 9.43* (0.96)					
Volume ( $m^3$ )	250 stems $ha^{-1}$	500 stems $ha^{-1}$	1000 stems $ha^{-1}$	2000 stems $ha^{-1}$	13.40	<0.01	5.18	0.06	1.53	0.29
	16.59* (4.83) Unfertilized 34.38 (5.84)	29.15** (6.51) Fertilized 40.61 (5.77)	45.64† (10.00) Fertilized 40.61 (5.77)	58.59* (4.95) Fertilized 40.61 (5.77)	58.59* (4.95) Fertilized 40.61 (5.77)					

Split-plot ANCOVA results are also provided. Within a row, mean values with different symbols are significantly different by Duncan's multiple range test, adjusted for multiple comparisons.

Table 5: Adjusted mean ( $n = 3$  replicate sites) (SE) difference in growth rates per hectare observed between the first and last 5 years of this 10-year study

	Split-plot ANCOVA									
	Density		Fertilizer		Density × fertilizer					
	$F_{3,5}$	$P$	$F_{1,7}$	$P$	$F_{3,7}$	$P$				
BA ( $m^2$ )	250 stems $ha^{-1}$	500 stems $ha^{-1}$	1000 stems $ha^{-1}$	2000 stems $ha^{-1}$	0.83	0.53	0.39	0.55	0.97	0.46
	-0.21 (0.11) Unfertilized 0.21 (0.19)	-0.14 (0.18) Fertilized 0.33 (0.36)	0.61 (0.55) Fertilized 0.33 (0.36)	0.81 (0.76) Fertilized 0.33 (0.36)	0.81 (0.76) Fertilized 0.33 (0.36)					
Volume ( $m^3$ )	250 stems $ha^{-1}$	500 stems $ha^{-1}$	1000 stems $ha^{-1}$	2000 stems $ha^{-1}$	1.58	0.31	19.76	<0.01	3.74	0.07
	34.08 (2.32) Unfertilized 35.21* (1.15)	36.06 (2.12) Fertilized 40.55* (2.03)	40.03 (1.25) Fertilized 40.55* (2.03)	41.35 (3.14) Fertilized 40.55* (2.03)	41.35 (3.14) Fertilized 40.55* (2.03)					

Positive values indicate the magnitude by which the growth rate increased during the last 5 years compared with the first 5 years, and vice versa. Split-plot ANCOVA results are also provided. Within a row, mean values with different symbols are significantly different by Duncan's multiple range test, adjusted for multiple comparisons.

Table 6: Mean ( $n=3$  replicate sites) (SE) crown attributes observed among the density and fertilizer treatments during the 1998 (pre-pruning) and 2003 sample periods

		Split-plot ANOVA									
		Density		Fertilizer		Density × fertilizer					
		$F_{3,6}$	$P$	$F_{1,8}$	$P$	$F_{3,8}$	$P$	$F_{3,8}$	$P$		
1998, Pre-pruning	Length (m)	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	2.65	0.14	0.27	0.62	0.45	0.72
		5.41 (0.57)	5.49 (0.53)	5.36 (0.45)	4.96 (0.29)						
		Unfertilized	Fertilized	Fertilized							
Area (m <sup>2</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	2.03	0.21	3.83	0.09	1.43	0.30	
	5.76 (0.98)	6.01 (1.63)	5.91 (1.32)	5.08 (1.06)							
	Unfertilized	Fertilized	Fertilized								
Volume (m <sup>3</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	2.80	0.13	2.66	0.14	1.48	0.29	
	11.35 (3.05)	12.31 (4.18)	11.55 (3.34)	9.43 (2.52)							
	Unfertilized	Fertilized	Fertilized								
LCR	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	1.96	0.22	0.11	0.75	0.68	0.59	
	0.91 (0.02)	0.91 (0.02)	0.89 (0.03)	0.87 (0.05)							
	Unfertilized	Fertilized	Fertilized								
2003	Length (m)	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	0.96	0.47	0.50	0.50	0.45	0.72
		5.25 (0.87)	5.18 (0.69)	5.30 (0.74)	6.01 (0.18)						
		Unfertilized	Fertilized	Fertilized							
Area (m <sup>2</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	0.88	0.50	12.85	<0.01	0.68	0.59	
	10.25 (2.62)	10.10 (1.86)	9.36 (1.80)	8.75 (1.14)							
	Unfertilized	Fertilized	Fertilized								
Volume (m <sup>3</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	0.13	0.94	3.28	0.11	0.17	0.91	
	20.24 (8.36)	19.52 (5.68)	18.01 (6.04)	18.64 (2.82)							
	Unfertilized	Fertilized	Fertilized								
LCR	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>	2.28	0.18	0.25	0.63	0.15	0.93	
	0.64 (0.02)	0.63 (0.01)	0.64 (0.01)	0.77 (0.08)							
	Unfertilized	Fertilized	Fertilized								

Split-plot ANOVAs are also provided. Within a row, mean values with different symbols are significantly different by Duncan's multiple range test, adjusted for multiple comparisons.

Table 7: Mean ( $n = 3$  replicate sites) (SE) 5-year increments in crown attributes observed from 1998 (post-pruning) to 2003 among density and fertilizer treatments

	Split-plot ANOVA											
	Density		Fertilizer		Density × fertilizer		Density		Fertilizer		Density × fertilizer	
	$F_{3,6}$	$P$	$F_{1,8}$	$P$	$F_{3,8}$	$P$	$F_{3,6}$	$P$	$F_{1,8}$	$P$	$F_{3,8}$	$P$
Length (m)	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>								
	2.02* (0.19) Unfertilized	1.99* (0.29)	2.18* (0.24) Fertilized	1.01† (0.20)	6.33	0.03	1.26	0.29	0.51	0.69		
Area (m <sup>2</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>								
	6.95 (1.74) Unfertilized	6.72 (1.16)	5.79 (1.25) Fertilized	3.59 (0.19)	3.70	0.08	17.99	<0.01	1.00	0.44		
Volume (m <sup>3</sup> )	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>								
	15.56 (5.86) Unfertilized	15.02 (4.18)	13.54 (4.63) Fertilized	8.99 (0.25)	1.36	0.34	8.12	0.02	0.28	0.84		
LCR	250 stems ha <sup>-1</sup>	500 stems ha <sup>-1</sup>	1000 stems ha <sup>-1</sup>	2000 stems ha <sup>-1</sup>								
	11.96† (3.36)	0.12* (0)	14.60* (3.86)	-0.10† (0.03)	48.52	<0.01	0.57	0.47	0.14	0.94		
	0.13* (0.01) Unfertilized	0.12* (0)	0.13* (0.01) Fertilized									
	0.08 (0.01)		0.07 (0.01)									

Split-plot ANOVAs are also provided. Within a row, mean values with different symbols are significantly different by Duncan's multiple range test, adjusted for multiple comparisons.

represents an extensive effort that sampled >5000 permanently tagged trees three times at 5-year intervals and incorporated operational-sized experimental units that totalled a combined area of 188 ha, of which 167 ha were thinned and 126 ha were pruned. In addition, during this 10-year study, ca. 63 000 kg of N were applied to 84 ha (a total of 750 kgN ha<sup>-1</sup>). These stands are the most intensively managed young forests in BC, and likely in all of Canada.

### *Experimental design*

Because of the wide geographical area covered by our replicated installations, the scope of inferences from this study may be extrapolated to lodgepole pine stands and habitats throughout the southern interior of BC. These inferences reflect responses in crop tree productivity. The size of our experimental units ranged from 4.4 to 12.6 ha at Summerland and Kelowna, which were within the range of typical forestry operations. Experimental units at the Cariboo study area ranged from 1.5 to 4.5 ha and we acknowledge the relatively smaller size of these units. However, it was unlikely that the size of these units had any effect on measurements of crop tree growth. At each of the three study areas, either the large management units and/or the wide range of treatments (9) precluded site replication. Thus, the three study areas acted as regional replicates in a design with true replication of experimental units.

As discussed by Hurlbert (1984), randomization and interspersed treatment units are essential elements of a sound experimental design. We acknowledge the concern that we did not actually intersperse the treatment units randomly within each block, *per se*. Assignment of target densities for PCT of lodgepole pine stands was random, but the fertilization treatments were applied to one-half of each of the original stand density areas. Because of the logistics of aerial application of fertilizer, fertilization treatment units were adjacent to each other at two of the Summerland units and at the four Kelowna units. However, because application logistics rather than experimenter bias (Hurlbert, 1984) tended to control assignment of treatment units within a block, this was considered a randomized split-plot design.

Uniformity (e.g. age and density) of pre-treatment lodgepole pine stands within blocks at all three study areas was determined by the lack of differences in diameters and heights of pine crop trees among pre-treatment experimental units in 1993. However, our treatment units may not have been completely independent since units were contiguous with adjacent units on one or two sides. Therefore, degree of independence may have been less than if each unit was physically separate from every other unit.

### *Foliar analysis*

With N applications every 2 years, elevated foliar N levels were maintained throughout the 10-year period. The small amount of N (100 kgN ha<sup>-1</sup>) that was added at the beginning of the study (fall 1994) resulted in a relatively small increase in foliar N at all three study areas. However, the higher N dosages used in subsequent applications (150–200 kgN ha<sup>-1</sup>) were much more effective at increasing, and maintaining, foliar N levels in fertilized trees.

By including S (as sulphate-S) in fertilizer prescriptions, favourable foliar N/S balance was maintained throughout the 10-year period at all three areas. Post-fertilization foliar N/S ratios in all fertilized treatments remained below a threshold value (~15), above which S deficiency is indicated for lodgepole pine (Ballard and Carter, 1986; Brockley, 2001). Combined N and S fertilization has proven effective in alleviating S deficiencies and in promoting tree growth of S-deficient lodgepole pine in central BC (Brockley, 2004). The small amount of B (1.5–3 kg ha<sup>-1</sup>) that was periodically included in fertilizer prescriptions was also readily taken up by lodgepole pine at all areas. Previous studies have also reported that, when combined with N, small amounts of B are sufficient to achieve, and maintain, favourable B status over a prolonged period (Brockley, 1990; 2003).

Although foliar N/K, N/P and N/Mg ratios were higher in fertilized treatments than in unfertilized treatments at all study areas, the ratios remained below probable deficiency thresholds in almost all cases (Brockley, 2001). Therefore, native soil fertility, and the amount of P, K and Mg applied in the initial fertilization, was

apparently sufficient to maintain favourable foliar nutrient balance in repeatedly N-fertilized trees at all study areas.

### *Stem growth*

According to Koch (1995), a minimum merchantable diameter of lodgepole pine would be 25 cm with an expected rotation age of 80 years. Depending on the degree of PCT and response to fertilization, this rotation age could be reduced by several decades to 50–60 years on sites similar to our study areas. As discussed below, this reduction in rotation age assumes that stand volume is not the only factor being considered in accelerating stand development. With enhanced diameter growth, a forest manager has two options to choose from: (1) harvest larger trees within a standard rotation or (2) harvest merchantable trees sooner. The first option produces larger diameter trees, which, in general, provide higher value products than smaller trees due to the premiums currently placed on sawlog products compared with pulp and composite wood products (Middleton *et al.*, 1995). In addition, the increased efficiency associated with harvesting, handling and milling large diameter trees provides additional financial returns relative to small diameter trees (Ballard and Long, 1988). The second option (reduced rotation) will provide mills with fiber sooner, which will become increasingly necessary to meet the growing global demands for forest products from an ever-decreasing landbase of managed forests (Brooks, 1997). Attaining merchantable timber within a reduced rotation is likely of critical significance to the long-term future of BC's forest industry. Such a strategy may be a viable means for addressing projected timber shortfalls resulting from the current mountain pine beetle epidemic, which has already decimated several million hectares of merchantable pine forest throughout BC's interior (B.C. Ministry of Forests, 2003).

In this study, five applications of fertilizer over 8 years (750 N in total) produced 10-year relative and absolute mean stand volume gains, over all densities, of only 18 per cent and 6.2 m<sup>3</sup> ha<sup>-1</sup>, respectively. The effects of fertilization on biological rotation length (i.e. culmination of mean annual increment) or technical rotation length (i.e. minimum merchantable harvest or target DBH)

can be predicted from TIPSy, a growth and yield program that interpolates managed stand yield tables generated by the tree and stand simulator growth and yield model (Mitchell *et al.*, 2007). The estimated reduction in harvest age of 1–2 years, based on stand volume, is probably too small to provide a positive return on investment from repeated fertilization in this study. However, larger growth responses have been previously reported from repeated fertilization experiments with lodgepole pine. Brockley (2005) reported the effects of factorial combinations of post-thinning density and fertilization (repeated every 5 years) on the growth of young lodgepole pine in central BC. Total volume increment in fertilized treatment plots averaged 15.2 m<sup>3</sup> ha<sup>-1</sup> (52 per cent) greater than in the unfertilized treatment plots over 10 years. In another study, two applications of a multi-nutrient fertilizer produced 17.2 m<sup>3</sup> ha<sup>-1</sup> more stand volume (36 per cent) than the unfertilized control over 12 years (Brockley, 2007). The larger growth responses reported in these studies, and less frequent fertilizer applications, would make fertilization a more attractive investment option.

At the stand level in this study, several factors, either acting separately or in combination, may be responsible for the relatively small increase in volume from repeated fertilization. Increased leaf area has been determined to be the primary mechanism governing growth response following fertilization (Vose and Allen, 1988). Although crowns apparently recovered rapidly following pruning, reduced live crown biomass may have negatively affected growth response to fertilization in the 250, 500 and 1000 trees ha<sup>-1</sup> treatments during the 6- to 10-year period. Low stand densities in two of the treatments (250 and 500 trees ha<sup>-1</sup>) may also have negatively affected fertilization response. Brockley (2005) reported that tree and stand volume gains following fertilization were less, in both relative and absolute terms, at 600 trees ha<sup>-1</sup> than at 1100 or 1600 trees ha<sup>-1</sup>. Vigorous response of understorey vegetation to nutrient additions (and strong competition for water and nutrients) at the low stand density may have reduced the effectiveness of fertilization on tree growth. Both herbaceous and shrubby vegetation can be strong competitors for soil moisture and nutrients in conifer stands, and induced water stress or direct competition for applied

nutrients can reduce or eliminate the positive effects of fertilization on conifer growth on brushy sites (Powers and Reynolds, 1999). Substantial moisture deficits are normal during the middle and latter parts of the growing season in drier sub-zones of the MS biogeoclimatic zone (Meidinger and Pojar, 1991).

Our significantly enhanced parameters of diameter, BA and volume growth per tree were consistent with those reported by several studies following PCT and fertilization treatments (Johnstone, 1985; Brockley, 1996; Weetman *et al.*, 1997; Brockley, 2005). Height growth was not significantly enhanced by thinning treatments and, within fertilized stands, appeared to be slightly decreased. Fertilization has been reported to increase the water flow to the lower branches, which may lead to water stress and decreased growth at the terminal during dry periods (Amponsah *et al.*, 2004; Brockley, 2005). Brockley and Simpson (2004) suggested that fertilization-induced nutrient imbalances may have been responsible for decreased height growth following repeated fertilization treatments; however, no such imbalances were observed during this study.

At the tree level, there may be several benefits associated with thinning in terms of enhanced growth. However, at the stand level, heavy thinning treatments will undoubtedly lead to growing space not being occupied by crop trees, which may reduce the volume available at harvest. The enhanced growth rates observed within both heavily thinned and fertilized stands may mitigate some of the losses of stand volume. While low-density thinning treatments may initially result in unoccupied growing space, the release of shade-tolerant crop trees as well as ingress of additional trees may provide a significant future source of crop tree volume (Sullivan *et al.*, 2006). In addition, Cochran (1989) reported that fertilization increased wood volume by increasing stand-level stocking. Our study reported on 10-year growth increments in the permanently tagged, dominant and co-dominant stems remaining after PCT and, as a result, did not account for the contributions made by other trees.

Thus, our hypothesis that thinning and repeated fertilization would enhance productivity (diameter, BA and volume) of lodgepole pine crop trees is supported by our results. At the stand level,

however, volume growth was decreased with heavy thinnings. Our results also revealed that BA/tree, volume/tree and volume/hectare growth was greater in heavily thinned and, in particular, repeatedly fertilized stands during the last 5 years compared with the first 5 years of the study. This pattern suggested that the effects of these incremental silviculture treatments may not have been fully expressed 10 years after the onset of treatments.

### *Crown architecture*

The architecture of a tree's live crown is of primary importance to the production of forest products as it directly determines the amount of photosynthates available for stem formation (Oliver and Larson, 1996; Zarnoch *et al.*, 2004), the geometry of the stem (Dean, 2004) as well as the cellular properties of the wood itself (Muhairwe, 1994). As a result, manipulating crown architecture allows forest managers to influence the growth rate, form and wood quality of a tree. Five years following thinning, crown area, volume and LCR all appeared to be enhanced by PCT and repeated fertilization; however, the differences were not statistically significant. At the end of our 10-year study, crown area and volume were similar among all density treatments, despite the lower density stands having been pruned 5 years earlier. This suggests that lodgepole pine trees recovered rapidly from pruning and that reduced growth rates associated with pruning, if any, would have been short-lived. Even though lodgepole pine does not produce epicormic branches, crown size recovered quickly from pruning treatments because of pine's relatively weak epinastic control and, therefore, ability to rapidly expand branch growth (Oliver and Larson, 1996; Kishchuk *et al.*, 2002). This was observed during our study and is indicated by the large crown area and volume within the very low and low-density stands 5 years after pruning.

The rapid recovery of crown size following pruning in young stands of lodgepole pine suggested that the benefits associated with pruning (see discussion on stem form and wood quality below) appear to be possible without sacrificing photosynthate production. Furthermore, repeated fertilization treatments were observed to

significantly enhance crown area, which likely facilitated the enhanced DBH, BA and volume growth observed within fertilized stands (Brockley and Simpson, 2004).

#### *Stem form and wood quality*

Enhanced growth of crop trees is an important condition that can provide for increased financial returns and/or mitigate timber supply shortfalls. However, accelerated growth rates may have negative impacts on both stem form and wood quality that must be considered. The amount of dimensional lumber that is recovered from a given unit volume of wood is directly related to stem form and decreases with increasing taper (Ballard and Long, 1988; Middleton *et al.*, 1995). Stem taper can largely be explained by the uniform stress principle of stem formation, which predicts a stem's form based on the physics of withstanding external stresses such as wind drag and snow loading; stems become increasingly tapered in response to increasing external stresses (Dean, 2004). Taper has been shown to increase with both thinning (Ballard and Long, 1988; Middleton *et al.*, 1995) and fertilization (Mead and Tamm, 1988), and is likely explained by the increased wind and snow-load stresses associated with increased crown length (Muhairwe, 1994). During this study, stem diameter was only measured at breast height. As a result, stem taper could not be quantified. However, taper is assumed to have increased with both thinning and fertilization treatments due to the enhanced diameter growth without a corresponding increase in height growth. Brockley (2005) observed increased taper for young lodgepole pine stems growing in heavily thinned stands compared with those in lightly thinned stands. We recommend that future sampling in these study areas include destructive sampling to facilitate an accurate assessment of treatment effects on stem taper. While increased stem taper and decreased wood quality are sometimes argued to outweigh the benefits of enhanced wood production, pruning may mitigate some of these negative attributes associated with fast-growing trees. The rapid recovery of lodgepole pine crowns to pruning disturbance suggested that pruning may benefit stem form and wood quality without sacrificing stem growth.

Wood density is often considered to be the most important indicator of clear-wood quality, with high-density wood being preferred to low-density wood (Jozsa and Brix, 1989). Thinning and fertilization treatments are often associated with decreased wood density (Ballard and Long, 1988; Amponsah *et al.*, 2004; Kang *et al.*, 2004), primarily because of the disproportionately large increase in low-density earlywood production compared with high-density latewood.

Juvenile wood is produced within and near the live crown and has several undesirable wood properties, including lower density, higher fibril angle and shorter cells compared with mature wood, which is produced along the branch-free portion of the lower stem (Snellgrove *et al.*, 1988). Because thinning and fertilization treatments tend to increase the size of crowns and decrease the rate of crown recession, it follows that these silvicultural treatments would increase the juvenile to latewood ratio throughout the lower stem. As a result, artificial pruning can mitigate some of the negative effects of thinning and fertilization by decreasing the LCR, thereby accelerating the transition from juvenile wood to mature wood (Macdonald and Hubert 2002). Pruning was shown to increase wood density up to 7 per cent at 2–3 years after treatment within radiata pine (*Pinus radiata* D. Don) (Cown, 1973). In addition, pruning provides for increased volume of clear wood (Ballard and Long, 1988; Kellomaki *et al.*, 1989) and has even been demonstrated to reduce the degree of taper following thinning treatments (Muhairwe, 1994).

#### *Indirect consequences of treatments on stand productivity*

The mountain pine beetle is the most severe insect pest of lodgepole pine and, while it is a natural component of the ecosystem which may even enhance the long-term competitive performance of lodgepole pine, losses due to periodic epidemics of this insect seriously affect the sustained yield and regulation of managed stands (Lotan and Critchfield, 1990). Several studies indicate that losses to this beetle can be significantly reduced or avoided with treatments such as thinning and fertilization that increase tree vigour (Oliver and Larson, 1996; Whitehead and Russo, 2005), as

well as modified microclimate including increased light intensity, wind movement and reduced humidity (Amman *et al.*, 1988). While increased tree vigour may enhance the ability of a tree to survive (i.e. pitch out) a bark beetle attack, the high number of beetles associated with the epidemic that is currently decimating pine forests throughout BC's interior is also killing stands of young, vigorous pine. If thinned and fertilized stands are killed by bark beetles, the advance regeneration in the understorey of low-density stands may significantly reduce reforestation costs and decrease time for stands to attain merchantable-sized trees. The potential for advance regeneration to provide a new stand of crop trees remains speculative and is related to the suitability of species composition, stocking density and spacing. Therefore, it is recommended that future studies carefully consider the attributes of the younger cohort of trees that develop within the understorey of low-density stands (Sullivan *et al.*, 2006).

## Conclusion

Our results indicate that PCT and repeated fertilization will enhance diameter, BA and volume growth of young lodgepole pine crop trees. At the tree level, the use of these intensive management practices appeared to enhance wood production 10-years after treatment. At the stand level, volume yields will undoubtedly decrease following heavy thinning. However, within these low-density open canopy stands, release of suppressed trees and ingress of new trees may mitigate some of the initial losses related to thinning, if this younger cohort of trees includes commercially desirable species.

The decision to apply intensive silviculture treatments should consider the impacts that treatments such as thinning and repeated fertilization have on enhancing tree growth, mitigating timber supply shortfalls, decreasing the potential for timber loss due to crown fires and bark beetle infestations, reducing hazards associated with urban-residential interface fires and biodiversity conservation.

Monitoring the long-term response of lodgepole pine to incremental silviculture treatments of thinning, fertilization and pruning will provide valuable insight as to when and where the most

significant benefits for wood production can be achieved. Incorporating a diversity of silvicultural practices, including heavy thinning and repeated fertilization regimes, should help meet the goals of enhanced wood production.

## Funding

Silviculture Branch, BC Ministry of Forests, Victoria, BC; the Canada-British Columbia Partnership Agreement on Forest Resource Development (FRDA II); Forest Renewal BC; Forest Innovation Investment; Gorman Bros. Lumber Ltd; Riverside Forest Products Ltd; Alex Fraser Research Forest; University of British Columbia.

## Acknowledgements

Operational treatments were conducted by the Silviculture sections of Penticton and Horsefly Forest Districts (MoF). We thank A. Kozak and L. Zabek for assistance with statistical analysis and C. Nowotny, J. Hickson, C. Houwers, C. Kohler, B. Runciman, S. Lang and H. Sullivan for assistance with the fieldwork.

## Conflict of Interest Statement

None declared.

## References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M. and Johnsen, K.H. 2004 Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manage.* **192**, 3–19.
- Alverson, W.S., Kuhlman, W. and Wallen, D.M. 1994 *Wild Forests: Conservation Biology and Public Policy*. Island Press, Washington, DC.
- Amman, G.D., McGregor, M.D., Schmitz, R.F. and Oakes, R.D. 1988 Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Can. J. For. Res.* **18**, 688–695.
- Amponsah, I.G., Liefers, V.J., Comeau, P.G. and Brockley, R.P. 2004 Growth response and sapwood hydraulic properties of young lodgepole pine following repeated fertilization. *Tree Physiol.* **24**, 1099–1108.
- Ballard, T.M. and Carter, R.E. 1986 Evaluating Forest Stand Nutrient Status. *Land Management Report No. 20*. B.C. Ministry of Forests, Victoria, British Columbia.

- Ballard, L.A. and Long, J.N. 1988 Influence of stand density on log quality of lodgepole pine. *Can. J. For. Res.* **18**, 911–916.
- B.C. Ministry of Forests 2003 *Timber Supply and the Mountain Pine Beetle Infestation in British Columbia*. British Columbia Ministry of Forests, Forest Analysis Branch, Victoria, British Columbia.
- Brockley, R.P. 1990 Response of thinned, immature lodgepole pine to nitrogen and boron fertilization. *Can. J. For. Res.* **20**, 579–585.
- 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. 2001 Foliar Sampling Guidelines and Nutrient Interpretative Criteria for Lodgepole Pine. *Extension Note 52*. B.C. Ministry of Forests, Victoria, British Columbia.
- Brockley, R.P. 2003 Effects of nitrogen and boron fertilization on foliar boron nutrition and growth in two different lodgepole pine ecosystems. *Can. J. For. Res.* **33**, 988–996.
- Brockley, R.P. 2004 Effects of different sources and rates of sulphur on the growth and foliar nutrition of nitrogen-fertilized lodgepole pine. *Can. J. For. Res.* **34**, 728–743.
- 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 twelve 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.*, (in press).
- Brockley, R.P. and Simpson, D.G. 2004 Effects of Intensive Fertilization on the Foliar Nutrition and Growth of Young Lodgepole Pine and Spruce Forests in the Interior of British Columbia (E.P. 886.13): Establishment and Progress Report. *Technical Report 018*. B.C. Ministry of Forests, Research Branch, Victoria, British Columbia.
- Brockley, R.P., Trowbridge, R.L., Ballard, T.M. and Macadam, A.M. 1992 Nutrient management in interior forest types. *Proceedings Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests*. Contribution 73, Institute of Forest Resources, University of Washington, Seattle, WA, pp. 43–64.
- Brooks, D.J. 1997 The outlook for demand and supply of wood: implications for policy and sustainable management. *Commonw. For. Rev.* **76**, 31–36.
- Carey, A.B., Lippke, B.R. and Sessions, J. 1999 Intentional systems management: managing forests for biodiversity. *J. Sust. For.* **9**, 83–125.
- Cochran, P.H. 1989 Growth rates after fertilizing lodgepole pine. *West. J. Appl. For.* **4**, 18–20.
- Cole, D.M. and Koch, P. 1996 *Managing Lodgepole Pine to Yield Merchantable Thinning Products and Attain Sawtimber Rotations*. Research Paper INT-RP-482, Ogden, Utah, USDA Forest Service Intermountain Research Station.
- Cown, D.J. 1973 Effects of severe thinning and pruning treatments on the intrinsic wood properties of young radiata pine. *N. Z. J. For. Sci.* **3**, 379–389.
- Dean, T.J. 2004 Basal area increment and growth efficiency as functions of canopy dynamics and stem mechanics. *For. Sci.* **50**, 106–116.
- Farnden, C. 1996 *Stand Density Management Diagrams for Lodgepole Pine, White Spruce and Interior Douglas-fir*. Information Report BC-X-360, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, pp 37.
- Farnum, P., Timmis, R. and Kulp, J.L. 1983 The biotechnology of forest yield. *Science*. **219**, 694–702.
- Gaines, T.P. and Mitchell, G.A. 1979 Boron determination in plant tissues by the azomethine H method. *Commun. Soil Sci. Plant Anal.* **10**, 1099–1108.
- Groot, A., Brown, K.M., Morrison, I.K. and Barker, J. E. 1984 A 10-year tree and stand response of jack pine to urea fertilization and low thinning. *Can. J. For. Res.* **14**, 44–50.
- Hunter, M.L. Jr 1999 *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge, UK.
- Hurlbert, S.H. 1984 Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**, 187–211.
- Johnstone, W.D. 1985 Thinning lodgepole pine. In *Lodgepole Pine: the Species and Its Management*. D.M. Baumgartner, R.G. Krebill, J.T. Arnott and G.F. Weetman (eds). Washington State University Cooperative Extension, Spokane, WA, pp. 253–262.
- Jokela, E.J., Dougherty, P.M. and Martin, T.A. 2004 Long-term production dynamics of loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. *For. Ecol. Manage.* **192**, 117–130.

- Jozsa, L.A. and Brix, H. 1989 The effects of fertilization and thinning on wood quality of a 24-year-old Douglas-fir stand. *Can. J. For. Res.* **19**, 1137–1145.
- Kang, K., Zhang, S.Y. and Mansfield, S.D. 2004 The effects of initial spacing on wood density, fibre and pulp properties in jack pine (*Pinus banksiana* Lamb.). *Holzforschung.* **58**, 455–463.
- Kellomaki, S., Oker-Blom, P., Valtonen, E. and Vaisanen, H. 1989 Structural development of Scots pine stands with varying initial density effect of pruning on branchiness of wood. *For. Ecol. Manage.* **27**, 219–234.
- Kishchuk, B.E., Weetman, G.F., Brockley, R.P. and Prescott, C.E. 2002 14-year growth response of young lodgepole pine to repeated fertilization. *Can. J. For. Res.* **32**, 153–160.
- Koch, P. 1995 *Lodgepole Pine in North America*. Forest Products Society, Madison, WI.
- Linder, S. 1987 Responses to water and nutrients in coniferous systems. *Ecol. Stud.* **61**, 180–202.
- Linder, S. 1995 Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. *Ecol. Bull.* **44**, 178–190.
- Lotan, J.E. and Critchfield, W.B. 1990 Pinus contorta Dougl. ex. Loud, or lodgepole pine. In *Silvics of North America: 1. Conifers*. Agriculture Handbook. 654, R.M. Burns and B.H. Honkala (eds). USDA Forest Service, Washington, DC, pp. 302–315.
- Malkonen, E. and Kukkola, M. 1991 Effect of long-term fertilization on the biomass production and nutrient status of Scots pine stands. *Fert. Res.* **27**, 113–127.
- Mead, D.J. and Tamm, C.O. 1988 Growth and stem form changes in *Picea abies* as affected by stand nutrition. *Scand. J. For. Res.* **3**, 505–513.
- Meidinger, D. and Pojar, J. 1991 Ecosystems of British Columbia. *Special Report Series No. 6*. Research Branch, Ministry of Forests, Victoria, British Columbia.
- Middleton, G.R., Jozsa, L.A., Palka, L.C., Munro, B.D. and Sen, P. 1995 Lodgepole pine product yields related to differences in stand density. *Special Publication SP-35*. Forintek Canada Corp., Vancouver, British Columbia.
- Mitchell, K.J., Stone, M., Grout, S.E., DiLucca, C.M., Night, G.D. and Goudie, J.W. et al. 2007 *TIPSY Version 4.1*. B.C. Ministry of Forests and Range, Victoria, British Columbia. <http://www.gov.bc.ca/hregymodels/TIPSY/index.htm> [online].
- Muhairwe, C.K. 1994 Tree form and taper variation over time for interior lodgepole pine. *Can. J. For. Res.* **24**, 1904–1913.
- Oliver, C.D. and Larson, B.C. 1996 *Forest Stand Dynamics, updated edition*. Wiley, New York, pp 521.
- Parkinson, J.A. and Allen, S.E. 1975 A wet oxidation procedure for the determination of nitrogen and mineral nutrients in biological material. *Commun. Soil Sci. Plant Anal.* **6**, 1–11.
- Powers, R.F. and 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. and 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.
- 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.
- Sedjo, R.A. and Botkin, D. 1997 Using forest plantations to spare natural forests. *Environment.* **39**, 15–20.
- Sedjo, R.A., Goetzl, A. and Moffat, S.O. 1998 *Sustainability of Temperate Forests*. Resources for the Future, Washington, DC.
- Snellgrove, T.A., Cahill, J.M., and Fahey, T.M. 1988. Timber quality considerations for forest managers. In *Proc. Future Forests of the Mountain West: a Stand Culture Symposium*. USDA Forest Service, *Gen. Tech. Rep.* INT-243. pp. 35–41. Ogden, Utah.
- Sullivan, T.P., Sullivan, D.S., and Lindgren, P.M.F. 2001 Stand structure and small mammals in young lodgepole pine forest: 10-year results after thinning. *Ecol. Applic.* **11**, 1151–1173.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. and 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.
- 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. and Haywood, J.D. et al. 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. and Flower-Ellis, J. 1999 Optimum nutrition and nitrogen saturation in Scots pine stands. *Stud. For. Suec.* **206**.
- Valinger, E., Elfving, B. and Morling, T. 2000 Twelve-year growth response of Scots pine to thinning and

- nitrogen fertilization. *For. Ecol. Manage.* **134**, 45–53.
- Vose, J.M. and Allen, H.L. 1988 Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *For. Sci.* **3**, 547–563.
- Watanabe, F.S. and Olson, S.R. 1965 Test of an ascorbic acid method for determining phosphorus in water and  $\text{NaHCO}_3$  extracts from soil. *Soil Sci. Soc. Am. Proc.* **49**, 677–678.
- 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.
- Weetman, G.F., Prescott, C.E., Kohlberger, F.L. and Fournier, R.M. 1997 Ten-year growth response of coastal Douglas-fir on Vancouver Island to N and S fertilization in an optimum nutrition trial. *Can. J. For. Res.* **27**, 1478–1482.
- Whitehead, R.J. and Russo, G.L. 2005 “Beetle-Proofed” Lodgepole Pine Stands in Interior British Columbia Have Less Damage from Mountain Pine Beetle. *Report BCX-402.*, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, pp 18.
- Yang, R.C. 1998 Foliage and stand growth responses of semimature lodgepole pine to thinning and fertilization. *Can. J. For. Res.* **28**, 1794–1804.
- Zarnoch, S.J., Bechtold, W.A. and Stolte, K.W. 2004 Using crown condition variables as indicators of forest health. *Can. J. For. Res.* **34**, 1057–1070.

*Received 26 March 2007*