Effects of post-thinning density and repeated fertilization on the growth and development of young lodgepole pine

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Abstract: The effects of factorial combinations of post-thinning density and fertilization on the growth and development of young lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) were investigated in central British Columbia. The effects of density and fertilization (repeated every 5 years) on tree height were small relative to the effects on stem radial growth. Tree radial growth increased with thinning intensity, whereas per-hectare growth was greatest at the highest residual density. Fertilizer effects varied across the range of residual densities tested. Tree and stand volume gains following fertilization were less, in both relative and absolute terms, at 600 trees/ha than at 1100 or 1600 trees/ha. Vigorous response of understory vegetation to nutrient additions (and strong competition for water and nutrients) may have reduced the effectiveness of fertilization on tree growth at 600 trees/ha relative to higher stand densities. Results indicate that the combined positive effects of thinning and fertilization on the growth of young lodgepole pine will accelerate stand development, thereby shortening technical rotation length. Results also indicate that significant growth gains following fertilization of thinned lodgepole pine will partially compensate for stand volume losses due to thinning. However, fertilization may be less effective at low stand densities, where negative effects of thinning on harvest volume are greatest.

Résumé : Les effets combinés de la densité et de la fertilisation après éclaircie sur la croissance et le développement de jeunes pins tordus (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) ont été étudiés dans le centre de la Colombie-Britannique. Les effets de la densité et de la fertilisation (répétées à tous les 5 ans) sur la hauteur des arbres étaient faibles comparativement aux effets sur la croissance radiale de la tige. La croissance radiale des arbres augmentait avec l'intensité de l'éclaircie, alors que la croissance à l'hectare était maximale lorsque la densité résiduelle était la plus forte. Les effets de la fertilisation ont varié en fonction des densités résiduelles testées. Les gains en volume des arbres et du peuplement après la fertilisation, tant en valeur relative qu'absolue, étaient moindres à une densité de 600 arbres/ha qu'à 1100 ou 1600 arbres/ha. Une réaction vigoureuse de la végétation de sous-bois à l'ajout de nutriments ainsi qu'une forte compétition pour l'eau et les nutriments peuvent avoir diminué l'efficacité de la fertilisation pour la croissance des arbres à une densité de 600 arbres/ha comparativement à des densités plus fortes. Les résultats indiquent que les effets combinés positifs de l'éclaircie et de la fertilisation sur la croissance des jeunes pins tordus accéléreront le développement du peuplement et raccourciront ainsi la durée de la rotation technique. Les résultats indiquent aussi que pour les pins tordus éclaircis, les gains significatifs de croissance causés par la fertilisation compenseront en partie les pertes en volume du peuplement attribuables à l'éclaircie. Cependant, la fertilisation peut être moins efficace dans le cas des peuplements à faible densité, là où les effets négatifs de l'éclaircie sur le volume à récolter sont les plus importants.

[Traduit par la Rédaction]

Introduction

A smaller timber harvesting land base, combined with age-class imbalances in the timber inventory and large mortality losses caused by the mountain pine beetle (*Dendroctonus ponderosae* Hopk.), is creating serious timber supply challenges for the forestry sector in the interior of British Columbia. Without strategic intervention, significant mid-term timber supply shortfalls are forecast for many interior forest management units (B.C. Ministry of Forests 2003). Because they are the primary silvicultural options for accelerating the operability of established stands, fertilization and thinning are key components of several timber supply mitigation strategies being developed to improve the size, and timing, of future harvests. Accelerating the development of extensive stands of young fire- and harvest-origin lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) may be particularly important in this regard.

The effects of thinning on the growth and development of lodgepole pine forests are well documented (Johnstone 1985; Johnstone and Cole 1988). Thinning reduces intertree competition in excessively dense stands, thereby redistributing growth on selected crop trees. The intensity of thinning has large potential impacts on the amount, size, and value of tim-

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ber harvested from managed forests and on biological and technical rotation lengths. Because stand and individual-tree growth cannot be simultaneously maximized, density management is typically a compromise between maximum production per unit area and individual-tree growth and size (Johnstone and Cole 1988). Forest managers must weigh the advantages of shorter rotation length and larger piece size (and lower harvesting, transportation, and milling costs) against the likelihood of reduced harvest volume and the possibility of producing trees with undesirable characteristics (e.g., larger branches and greater proportion of juvenile wood) that may negatively affect timber quality and value (Ballard and Long 1988).

Nutrient deficiencies are widespread throughout the British Columbia interior, and several investigators have reported improved growth of young lodgepole pine forests following fertilization with nitrogen (N) and other nutrients (Weetman et al. 1988; Yang 1998; Brockley 2000, 2003, 2004; Kishchuk et al. 2002; Brockley and Simpson 2004). Unlike thinning, fertilization accelerates stand development and increases piece size without sacrificing stand volume. As such, fertilization may be particularly useful for addressing age-class imbalances and for increasing long-term harvest levels.

Several studies have compared growth responses of *Pinus* species to fertilization in thinned and unthinned stands (Groot et al. 1984; Morrison and Foster 1990; Yang 1998; Valinger et al. 2000). Unthinned stands respond positively to fertilizer, but mortality losses are often higher in unthinned stands than in thinned stands. Thinning reduces the likelihood of competition-induced mortality of fertilized trees later in the rotation, and the growth increment of fertilized trees compensates for the volume sacrificed by reducing stand density. Because density control creates room for crown expansion, opportunities for refertilization may be greater in thinned than in unthinned stands.

Most lodgepole pine fertilization research in the British Columbia interior has been conducted in thinned, fire- or harvest-origin stands (Brockley 1996). Several stand densities have been used, but no studies have compared fertilization response across a range of post-thinning densities on the same site. This information is needed to determine optimum fertilization and thinning regimes for achieving specific yield and product objectives. In jack pine (*Pinus banksiana* Lamb.), the response to fertilization varied among post-thinning levels, with the largest relative and absolute growth increases occurring at the lowest stand density (Morrison and Foster 1990). Similar results were obtained from two fertilization × density factorial studies with Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) (Miller et al. 1986; Gardner 1990).

This paper reports 10-year results of a long-term field experiment designed to investigate the effects of differing levels of post-thinning stand density (600, 1100, 1600 trees/ha) on the growth and development of fertilized and unfertilized lodgepole pine in south-central British Columbia.

Methods

Location and site description

The Spokin Lake study site is located approximately 24 km southwest of Horsefly (52°9′N, 121°37′W) within the moist cool subzone of the Sub-Boreal Pine–Spruce biogeoclimatic zone (SBPSmk) (Steen and Coupe 1997). Annual precipitation in this subzone averages about 500 mm, slightly less than half of which occurs during the May through September period. Substantial moisture deficits are normal during the middle and latter parts of the growing season. Soil and vegetation description indicates the site belongs to the zonal Pl – Pinegrass – Arnica (01) site series (Steen and Coupe 1997). The site is flat and occurs on an imperfectly drained morainal blanket at an elevation of 1040 m. The rooting zone has a loamy texture with about 30% volume of gravel and cobbles. There is a clay-rich horizon at a depth of about 30 cm, below which rooting is restricted. The soil is classified as an Orthic Gray Luvisol (Soil Classification Working Group 1998).

The site is occupied by a naturally regenerated lodgepole pine stand that originated from a 1977 clearcut and subsequent drag scarification. At the time of installation establishment in 1989, the 10-year-old stand had an average density of about 42 000 stems/ha. The stand was generally of good health, with low levels of infection with western gall rust (caused by *Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka). With growth intercept methodology (Nigh 1997), the estimated site index of lodgepole pine occupying the site is 20 m at 50 years.

Pretreatment mean foliar N levels (10.4 g/kg) indicated severe N deficiency according to foliar nutrient diagnostic criteria developed for lodgepole pine (Ballard and Carter 1986; Brockley 2001). Pretreatment mean foliar sulphate-S (SO_4) concentration (44 mg/kg) indicated probable S deficiency, based on published foliar SO_4 interpretative criteria for conifers (Turner et al. 1977; Brockley 2000). With the exception of boron (B) (9 mg/kg), other plant nutrients were generally well supplied. Foliar B levels are a characteristically low in lodgepole pine forests throughout central British Columbia (Brockley 2003).

Study establishment

The study was designed as a 3 × 2 factorial experiment: three levels of post-thinning density (600, 1100, and 1600 trees/ha) and two levels of fertilization (unfertilized and fertilized).

During August 1989, areas of uniform site conditions and lodgepole pine cover within the cutblock were identified for plot location. Each of the six treatment combinations was randomly assigned to three of the plot locations. Treatment plots were rectangular in shape and varied in size from 0.105 to 0.280 ha depending on post-thinning density. A minimum distance of 5 m separated the outer boundaries of adjacent treatment plots.

The 600, 1100, and 1600 trees/ha thinning regimes were created by establishing a 12 × 14 grid within each treatment plot. Grid intervals corresponded to the square intertree spacing dictated by each post-thinning density (Table 1). A healthy, vigorous "leave" tree was selected near each of the 168 grid intersections. All nonselected trees within each treatment plot were cut with brushsaws in August 1989. All thinned material was retained within treatment plot boundaries.

A square assessment plot was established within each treatment plot to monitor the growth and development of retained lodgepole pine. The assessment plot was offset at one end of the rectangular treatment plot to reserve an area for future

Table 1. Treatment plot and assessment plot specifications for the 600, 1100, and 1600 trees/ha thinning regimes.

	Treatment plot			Assessment plot			
Thinning regime (trees/ha)	Dimensions (m)	Size (ha)	No. of trees	Dimensions (m)	Size (ha)	No. of trees	Intertree spacing (m)
600	49.0 × 57.1	0.280	168	32.6 × 32.6	0.107	64	4.08
1100	36.2 × 42.3	0.153	168	24.2 × 24.2	0.058	64	3.02
1600	30.0 × 35.0	0.105	168	20.0 × 20.0	0.040	64	2.50

destructive sampling. Three sides of the assessment plot were surrounded by two rows of trees at the specified spacing interval; the buffer on the fourth side was four trees wide. Numbered metal tags were attached to each of the 64 lodgepole pine leave trees within each assessment plot.

Treatment plot and assessment plot specifications are fully described in Table 1.

Fertilization

In a previous study, fertilization of a young, densely stocked stand at the time of thinning resulted in severe snow-press damage to lodgepole pine leave trees (R.P. Brockley, unpublished data). At Spokin Lake, fertilization was delayed for 3 years after thinning to minimize snow-press losses.

A customized, multinutrient fertilizer was applied to fertilized treatment plots in October 1992. Urea (46:0:0, N–P–K) was the major source of N. A small amount of N (24% of the total) was added as monoammonium phosphate (11:52:0; N–P–K), which also served as the phosphorus (P) source. Potassium (K) was delivered as potassium chloride (0:0:60; N–P–K) and sulphate potash magnesia (0:0:22:22:11; N–P–K–S–Mg). The latter fertilizer was also the source of sulphur (S) and magnesium (Mg). Boron was added as granular borate (14% B). At an application rate of 1208 kg/ha, the blended fertilizer delivered amounts of individual nutrients as follows: 200 kg N/ha, 100 kg P/ha, 100 kg K/ha, 75 kg S/ha, 37 kg Mg/ha, and 3 kg B/ha. The same blended fertilizer, at the same application rate, was reapplied to treatment plots in October 1997 and in October 2002.

The 600, 1100, and 1600 trees/ha treatment plots were divided into 12, 16, and 32 sections, respectively, prior to each fertilizer application. The size of each section was the same within a thinning regime, but differed slightly among regimes. Premeasured amounts of the fertilizer blend were uniformly broadcast applied by hand to each of the sections.

Tree growth

The diameter at breast height (DBH), total height, height to the base of the live crown, and tree form and condition were recorded for all tagged trees within each assessment plot in October 1992, immediately after fertilization. Diameter measurements were taken with a steel diameter tape at a permanently marked point approximately 130 cm above the ground. A telescoping height pole was used for tree height and live crown measurements. The initial tree and stand characteristics for each of the thinning regimes immediately after fertilization are shown in Table 2.

Measurements were repeated in the fall of 1997 (fifth year) and in the fall of 2002 (tenth year). In 1997 and 2002, height measurements were taken with a Forestor Vertex® hypsometer.

Table 2. Tree and stand characteristics by thinning regime in October 1992, immediately after fertilization.

Thinning regime (trees/ha)	Dq (cm)*	Height (m)	DBH/height (cm/m)	SDI†	Basal area (m^2/ha)	Volume (m^3/ha)
600	4.98	3.46	1.41	45	1.14	1.87
1100	4.66	3.34	1.36	75	1.84	2.97
1600	4.34	3.24	1.30	97	2.34	3.73

*Dq, quadratic mean diameter.
†SDI, stand density index = trees per hectare × $(Dq/25)^{1.6}$ (Long 1985).

A small amount of mortality occurred in most treatment plots during the initial 5-year measurement period. However, there was very little mortality thereafter, and survival in the six treatment regimes ranged from 92% to 98% after 10 years. Most of the mortality was associated with snow and (or) wind damage.

Understory vegetation

Understory vegetation was destructively sampled in 2004 to determine whether differences in understory biomass could partially explain the differing effects of thinning and fertilization regimes on lodgepole pine growth and development that were measured after 10 years. Understory vegetation was collected from five randomly located subplots within each of the 18 treatment plots in late July at the period of peak vegetation development. At each sampling point, a 0.5-m^2 circular hoop was placed on the ground, and all herbaceous vegetation, grasses, and shrubs originating within the sampling area were cut at ground level and placed in a plastic bag. The collected vegetation was not sorted by species or life form. Mosses and lichens were not sampled. The individual samples were transferred to large paper bags and subsequently dried in a forced-air oven at 70 °C for 24 h.

Leaf area index

An indirect estimate of stand leaf area index (LAI), commonly referred to as effective LAI (LAI_e) (Chen and Black 1991), was obtained for each treatment plot in 2003 following the tenth growing season after initial fertilization. LAI measurements followed foliage abscission in the fall and preceded bud flush in the spring.

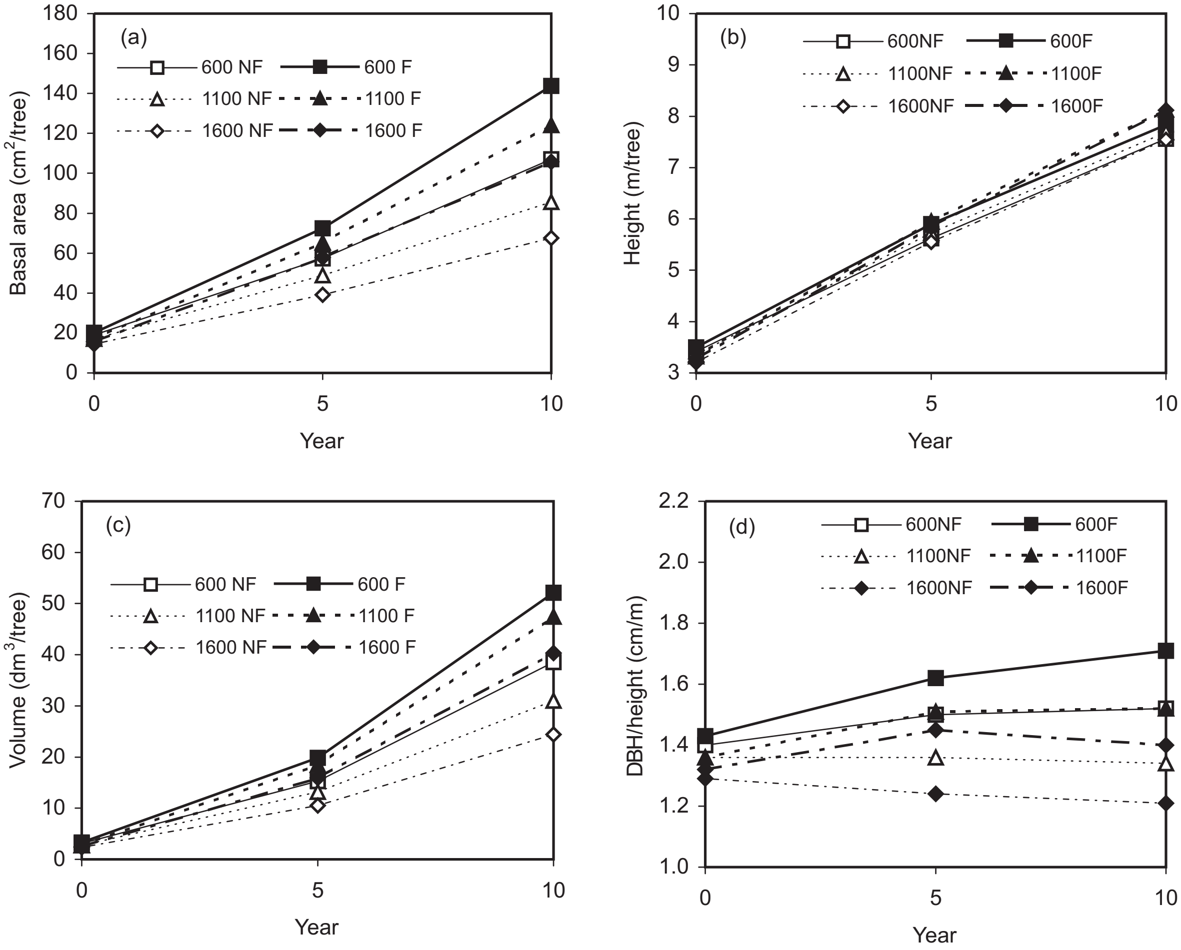
Effective LAI was measured with a LI-COR LAI-2000 plant canopy analyzer (LI-COR 1991). Several studies have shown a strong positive correlation, but negative bias (due to tree and stand foliage clumping), between LAI_e estimates obtained with the LAI-2000 in conifer stands and direct LAI

Table 3. Repeated measures ANOVA summary table for tree basal area, height, volume, and DBH/height, showing variance ratios (*F*), *p* values, and error mean squares.

		Basal area		Height		Volume		DBH/height	
Source of variation	df	*F*	*p* >*F*	*F*	*p* >*F*	*F*	*p* >*F*	*F*	*p* >*F*
Between subjects									
D	2	13.06	0.001	0.10	0.902	6.15	0.014	138.32	<0.001
F	1	33.24	<0.001	1.40	0.259	23.19	<0.001	133.33	<0.001
D × F	2	0.03	0.966	0.04	0.962	0.09	0.916	1.05	0.379
Error mean square	12	8373.11		34.25		1639.94		0.091	
Within subjects									
Y	2	2327.45	<0.001	6931.93	<0.001	978.25	<0.001	63.96	<0.001
Y × D	4	29.81	<0.001	4.59	0.007	9.34	<0.001	20.42	<0.001
Y × F	2	100.58	<0.001	13.81	<0.001	42.88	<0.001	46.58	<0.001
Y × D × F	4	0.16	0.314	1.29	0.301	0.20	0.939	1.28	0.306
Error mean square	24	934.34		0.80		380.89		0.046	

Note: D, density; F, fertilizer; Y, year.

Fig. 1. Effects of stand density and fertilization on (*a*) tree basal area, (*b*) tree height, (*c*) tree volume, and (*d*) tree DBH/height over 10 years. For each year, plotted values are means of all measurements combined. 600NF: 600 trees/ha, unfertilized; 600F: 600 trees/ha, fertilized; 1100NF: 1100 trees/ha, unfertilized; 1100F: 1100 trees/ha, fertilized; 1600NF: 1600 trees/ha, unfertilized; 1600F: 1600 trees/ha, fertilized.

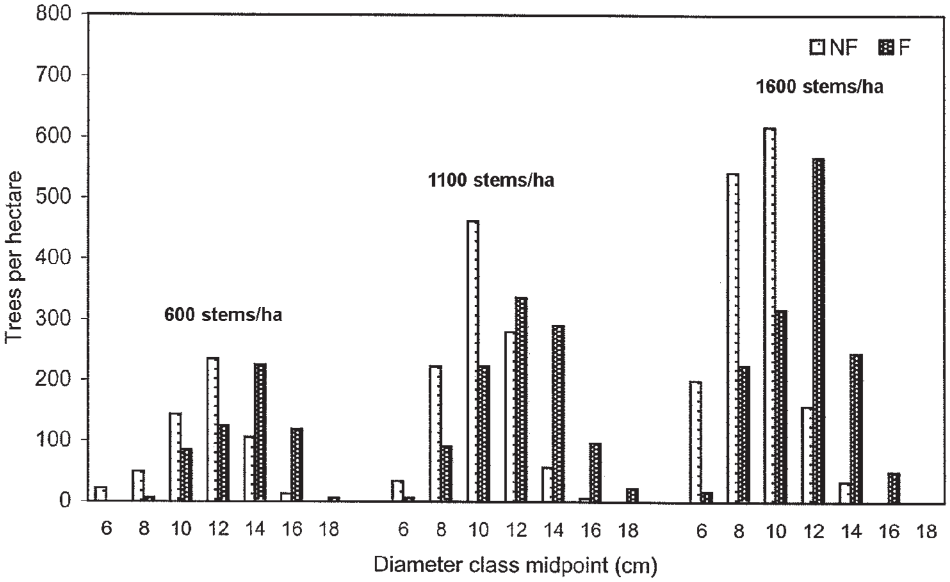


values determined by dimension analysis (Gower and Norman 1991; Smith et al. 1993; Barclay and Trofymow 2000).

Within each treatment plot, measurements were obtained at a height of 80–100 cm above the ground at the five permanently marked points. One measurement point was located at the centre of each treatment plot. The other four points were located by measuring a distance of 8 m from plot centre in each of the four cardinal directions.

Two readings were obtained at each point, one facing northwest and the other facing northeast before and after so-

Fig. 2. Distribution of unfertilized and fertilized trees by diameter class at different stand densities at year 10. NF, unfertilized; F, fertilized.



lar noon, respectively. Sensors were equipped with a 180° view cap. Simultaneously, above-canopy light measurements were collected in an open area adjacent to the study site where the light sensor had an unobstructed view of the sky. All measurements were made under uniformly overcast conditions.

Foliar analysis

Replicated samples of current-year foliage were collected from all treatment plots in October 1992 prior to initial fertilization and after the first, fifth, tenth, and eleventh growing seasons after initial fertilization. The first- and eleventh-year sampling corresponded to the first growing season following the initial and third fertilizer applications, respectively. Inclement weather and access problems prohibited foliage sample collection after year 6.

At each sampling date, current-year foliage was collected from 10 representative healthy dominant or codominant trees that were evenly distributed within each assessment plot. Samples were collected from the lower portion of the top third of the live crown, consistent with standardized foliar sampling guidelines (Brockley 2001). Whenever possible, the same trees were sampled each year. Individual foliage samples were frozen following field collection and then dried in a forced-air oven at 70 °C for 24 h before analysis. One composite sample, consisting of equal amounts of foliage from each of the 10 trees per treatment plot, was prepared for chemical analysis. Dried composite samples were ground in an electric coffee grinder before shipment to a laboratory for chemical analysis.

Foliage collected prior to fertilization and after the first and fifth growing seasons was analyzed by a commercial laboratory. Subsamples of foliage were digested using a variation of the sulphuric acid – hydrogen peroxide procedure described by Parkinson and Allen (1975). The digests were analyzed colorimetrically for N on a Technicon Autoanalyzer using the Bertholot (phenol–hypochlorite) reaction (Weatherburn 1967). 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, Mn, and Al were determined by atomic absorption spectrophotometry. Separate subsamples were dry ashed and copper (Cu), zinc (Zn), and iron (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). Total S was determined by combustion using a LECO sulphur analyzer. Inorganic sulphate S was extracted with boiling 0.01 mol/L hydrochloric acid (HCl) and determined colorimetrically on a hydriodic acid – bismuth reducible distillate (Johnson and Nishita 1952).

The foliage samples collected after the tenth and eleventh growing seasons were sent to the British Columbia Ministry of Forests laboratory. Analysis of total N and total S was by combustion using a Fisons NA-1500 elemental analyzer, followed by determination by inductively coupled plasma optical emission spectrometer. All other macronutrients and micronutrients were wet ashed with concentrated HNO_3-HCl acid (vanadium added as internal standard) and hydrogen peroxide, using a closed vessel microwave digestion system (Kalra and Maynard 1991). The digest solutions were diluted with HCl and individual nutrients were determined by inductively coupled plasma as above. Sulphate S was extracted with dilute HCl and determined by ion chromatography (Waters IC system).

Data analysis

The main effects of post-thinning density (D) and fertilization (F) and the D × F interaction were determined for several tree and stand characteristics. Individual-tree basal area (BA), total height, and volume values for the three measurement periods (0, 5, and 10 years) were analyzed with a repeated measures analysis of variance (ANOVA) (SAS Institute Inc. 1989). Only those trees alive after 10 years were used to determine stand BA and volumes per hectare for each measurement by summing individual-tree values in each plot and converting plot area to a per-hectare basis. Per-hectare stand values for each treatment plot were subjected

Table 4. ANOVA summary table for 10-year tree height increment, basal area increment, and volume increment, showing variance ratios (*F*), *p* values, and error mean squares.

		Height increment		Basal area increment		Volume increment	
Source of variation	df	*F*	*p* >*F*	*F*	*p* >*F*	*F*	*p* >*F*
D	2	9.61	0.003	12.92	<0.001	7.62	0.007
Linear	1	15.51	0.002	25.82	<0.001	14.99	0.002
Quadratic	1	3.69	0.079	0.02	0.879	0.24	0.631
F	1	23.04	<0.001	111.42	<0.001	123.85	<0.001
D × F	2	2.05	0.172	0.32	0.730	0.86	0.446
Covariate	1	9.98	0.008	137.12	<0.001	273.97	<0.001
Error mean square	12	1.79		2928.62		445.67	

Note: D, density; F, fertilizer.

to repeated-measures ANOVA. Individual-tree volumes (inside bark) were calculated from a variable-exponent taper function that was developed for lodgepole pine in the central interior of British Columbia (Kozak 1988).

One- to 10-year BA, height, and volume increments were calculated for all trees alive after 10 years and were adjusted by covariance analysis, using initial height, BA, and volume, respectively, as covariates. The 1- to 10-year stand BA and volume increments were analyzed in a similar fashion. Orthogonal polynomial contrasts were used to test the linear and quadratic effects of post-thinning density among the quantitative means of all tree and stand variables (Steel and Torrie 1980).

The crown width, LAI, and percent live crown ((live crown length / total height) × 100) measurements that were obtained at year 10 were subjected to analysis of variance. Percent live crown was converted with an arcsine square-root transformation prior to analysis. A level of significance of $\alpha = 0.05$ is used throughout the text for inferring statistical significance.

Results

Individual-tree growth

Tree mean BA, volume, and DBH/height ratio were significantly affected by stand density and fertilization over 10 years (Table 3). For these variables, both the year (Y) × D and Y × F interactions were highly significant. Overall, tree height was unaffected by either density or fertilization, but the effects of both treatments on tree height varied with time (Table 3). The individual-tree growth trends and interactions are illustrated in Figs. 1*a*–1*d*.

Post-thinning density resulted in major changes in the diameter distribution of lodgepole pine (Fig. 2). After 10 years, one-third of the trees in the 1600 trees/ha treatment had a DBH ≤8 cm, whereas only 7% of the trees in the 600 trees/ha treatment were below this threshold. Conversely, 41% and 12% of trees in the 600 and 1600 trees/ha density regimes, respectively, had a DBH ≥14 cm after 10 years. Fertilization was also very effective in shifting diameter distribution toward larger trees (Fig. 2). For example, 41% of fertilized trees and only 10% of unfertilized trees across all density regimes had a DBH ≥14 cm after 10 years.

Ten-year height increment was significantly affected by both stand density and fertilization (Table 4). The density effect was linear, with the smallest relative height increment measured at the lowest stand density (Fig. 3*a*). On average, the height increment of fertilized trees was 39 cm (9%) greater than that of unfertilized trees over 10 years. The D × F interaction was not statistically significant. However, both relative and absolute incremental height differences between fertilized and unfertilized trees were slightly less at 600 trees/ha than at 1100 and 1600 trees/ha (Fig. 3*a*).

The effects of density and fertilization on tree BA and volume increment were statistically significant over 10 years (Table 4). The density effects were strongly linear, with the largest BA and volume increments being measured at the lowest stand density (Figs. 3*b*, 3*c*). Relative BA and volume growth gains in response to fertilization were smallest at the lowest stand density, but the D × F interactions were not statistically significant (Figs. 3*b*, 3*c* and Table 4).

Crown characteristics

After 10 years, percent live crown was significantly affected by stand density (Table 5). The density effect was strongly linear; the largest percent live crown was measured at the lowest stand density (Fig. 4). Percent live crown was unaffected by fertilization (Table 5).

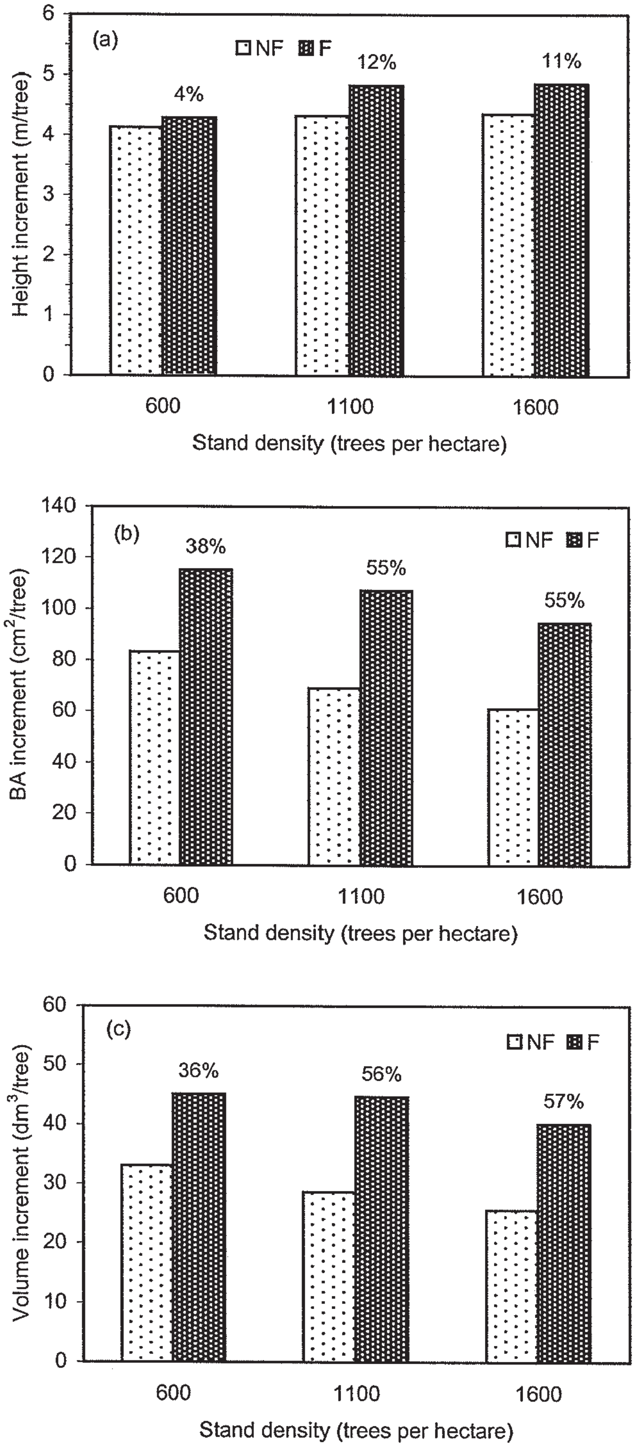
Crown width at year 10 was significantly affected by both density and fertilization (Table 5). The effect of density was strongly linear, with the lowest stand density producing the largest crown width (Fig. 5). Fertilization increased crown width across all stand densities, with the smallest absolute and relative increases measured at the lowest residual density (Fig. 5). However, the D × F interaction was not statistically significant (Table 5).

At year 10, effective leaf area index ($\mathrm{LAI_e}$) showed a statistically significant D × F interaction (i.e., the effects of fertilization on LAI varied differentially with stand density) (Table 5). In both absolute and relative terms, fertilization was least effective at stimulating $\mathrm{LAI_e}$ at the lowest stand density (Fig. 6).

Stand growth

Stand BA and volume development were significantly affected by density and fertilization (Table 6). For these variables, the Y × D and Y × F interactions were highly significant. Overall, there was no D × F interaction. However, the Y × D × F interaction was statistically significant (i.e., the effects of density on fertilizer response varied over time) for both BA and volume. The BA and volume stand growth trends and interactions are illustrated in Figs. 7*a* and 7*b*.

Fig. 3. One- to 10-year (*a*) height increment, (*b*) basal area increment, and (*c*) volume increment of unfertilized and fertilized lodgepole pine by stand density. Values above bars indicate change relative to unfertilized treatment for each stand density. NF, unfertilized; F, fertilized.



For the whole-stand component (all trees), the effect of fertilization on 10-year stand BA increment varied with stand density (i.e., a significant D × F interaction) (Table 7). Fertilization was least effective (both in relative and absolute terms) at stimulating stand BA increment at the lowest stand density (Fig. 8*a*). For 10-year stand volume increment (all trees), the effects of both density and fertilization were statistically significant (Table 7). The effect of density was linear, with the lowest stand density producing the smallest stand volume increment. Over 10 years, total volume increment in fertilized treatment plots was, on average, 7.3 m^3/ha (36%) greater than that in the unfertilized treatment plots at a density of 600 trees/ha. At 1100 and 1600 trees/ha, 10-year fertilization volume gains averaged 17.7 m^3/ha (59%) and 20.5 m^3/ha (60%), respectively (Fig. 8*b*). However, the D × F interaction was not statistically significant ($p = 0.089$).

For the largest 250 trees/ha, 1- to 10-year stand BA increment was significantly affected by stand density (Table 7). The density effect was linear, with the largest absolute stand BA increment being measured at the lowest stand density. Stand volume increment for the largest 250 trees/ha was unaffected by density. Fertilization increased BA and volume increments of the largest 250 trees/ha, with the smallest absolute and relative increases measured at the lowest density (Table 7 and Figs. 8*a*, 8*b*). However, the D × F interaction was not statistically significant for either BA or volume (Table 7).

Foliar nutrition

Foliar N levels were largely unaffected by stand density during the 11 years following installation establishment (Table 8). Foliar N levels were significantly higher in fertilized trees than in unfertilized trees 1 year following the initial fertilization, but there was no difference between fertilized and unferilized trees after 5 years (Table 8). Foliar sampling was not undertaken in year 6 (1 year after the first refertilization), but foliar N levels were significantly higher in fertilized trees than in unfertilized trees in year 10 (5 years after the first refertilization) (Table 8). In year 11 (1 year after the second refertilization), the relative effectiveness of fertilization in stimulating foliar N varied with stand density ($p = 0.027$). Foliar N differences between fertilized and unfertilized trees were smaller at the lowest stand density (600 trees/ha) compared with 1100 and 1600 trees/ha (Table 8). The D × F interactions were not statistically significant at the other sampling dates.

Foliar S, SO_4, and B levels were unaffected by stand density but were significantly improved by fertilization (data not shown). Higher foliar levels of these nutrients were maintained in fertilized trees throughout the study period. Other foliar nutrients were largely unaffected by either density or fertilization (data not shown).

Discussion

The effect of stand density on tree growth is consistent with the results reported from several previous studies with lodgepole pine and Scots pine (*Pinus sylvestris* L.) (Johnstone 1985; Johnstone and Cole 1988; Johnstone and van Thienen 2004; Makinen and Isomaki 2004). Trees responded primarily in radial growth, and the magnitude of radial increment increased with thinning intensity. This has resulted in an upward shift in the diameter distribution at the lower stand densities. The inverse relationship between tree radial increment and stand density is likely primarily a function of the size and persistence of tree crowns and higher LAI_e at

Table 5. ANOVA summary table for percent live crown, crown width, and leaf area index at year 10, showing variance ratios (*F*), *p* values, and error mean squares.

		Percent live crown		Crown width		Leaf area index	
Source of variation	df	*F*	*p* >*F*	*F*	*p* >*F*	*F*	*p* >*F*
D	2	66.39	<0.001	20.97	<0.001	62.84	<0.001
Linear	1	132.55	<0.001	41.57	<0.001	108.08	<0.001
Quadratic	1	0.19	0.667	0.40	0.539	17.61	0.001
F	1	0.14	0.715	84.86	<0.001	126.59	<0.001
D × F	2	0.56	0.584	1.24	0.324	9.65	0.003
Error mean square	12	0.0215		1.2296		0.0464	

Note: D, density; F, fertilizer.

Fig. 4. Effects of stand density and fertilization on percent live crown over 10 years. For each year, plotted values are means of all measurements combined. See caption of Fig. 1 for a description of the treatments.

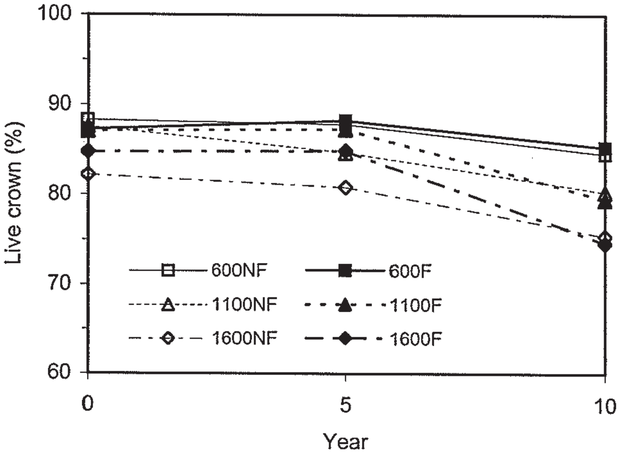


Fig. 5. Crown width of unfertilized and fertilized lodgepole pine at year 10 by stand density. Values above bars indicate change relative to unfertilized treatment for each stand density. NF, unfertilized; F, fertilized.

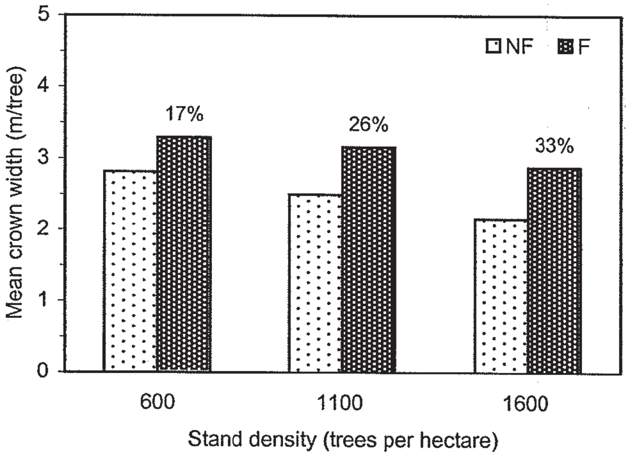


Fig. 6. Effective leaf area index of unfertilized and fertilized lodgepole pine at year 10 by stand density. Values above bars indicate change relative to unfertilized treatment for each stand density. NF, unfertilized; F, fertilized.

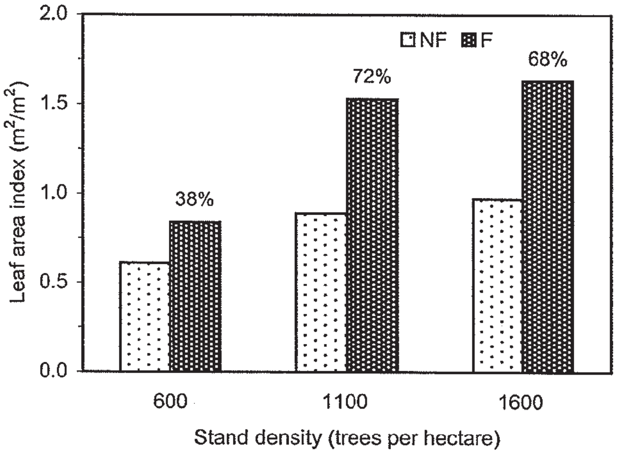


Table 6. Repeated measures ANOVA summary table for stand basal area and total volume, showing variance ratios (*F*), *p* values, and error mean squares.

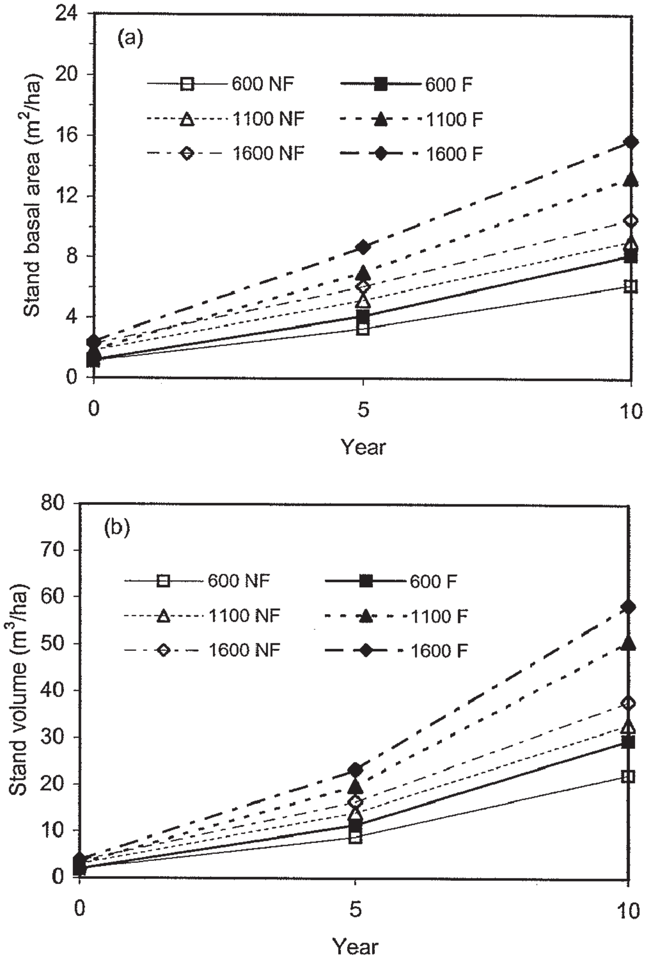
		Basal area		Volume	
Source of variation	df	*F*	*p* >*F*	*F*	*p* >*F*
Between subjects					
D	2	30.79	<0.001	18.38	<0.001
F	1	24.22	<0.001	18.99	<0.001
D × F	2	1.64	0.234	1.30	0.309
Error mean square	12	1.963		32.93	
Within subjects					
Y	2	2177.71	<0.001	955.95	<0.001
Y × D	4	56.07	<0.001	27.50	<0.001
Y × F	2	98.89	<0.001	43.45	<0.001
Y × D × F	4	6.27	0.001	3.05	0.036
Error mean square	24	0.159		6.20	

Note: D, density; F, fertilizer; Y, year.

lower densities. Increased crown longevity is generally associated with larger branch (knot) size and greater proportion of juvenile wood (Brazier 1977; Bendtsen 1978; Ballard and Long 1988). However, it is too early to speculate about the relative importance of characteristics such as log size and crown form in determining the quality and value of harvested material from low-density stands.

The apparent effect of stand density on tree size and radial increment is somewhat surprising given the low levels of

Fig. 7. Effects of stand density and fertilization on (*a*) stand basal area and (*b*) stand total volume over 10 years. For each year, plotted values are means of all measurements combined. See caption of Fig. 1 for a description of the treatments.



growing stock at this study site. Following thinning, stand density index (SDI) ranged from 45 at 600 trees/ha to 97 at 1600 trees/ha. These values represented only 3% and 6% of maximum SDI, respectively, based on a maximum SDI of 1700 for lodgepole pine (Long 1985). After 10 years, SDIs ranged from 200 (12% of maximum SDI) at 600 trees/ha to 395 (23% of maximum SDI) at 1600 trees/ha. The latter SDI value is just beginning to approach the level at which strong intertree competition generally begins (Long 1985). Density-related differences in mean tree characteristics shortly after thinning may partially explain the density effects on bole size and radial increment that were measured in this study. The "chainsaw effect" resulted in a small upward shift in quadratic mean diameter and height as residual stand density was decreased (see Table 2). However, the effects of stand density on tree radial increment persisted even when initial tree size was included as a covariate in the analysis.

The effects of stand density on lodgepole pine tree height were small relative to the density effects on stem radial growth. The slightly smaller height increments measured at the lowest density support previously reported findings that a limited degree of crowding is required to maximize the height growth of lodgepole pine and Scots pine (Johnstone 1985; Johnstone and Cole 1988; Johnstone and van Thienen 2004; Makinen and Isomaki 2004).

Increased leaf area has been determined to be the primary mechanism governing growth response following fertilization (Fagerstrom and Lohm 1977; Brix 1983). At Spokin Lake, the positive effects of fertilization on crown size and LAI_e resulted in increased tree radial increment at all thinning levels. Tree BA and volume increments of fertilized trees in the 1- to 5-year measurement period were, in relative terms, in the mid to upper range of growth responses previously reported for lodgepole pine in British Columbia following a single fertilizer application (Brockley 1996, 2000, 2004). The generally positive, but modest, effects of fertilization on height increment are consistent with previously reported findings that increased N supply stimulates crown and stem radial growth more than height growth in thinned, nonrepressed lodgepole pine (Brockley 1996; Brockley and Simpson 2004). Across the range of densities tested, the proportional difference between radial growth and height growth was larger in fertilized trees than in unfertilized trees. This exacerbated the more conical shape (i.e., higher DBH/height ratio) of trees growing at lower densities.

The most interesting result from this study may be the apparent differential response of lodgepole pine to fertilization across the range of residual densities tested. Although D × F interactions were not statistically significant, individual-tree height and volume responses to added nutrients were less, in both relative and absolute terms, at 600 trees/ha than at 1100 or 1600 trees/ha. At the stand level, absolute fertilization volume gains (m³/ha) were directly proportional to residual stand density (i.e., the smallest absolute stand volume gains following fertilization were obtained at the lowest stand density). As with individual-tree responses, however, the relative stand volume gains attributable to fertilization were also substantially lower at 600 trees/ha than at 1100 or 1600 trees/ha. Significant Y × D × F interactions for stand BA and volume development indicate that the differential effects of residual stand density on fertilization response are increasing over time. These growth trends differ from several previously reported density × fertilizer studies with other species, where the relative effectiveness of fertilization was the same, or greater, at lower post-thinning densities (Miller et al. 1986; Gardner 1990; Morrison and Foster 1990). The possibility that trees at 600 trees/ha are less nutrient stressed because of lower intertree competition or because of the extra nutrients added from the larger amount of decomposing thinning material is not borne out by foliar nutrient data from this site. Other factors, either acting separately or in combination, are apparently responsible for the relative ineffectiveness of fertilization in the 600 trees/ha treatment at the Spokin Lake study site.

Several investigators have suggested branch size and longevity are increased at low stand density (Ballard and Long 1988; Johnstone and Pollack 1990; Gillespie et al. 1994; Makinen 1996, 1999). Others have reported that foliage and branch growth of *Pinus* is stimulated by fertilization (Linder and Axelsson 1982; Makinen and Uusvaara 1992; Snowdon and Benson 1992; Tamm et al. 1999; Albaugh et al. 2004). Using allometric approaches to separate treatment effects from developmental stage, several studies have reported that fertilization of *Pinus* results in proportionally more partition-

Table 7. ANOVA summary table for 10-year stand basal area increment and stand volume increment by stand component, showing variance ratios (*F*), *p* values, and error mean squares.

		Basal area				Volume			
		All trees		Largest 250 trees/ha		All trees		Largest 250 trees/ha	
Source of variation	df	*F*	*p* >*F*	*F*	*p* >*F*	*F*	*p* >*F*	*F*	*p* >*F*
D	2	60.92	<0.001	12.71	0.001	27.53	<0.001	3.11	0.082
Linear	1	115.73	<0.001	21.49	<0.001	51.48	<0.001	3.31	0.094
Quadratic	1	6.11	0.029	3.92	0.071	3.57	0.083	2.90	0.114
F	1	107.14	<0.001	154.69	<0.001	42.52	<0.001	74.20	<0.001
D × F	2	6.77	0.011	1.34	0.299	2.98	0.089	1.89	0.193
Error mean square	12	0.585		0.051		24.342		2.023	

Note: D, density; F, fertilizer.

Fig. 8. One- to 10-year (*a*) stand basal area increment and (*b*) stand volume increment of unfertilized and fertilized lodgepole pine by stand density for all trees and largest 250 trees per hectare. Values above bars indicate change relative to unfertilized treatment for each stand density. NF, unfertilized; F, fertilized.

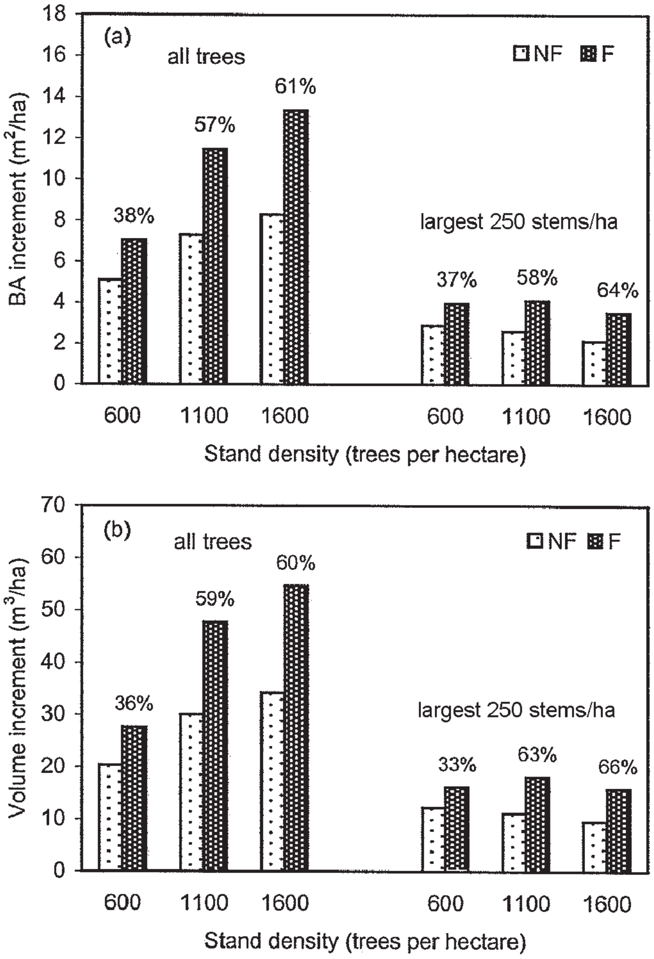


Table 8. Mean foliar nitrogen concentration (g/kg) by year and factor (density (D), fertilizer (F), D × F).

	Years after initial fertilization			
	1	5	10	11*
Density[†]				
600	11.82a	11.15a	11.32a	11.63a
1100	11.60a	11.32a	11.57a	12.17a
1600	11.57a	11.22a	10.98a	11.82a
Fertilizer[‡]				
F	12.40a	11.24a	11.08a	13.27a
NF	10.92b	11.21a	11.50b	10.48b
D × F				
600F	12.27	11.27	11.10	12.60
600NF	11.37	11.03	11.53	10.67
1100F	12.43	11.20	11.23	14.00
1100NF	10.77	11.43	11.90	10.33
1600F	12.50	11.27	10.90	13.20
1600NF	10.63	11.17	11.07	10.43

Note: For density, fertilizer, and D × F, values represent means of six, nine, and three composite samples, respectively. For each factor, values with different letters are significantly different at $p = 0.05$.

*One growing season after re-fertilization in Fall 2002.

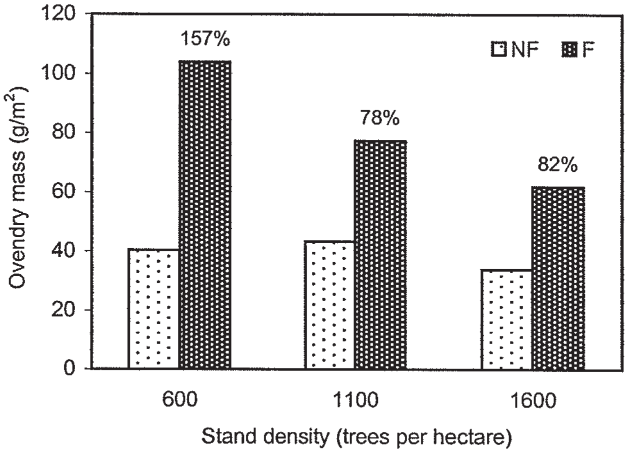
[†] 600, 600 trees/ha; 1100, 1100 trees/ha; 1600, 1600 trees/ha.

[‡] F, fertilized; NF, not fertilized.

ing of biomass to branches and (or) foliage relative to stems (Gholz et al. 1991; Gower et al. 1993; King et al. 1999). Disproportionately large allometric shifts (i.e., proportionally greater response of branches and (or) foliage than radial growth) in low density stands may partially explain the poor response of lodgepole pine to fertilization at 600 trees/ha relative to fertilizer responses at the higher stand densities at Spokin Lake. The lower absolute and relative LAI and crown width responses following fertilization at 600 trees/ha than at either 1100 or 1600 trees/ha appear to contradict this hypothesis. However, density-dependent differences between actual LAI and LAI$_e$ values have been reported, with the highest conversion factors (LAI/LAI$_e$) being associated with stands with low stocking and larger diameter trees (Barclay and Trofymow 2000). As such, the LAI$_e$ values measured in our study may proportionally underestimate the true LAI response in the 600 trees/ha density regime. Also, the large positive density effect on crown width at 600 trees/ha may have reduced the likelihood of further increases following fertilization. Future quantitative field studies are needed to evaluate allometric relationships and aboveground biomass partitioning in the fertilizer and density treatments at the Spokin Lake study site.

Both herbaceous and shrubby vegetation can be strong competitors for soil moisture and nutrients in conifer plantations (White and Newton 1989; Messier 1993; Nambiar and Sands 1993). Oliver (1984) documented a significant thinning ×

Fig. 9. Ovendry mass of understory vegetation of unfertilized and fertilized lodgepole pine at year 12 by stand density. Values above bars indicate change relative to unfertilized treatment for each stand density. NF, unfertilized; F, fertilized.



brushing interaction in a ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) stand in northern California. The DBH increment of trees growing at post-thinning densities from approximately 500 to 3000 trees/ha was about the same when brush cover was high. Conversely, DBH increment was inversely related to thinning intensity following brush removal. Induced water stress or direct competition for applied nutrients can also reduce or eliminate the positive effects of fertilization on conifer growth on brushy sites (Powers and Jackson 1978; Powers and Reynolds 1999). Periodic observation of understory development at Spokin Lake has indicated that noncrop biomass is higher in fertilized than in unfertilized plots, and that biomass differences between fertilized and unfertilized treatments are disproportionately large at the lowest stand density. These observations are consistent with reports that understory response was larger in low-density stands than in high-density stands following fertilization (VanderSchaaf et al. 2002). In 2004 quantitative biomass sampling of understory vegetation at Spokin Lake confirmed a D × F interaction ($p = 0.013$). In both absolute and relative terms, the response of noncrop vegetation to fertilization was largest at the lowest stand density (Fig. 9). Almost 2 years after the most recent fertilization (in fall 2002), noncrop biomass in the 600 trees/ha fertilized treatment was 34% and 68% greater than that in the 1100 and 1600 trees/ha fertilized treatments, respectively. These results indicate that vigorous response of understory vegetation to nutrient additions (and strong competition for water) may have reduced the effectiveness of fertilization on conifer growth at 600 trees/ha relative to higher stand densities. Although inconclusive (because of possible foliar dilution effects), the smaller difference in foliar N levels between fertilized and unfertilized trees at 600 trees/ha than at the other stand densities following the third fertilization (year 11) may also indicate vigorous competition for applied N by understory vegetation. Substantial moisture deficits are normal during the middle and latter parts of the growing season in the SBPS biogeoclimatic zone (Steen and Coupe 1997). The competitive effects of understory vegetation on the growth of fertilized, low-density lodgepole pine at Spokin Lake may be exacerbated by soil conditions (i.e., compact glacial till) that restrict effective rooting depth to the upper 30 cm of mineral soil. Also, because of lower canopy closure and a greater amount of solar radiation reaching the forest floor, there may be more evaporation of water from the soil surface and greater evapotranspiration from understory vegetation at low residual stand densities. Other possible contributing factors are high hydraulic resistance and maintenance respiration associated with larger crowns and allometric shifts in low-density, fertilized trees. Results from recently completed exploratory soil moisture monitoring and tree moisture stress measurements at Spokin Lake are inconclusive (D. Simpson, unpublished data). More rigorous testing is needed to fully test this hypothesis.

Results from this study indicate that the combined positive effects of thinning and fertilization on the radial increment of young lodgepole pine will accelerate stand development, thereby shortening technical rotation length. In the interior of British Columbia, fertilization and thinning in immature stands may be potentially valuable tools for mitigating “pinch points” in the midterm timber supply caused by age-class imbalances and catastrophic losses from the mountain pine beetle. The results also indicate that significant growth gains following fertilization of thinned lodgepole pine will partially compensate for the expected stand volume losses due to thinning. However, preliminary results indicate that fertilization may be less effective at low stand densities, where the negative effects of thinning on harvest volume are greatest. Also, fertilization of low-density stands may exacerbate undesirable tree characteristics (e.g., branchiness, stem taper) that may reduce lumber quality and recovery.

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