Effects of nitrogen and boron fertilization on foliar boron nutrition and growth in two different lodgepole pine ecosystems

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Abstract: The 9-year effects of nitrogen (N) and boron (B) fertilization on the growth and foliar B nutrition of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) were evaluated in two different ecosystems in the interior of British Columbia. When added alone, B had no effect on basal area or height increment. However, combined applications of N and B were superior to N alone in stimulating height development at both study sites. At one site, fertilization with N, alone and in combination with sulphur (S), resulted in a significant amount of top dieback symptomatic of severe B deficiency. No visible deficiency symptoms were observed when B was combined with N or N + S. Boron fertilization significantly increased foliar B concentrations at both study sites, and higher foliar B levels were maintained throughout the 9-year study period. Results suggest that significant visible symptoms of B deficiency in lodgepole pine are unlikely to occur at foliar levels >6 mg/kg, although subacute B deficiency may suppress height development in the absence of deficiency symptoms. When combined with nitrogenous fertilizers, B applications of 1.5–3.0 kg/ha are likely sufficient to achieve, and maintain, favourable B status and healthy growth of trees over a prolonged period.

Résumé : Les effets de la fertilisation à l’azote (N) et au bore (B) sur la croissance et le B foliaire du pin lodgepole (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) ont été évalués dans deux écosystèmes différents de l’intérieur de la Colombie-Britannique durant une période de 9 ans. Ajouté seul, le B n’a eu aucun effet sur la croissance en surface terrière ou en hauteur. Toutefois, les applications combinées de N et de B ont eu des effets supérieurs à l’application seule de N en stimulant la croissance en hauteur dans les deux sites étudiés. À l’un des sites, la fertilisation avec N, seul ou en combinaison avec le soufre (S), s’est traduite par un dépérissement de la flèche terminale symptomatique d’une carence en B. Aucun symptôme visible n’a été observé lorsque B était combiné avec N ou N + S. La fertilisation au bore a significativement augmenté la concentration foliaire en B aux deux sites, et des niveaux plus élevés de B foliaire ont été maintenus durant les 9 années de l’étude. Les résultats indiquent qu’il y a peu de chance d’apercevoir des symptômes visibles de déficience en B chez le pin lodgepole lorsque la concentration de B est supérieure à 6 mg/kg, bien qu’une déficience subaiguë en B puisse diminuer le développement en hauteur en absence de symptômes de déficience. Lorsque combinées avec les fertilisants azotés, des applications de B de 1,5–3,0 kg/ha sont probablement suffisantes pour atteindre et maintenir un statut en B favorable ainsi qu’une croissance vigoureuse des arbres sur une période prolongée.

[Traduit par la Rédaction]

Introduction

Low to marginal foliar boron (B) levels are a characteristic found in many immature lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forests in the interior of British Columbia. In a summary of foliar B concentrations in 52 lodgepole pine fertilization research trials, Brockley (2001*a*) reported that mean foliar B levels in unfertilized trees were <12 mg/kg in one-third of the stands, indicating the possibility of B deficiency, or deficiency induced by nitrogen (N) fertilization (Stone 1990). Low foliar B levels in the north-central interior of British Columbia are often found in stands established on glacial morainal soils derived from igneous rocks, with thin surface organic layers. Underlying basal tills are typically clay rich, often restricting rooting depth to 20–30 cm. As such, many sites may be susceptible to soil moisture deficit during the growing season. Boron deficiencies are well documented under these soil conditions (Wikner 1983; Stone 1990). Although less common, low foliar B levels have also been documented in immature lodgepole pine forests growing on coarse-textured glacial outwash soils in wetter climatic regions in southeastern British Columbia (Brockley 1996). In high rainfall environments, sandy soils may be particularly susceptible to B deficiencies, since borate is very easily lost in leaching (Mengel and Kirkby 1987; Marschner 1995).

In the interior of British Columbia, lodgepole pine with low to marginal B status generally exhibits normal growth characteristics under natural conditions. However, acute B deficiency symptoms have been documented following N and N + sulphur (S) fertilization of these stands (Brockley 1989, 1996). Morphologically, the most prominent symptoms are top dieback and multi-leadered, bushy crowns.

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Similar symptoms have been reported in fertilized and unfertilized Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) in Scandinavia (Aronsson 1983; Braekke 1983*a*; Moller 1983) and radiata pine (*Pinus radiata* D. Don) in New Zealand (Will 1985). For these other species, B deficiency symptoms have been alleviated by applying B either alone or in combination with N (Mead and Gadgil 1978; Aronsson 1983; Braekke 1983*b*; Hopmans and Clerehan 1991).

This paper reports 9-year results of two studies designed to investigate the effects of added B on the foliar nutrition and growth of N and N + S fertilized trees in two different lodgepole pine ecosystems in the interior of British Columbia. One of the sites is in the north-central interior, near Burns Lake; the other site is in the southeast interior, near Golden. Both study sites are adjacent to lodgepole pine stands in which B deficiencies have previously been documented, based on low foliar B concentrations and significant top dieback following N fertilization (Brockley 1989, 1996). Preliminary results from the Burns Lake study were previously reported by Brockley (1990).

Materials and methods

Location and site description

The Lord Lake study was established in a thinned, 27-year-old stand of fire-origin lodgepole pine located about 30 km northeast of Burns Lake, B.C. (54°14′N, 125°25′W). The study area lies within the Babine variant of the moist cold subzone of the Sub-Boreal Spruce biogeoclimatic zone (SBSmc2; Banner et al. 1993) at an elevation of 1200 m. This portion of the SBS zone has a continental climate characterized by seasonal extremes of temperature, snowy winters, and relatively low annual precipitation (440–650 mm). Mean annual temperature ranges from –0.7 to 3.6°C. Growing degree-days (>5°C) and frost-free days range from 844 to 1145 and 45 to 125, respectively. Soil and vegetation reconnaissance indicates the site belongs to the submesic phase (01c) of the Sxw-Huckleberry site series (Banner et al. 1993). It occurs on a gently undulating morainal blanket with weakly developed drainage patterns. The overlying ablation till has a large volume of cobbles and stones of acidic, igneous intrusive lithology. The underlying basal till is more clay rich with fewer coarse fragments. Rooting depth is restricted to 25–30 cm. Soil development is transitional between Brunisolic Gray Luvisols and Podzolic Gray Luvisols (Soil Classification Working Group 1998). The forest floor is very thin with little incorporation of organic matter in the underlying mineral soil. Soils are cold, and moisture deficits commonly occur during the growing season (Banner et al. 1993). Using growth intercept methodology (Nigh 1997), the estimated site index of lodgepole pine occupying the site is 17 m at 50 years. When the study began in 1984, stem breast height diameters and total heights of dominant and codominant trees averaged 11 cm and 8.2 m, respectively. The stand had been thinned from approximately 8000 to 1600 stems/ha in 1979.

The Blackwater Creek study was established in a thinned, 18-year-old stand of fire-origin lodgepole pine located about 30 km northwest of Golden, B.C. (51°33′N, 117°17′W). The study area lies within the Golden variant of the moist warm subzone of the Interior Cedar–Hemlock biogeoclimatic zone (ICHmw1; Braumandl and Curran 1992) at an elevation of 920 m. The ICH biogeoclimatic zone is the most productive forest zone in the interior of British Columbia (Meidinger and Pojar 1991). It is considerably wetter and warmer than the SBS zone, with about twice as many growing degree-days (>5°C) and frost-free days. Soil and vegetation reconnaissance indicates the site belongs to the subxeric to submesic HwCw-Falsebox-Pipecleaner moss (03) site series (Braumandl and Curran 1992). It occurs on a flat to gently sloping glaciofluvial terrace, with metamorphic parent materials predominantly of schistose origin. Soils are rapidly drained with textures ranging from sandy loam near the surface to loamy sands and sands at depth. The volume of gravels and cobbles increases with depth. Soil development is consistent with an Orthic Humo-Ferric Podzol (Soil Classification Working Group 1998). The forest floor is very thin with little incorporation of organic matter in the underlying mineral soil. Using growth intercept methodology (Nigh 1997), the estimated site index of lodgepole pine occupying the site is 23 m at 50 years. When the study began in 1990, stem breast height diameters and total heights of lodgepole pine trees averaged 10.7 cm and 8.5 m, respectively. The stand had been thinned from approximately 8500 to 1800 stems/ha in 1978.

Study establishment

The Lord Lake study was designed as a 3 × 2 factorial experiment: three levels of B (0, 1.5, and 3.0 $kg \cdot ha^{-1}$ as Solubor®) and two levels of N (0 and 200 $kg \cdot ha^{-1}$ as urea). An additional granulated "complete mix"[1] fertilizer treatment (combined with 200 $kg\ N \cdot ha^{-1}$) was included to assist in identifying other nutrients that may be limiting growth on the study site. Parallel grid lines were systematically laid out at 20-m intervals throughout the stand, with sampling points marked every 20 m along the lines. At each sampling point, an attempt was made to select a nearby healthy, dominant lodgepole pine "plot" tree. Sampling points that were unsuitable because of stand or site irregularities were discarded. A deliberate attempt was made to select trees that were similar in both diameter at breast height (DBH) and total height. Adjacent "single-tree" plots were separated by a minimum distance of 15 m. Each of the seven treatments was randomly assigned to 15 of the single-tree plots. Similar techniques have been used with considerable success to rapidly identify nutrient deficiencies and to evaluate the fertilizer response potential of various species in the interior of British Columbia (Brockley and Sheran 1994; Brockley 1995; Swift and Brockley 1994). Fertilizer was applied to a 5 m radius area (0.0079 ha) surrounding each selected plot tree in the fall of 1984. Premeasured amounts of urea (46:0:0, N–P–K) and the complete granulated fertilizer were broadcast applied by hand, whereas B (as Solubor®; 20.5% B) was dissolved in water and evenly sprayed on the soil surface within

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[1] At 1100 kg/ha of fertilizer applied, the amounts of nutrients added were as follows ($kg \cdot ha^{-1}$): P, 100; K, 102; Ca, 129; Mg, 51; S, 36; Fe, 9; Zn, 3.5; Mn, 3.7; Cu, 1.5; B, 1.5; Mo, 1.0.

the 5-m plot radius with a backpack sprayer. Plots treated with the complete fertilizer received a further 1.5 kg B·ha^{-1} as Solubor®.

At Blackwater Creek, each of five treatments was applied to five 0.031-ha (10 m radius) plots in a completely randomized design. Each plot consisted of an inner 7 m radius measurement plot surrounded by a 3-m treated buffer. Each measurement plot contained approximately 20 lodgepole pine trees. The outer boundaries of adjacent treatment plots were separated by a minimum distance of 5 m. In addition to an unfertilized control, fertilizer was applied as N (300 kg·ha^{-1}) and N + S (300 kg N·ha^{-1} + 75 kg S·ha^{-1}) alone, and in combination with B (3 kg·ha^{-1}). In the N + S and N + S + B treatments, N was added as a mixture of urea and ammonium sulphate (21:0:0:24, N–P–K–S). In the N and N + B treatments, N was added as urea and ammonium chloride (26:0:0, N–P–K), the latter used to substitute for the ammoniacal N in the ammonium sulphate. In all treatments, 78% of the added N was in the form of urea; the remaining 22% in ammoniacal form. Boron was added as Solubor®. Fertilizer was applied to each 10 m radius treatment plot in the fall of 1990. Before fertilization, each plot was divided into four pie-shaped segments to facilitate uniform application. Premeasured amounts of urea, ammonium sulphate, and ammonium chloride were broadcast by hand within each segment. The Solubor® was dissolved in water and uniformly sprayed onto the soil surface within each segment using a backpack sprayer.

Measurement

At the time of establishment and again after 9 years, the DBH and total height of all 105 selected plot trees were measured at Lord Lake. None of the other lodgepole pine trees (usually 12 to 15) within the 5 m radius fertilized area surrounding each central plot tree were measured. The same schedule was used to record the DBH and height of all trees (approximately 20) within each measurement plot at Blackwater Creek. Diameter measurements were taken with a steel diameter tape at a permanently marked point approximately 1.30 m above the ground. A telescoping height pole was used to measure initial tree heights at Lord Lake and at Blackwater Creek. After 9 years, height measurements were taken with an electronic measuring device (Criterion 400® survey laser or Forestor Vertex® hypsometer).

At Blackwater Creek, the condition of the leading shoot of all trees was assessed after the third growing season. For each tree, the leading shoot was assigned to one of two categories: (1) absence of any visual symptoms of B deficiency (i.e., strong apical dominance of leading shoot); (2) visual evidence of dieback of the leading shoot or secondary shoots produced from lateral buds at the dead apex. Trees with multiple leading shoots caused by prior damage, breakage of the leading shoot, or an aborted terminal bud were assigned to the “no symptoms” category.

Foliar analysis

At Lord Lake, samples of current-year’s foliage were collected from two lateral branches within the upper one-third of the live crown on each crop tree immediately prior to fertilization and in the fall (late September or October) after one, two, three, six, and nine growing seasons. One composite sample per treatment, consisting of equal amounts of foliage from each of the 15 trees, was prepared for total chemical analysis from the pre-treatment and 1-, 2-, and 3-year post-treatment foliage samples. For years 6 and 9, three composite samples per treatment, each sample consisting of equal amounts of foliage from five of the trees, were prepared for total chemical analysis. The five individual samples used for each composite were randomly selected, and the composites for both years were prepared using foliage from the same trees.

At Blackwater Creek, foliage samples were collected from 10 dominant or codominant trees within each measurement plot immediately prior to fertilization and again after the first, second, third, sixth, and ninth growing seasons. For each sampling year, one composite sample per measurement plot was prepared for chemical analysis.

At both study sites, 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 analyzed colorimetrically for N using the Berthelot (phenol-hypochlorite) reaction (Weatherburn 1967) in a Technicon Autoanalyzer II. A spectrophotometer was used for the determination of phosphorus (P) using a procedure based on the reduction of the ammonium molybdiphosphate complex by ascorbic acid (Watanabe and Olson 1965). Total calcium (Ca), magnesium (Mg), and potassium (K) were measured by atomic absorption spectrophotometry (Price 1978). Total S was determined by combustion with a Leco SC-132 sulphur analyzer, using the procedures of Guthrie and Lowe (1984). After dry ashing, B was determined by the azomethine H colorimetric method described by Gaines and Mitchell (1979).

At Lord Lake, B analysis was also undertaken on individual foliage samples (15 samples per treatment) collected prior to fertilization and after the first, second, and third year. As with composite samples, B was determined colorimetrically following dry ashing.

At Blackwater Creek, B was determined on individual samples collected from all trees within each treatment plot following the third growing season. For these individual samples, B was determined with an inductively coupled plasma spectrophotometer (ICP) following wet digestion with nitric acid.

At Lord Lake, the dry mass of needles (g/100 fascicles) that were produced in the first year after fertilization by each of the 15 crop trees per treatment were measured and recorded. At Blackwater Creek, fascicle masses were measured from 5 of the 10 trees per plot from which foliage samples were collected.

Data analysis

At Lord Lake, the effects of fertilization on first-year fascicle mass and 9-year basal area (BA) and height increment were subjected to analysis of variance (ANOVA) using the general linear model procedure (SAS Institute Inc. 1989). Basal area and height increments were calculated for all trees alive after 9 years, and were adjusted by covariance analysis, using initial BA and height, respectively, as the covariates. The covariate for height was not statistically significant ($p > 0.05$); thus adjusted treatment means are presented for BA increment only. A set of orthogonal contrasts was used to test the main effects of N and B as well as the N × B interaction effects. Additional single df contrasts were selected to answer specific a priori questions (Milliken and Johnson 1984). The first-year fascicle mass response at Lord Lake was previously reported by Brockley (1990), so these data are not presented in this paper.

At Blackwater Creek, BA and height increments were calculated for trees alive after 9 years within each measurement plot. Significant amounts of top damage (i.e., top dieback) were recorded at this site following treatment. Because damage appeared to be treatment related, most damaged trees were included in BA and height increment analyses. Trees were only excluded from analysis if damage was clearly not associated with B deficiency (e.g., broken stem). Fascicle masses and BA and height increments were subjected to ANOVA. Basal area and height increments were adjusted by covariance analysis, using the same covariates as at Lord Lake. The covariate for height was not statistically significant ($p > 0.05$); thus adjusted treatment means are presented for basal area increment only. The effects of B and S and the B × S interaction were tested with orthogonal contrasts. Contingency tables were constructed to examine the relationship between third-year leader condition and fertilizer treatment using the FREQ procedure and the chi-square statistic (SAS Institute Inc. 1989). Similar procedures were used to examine the relationship between third-year leader condition and foliar B concentration.

A probability threshold of $p = 0.05$ is used throughout the paper for inferring statistical significance. To compensate for the large number of ANOVA tests and the increased probability of committing a type I error, the reader may wish to apply a more stringent rule.

Results

Basal area

Fertilization significantly increased 9-year BA increment at Lord Lake (Tables 1 and 2). Basal area growth was significantly affected by N but not by B. There was no N × B interaction. Although not statistically significant, the N + B treatments resulted in a slightly larger response than N alone (Table 1). The largest response was obtained with the complete mix fertilizer treatment, although the incremental gain between the complete treatment and the N + B treatments was not statistically significant.

Fertilization also significantly increased 9-year BA increment at Blackwater Creek, although relative responses were much lower than those at Lord Lake (Tables 3 and 4). Neither B nor S significantly affected BA growth.

Height

Fertilization had little overall effect on 9-year height increment at Lord Lake. However, height growth was significantly affected by added B, with the N + B treatments having significantly greater height increment than N alone (Tables 1 and 2). Although statistically insignificant, the latter treatment apparently had a slightly negative effect on height increment. Fertilization with B alone had no effect on height growth.

Table 1. Mean 9-year tree basal area and height increment by treatment at Lord Lake.

	9-year increment	
Treatment*	Basal area (cm^2)	Height (m)
Control	61.7 (100)	3.04 (100)
1.5B	63.9 (104)	3.19 (105)
3.0B	65.7 (106)	3.19 (105)
200N	80.6 (131)	2.67 (88)
200N + 1.5B	82.8 (134)	3.19 (105)
200N + 3.0B	86.0 (139)	3.28 (108)
Complete	88.9 (144)	3.31 (109)
LSD ($p = 0.05$)	8.94	0.381

Note: Numbers in parentheses indicate response relative to the control. *N, nitrogen; B, boron. Values preceding the nutrients indicate the amount of nutrient applied in kilograms per hectare. Complete refers to the "complete mix" fertilizer treatment. LSD, least significant difference test.

Overall, fertilization had a significantly negative effect on 9-year height increment at Blackwater Creek (Tables 3 and 4). The effects of B were highly significant, with the N and N + S treatments having significantly smaller height increments than the corresponding treatments with added B. Height growth was unaffected by added S, and there was no B × S interaction.

Leader damage

At Blackwater Creek, the variation in third-year leader damage (i.e., top dieback) between treatments was highly significant ($p < 0.001$; χ^2). Extensive leader damage was observed in the N and N + S treatments, with about twice as many N + S fertilized trees experiencing damage as the N-fertilized trees (34% damage vs. 16% damage) (Fig. 1). There was no leader damage recorded in the control and the two B-fertilized treatments.

Although lodgepole pine height increments were smaller in treatments without added B, visual symptoms of B deficiency were not documented at Lord Lake.

Fascicle mass

Fertilization significantly increased first-year fascicle mass at Blackwater Creek (Tables 3 and 4). The effects of added S were highly significant, with the N and N + B treatments having significantly smaller first-year fascicle masses than the corresponding treatments with added S (Tables 3 and 4). Conversely, B had little effect on fascicle mass when combined with either N or N + S. There was no B × S interaction.

Foliar boron

Spray application of B to the soil surface significantly increased foliar B concentrations at both Lord Lake and Blackwater Creek (Figs. 2 and 3). Moreover, B-fertilized trees maintained significantly higher B concentrations throughout the 9-year study period.

In the N and N + S treatments at Blackwater Creek, the differences in foliar B between trees with observed top dieback and those with no dieback in year 3 were highly significant ($p < 0.001$). Third-year foliar B concentration in trees with top dieback ($n = 40$) averaged 1.4 mg/kg. For trees with no top dieback ($n = 143$), foliar B concentrations averaged 4.7 mg/kg. As shown in Fig. 4, 85% of trees with top dieback had <2 mg/kg of B in foliage; in all cases, foliar B was

Table 2. ANOVA summary table showing variance ratios (*F*), *p* values, and error mean squares for 9-year basal area and height increments at Lord Lake.

	Basal area			Height		
Source of variation*	df	*F*	*p* >*F*	df	*F*	*p* >*F*
Treatment	6	12.91	<0.001	6	2.58	0.023
Factorial partitions						
N	1	55.49	<0.001	1	0.25	0.615
B	2	1.09	0.341	2	5.46	0.006
N × B	2	0.03	0.967	2	2.03	0.137
Contrasts						
Control vs. others	1	22.08	<0.001	1	0.45	0.505
Control vs. B	1	0.62	0.432	1	0.83	0.363
N vs. N + B	1	0.96	0.329	1	14.11	<0.001
N + 1.5B vs. N + 3.0B	1	0.50	0.481	1	0.02	0.876
Complete vs. N + B	1	1.30	0.256	1	0.39	0.532
Covariate	1	10.35	<0.001	—	—	—
Error mean square	97	152.17		98	0.2768	

*N, nitrogen; B, boron. Values preceding the nutrients indicate the amount of nutrient applied in kilograms per hectare. Complete refers to the "complete mix" fertilizer treatment.

Table 3. Mean first-year fascicle mass and 9-year basal area and height increment by treatment at Blackwater Creek.

Treatment*	Fascicle mass (g/100 fascicles)	Basal area (cm^2)	Height (m)
Control	4.78 (100)	83.4 (100)	5.10 (100)
300N	5.59 (117)	98.3 (118)	4.40 (86)
300N + 75S	6.78 (142)	98.2 (118)	4.09 (80)
300N + 3B	5.72 (120)	86.9 (104)	4.88 (96)
300N + 75S + 3B	7.22 (151)	95.0 (114)	5.01 (98)
LSD (p = 0.05)	0.702	12.96	0.572

Note: Numbers in parentheses indicate response relative to the control.
*N, nitrogen; B, boron; S, sulphur. Values preceding the nutrients indicate the amount of nutrient applied in kilograms per hectare. LSD, least significant difference test.

<6 mg/kg. Conversely, only 19% of trees with no top dieback had <2 mg/kg foliar B; one-quarter of the trees with no top dieback had levels >6 mg/kg.

Discussion

The 9-year fertilization response at Lord Lake compares favourably with those reported previously for N-fertilized lodgepole pine in western Canada (Brockley 2001*b*). The slightly larger BA response obtained with the complete fertilizer treatment at Lord Lake is consistent with other studies in British Columbia where S additions have improved the growth response of N-fertilized lodgepole pine (Brockley and Sheran 1994; Brockley 2000). As discussed by Brockley (1990), the S contained in the complete fertilizer was apparently sufficient to maintain an adequate foliar N–S balance at Lord Lake.

The relatively small BA response to all fertilizer treatments at Blackwater Creek is rather surprising, given that pre-fertilization foliar N (11.0 g/kg) levels indicated moderate to severe N deficiency (Brockley 2001*c*; Thomson et al. 2001). The low pre-fertilization foliar sulphate-S levels (35 mg/kg) and high foliar N/S ratio (13.3) at Blackwater Creek indicate a probable S deficiency (Brockley 2001*c*). As such, large BA responses to N or N + B would not be expected at this site (Brockley 2000). However, relatively large differential responses between N alone and N + S have been documented on many S-deficient sites in the interior of British Columbia (Brockley 2000, 2001*b*). At Blackwater Creek, the expectation of a differential response between N and N + S was supported by the highly significant effects of added S on first-year fascicle mass. Previous studies (including Lord Lake) have shown positive correlations between first-year increases in fascicle mass and subsequent stemwood responses (Brockley 1990, 2000). The inability of added S to improve the 9-year BA response at Blackwater Creek can likely be largely explained by the severe B deficiency, and associated tree damage, in the N + S treatment plots. Although not statistically significant, there was some evidence of a small differential BA response between treatments with no visible damage (i.e., N + B vs. N + S + B).

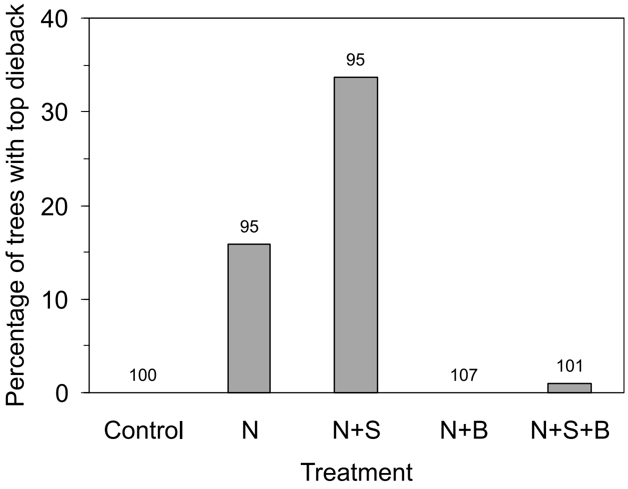
It is possible that the relatively large N application rate (i.e., 300 $kg \cdot ha^{-1}$), combined with marginal supplies of other nutrients in the coarse-textured glacial outwash soil, caused nutrient imbalances (and small growth response) at Blackwater Creek. Nitrification of applied urea and ammonium sulphate likely increased the concentration of anions (NO_3^- and SO_4^{2-}) in the soil solution. High anion levels, combined with relatively high precipitation and coarse soil texture, increase susceptibility of soils to base cation leaching losses (Brady and Weil 1998). Cation losses have been linked to symptoms of forest "decline" in European forests (Zoettl and Huettl 1986). Foliar N–K and N–Mg levels were significantly higher in fertilized foliage than in unfertilized foliage during each of the 3 years following fertilization at Blackwater Creek (data not shown). In year 1, foliar imbalances indicated slight to moderate K and Mg deficiencies (Brockley 2001*c*). Potassium deficiencies are well documented on sandy outwash soils of the northeastern U.S.A. and south-

Table 4. ANOVA summary table showing variance ratios (*F*), *p* values, and error mean squares for first-year fascicle mass and 9-year basal area and height increment at Blackwater Creek.

	Fascicle mass			Basal area			Height		
Source of variation*	df	*F*	*p* >*F*	df	*F*	*p* >*F*	df	*F*	*p* >*F*
Treatment	4	16.88	<0.001	4	2.52	0.074	4	3.90	0.017
Contrasts									
Control vs. others	1	40.41	<0.001	1	5.47	0.030	1	4.43	0.048
–B vs. +B	1	1.72	0.192	1	2.88	0.105	1	9.86	0.005
–S vs. +S	1	38.48	<0.001	1	0.87	0.361	1	0.23	0.638
B × S	1	0.53	0.469	1	0.92	0.349	1	1.49	0.237
Covariate	—	—	—	1	137.16	<0.001	—	—	—
Error mean square	100	1.18		463	435.02		464	0.8477	

*B, boron; S, sulphur.

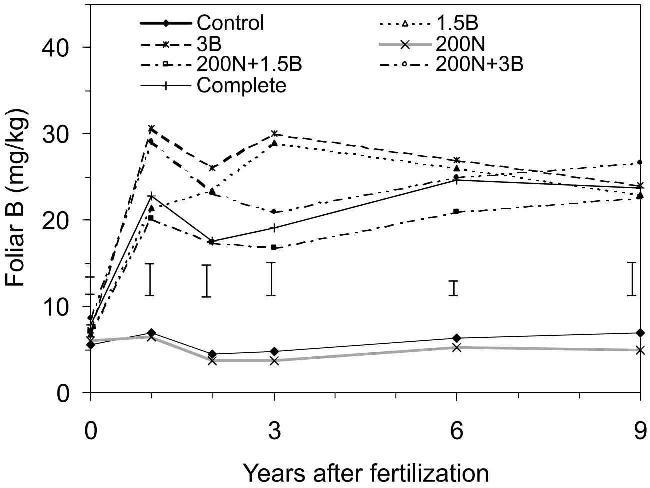
Fig. 1. Distribution of dieback of the terminal leader in year 3 by treatment at Blackwater Creek. The total number of trees in a given treatment is located above each bar.



eastern Canada (Truong dinh Phu and Gagnon 1975; Shepard and Mitchell 1990).

The inability of added B to improve the 9-year BA increment of lodgepole pine at either study site is consistent with results previously reported for radiata pine and black spruce (*Picea mariana* (Mill.) BSP) (Hopmans and Flinn 1984; Hopmans and Clerehan 1991; White and Krause 2001). In contrast, the positive effects of B additions on height development were clearly evident at both study sites. When added alone, B was ineffective in stimulating height growth at Lord Lake. This is consistent with results previously reported by Braekke (1983*b*) but contrary to those reported by others (Vail et al. 1961; Mead and Gadgil 1978; Veijalainen 1983; Hopmans and Clerehan 1991). At both study sites, however, B in combination with N (and N + S) resulted in significantly larger height increments than N (and N + S) without added B. At Blackwater Creek, the smaller height increments following N and N + S fertilization can be largely attributed to significant amounts of top dieback in fertilized trees, similar to symptoms in N-fertilized Scots pine described by Braekke (1983*a*), Moller (1983), and Aronsson (1983). At Lord Lake, however, height increments following fertilization with N alone were significantly smaller than with N + B in the absence of readily observable top dieback. These results agree with Stone (1990), who concluded that insufficient B supply may retard shoot growth even though visible symptoms do not appear.

Fig. 2. The effect of various fertilization treatments on foliar boron concentrations over 9 years at Lord Lake. For years 0, 1, 2, and 3, plotted values for each treatment represent the mean of 15 individual foliage samples. For years 6 and 9, plotted values for each treatment represent the mean of three composite samples (five trees/composite). For each year, error bars represent the least significant difference (*p* = 0.05). Values preceding the nutrients indicate the amount of nutrient applied in kilograms per hectare.



Other studies have shown that B deficiency symptoms can be readily alleviated by applying B either alone or in combination with N (Mead and Gadgil 1978; Aronsson 1983; Braekke 1983*b*; Hopmans and Clerehan 1991). Because typical symptoms were not visible prior to treatment in control or B-fertilized plots, the effectiveness of added B in alleviating symptoms could not be tested in the present studies.

At Lord Lake, mean foliar B concentrations in control and N-fertilized trees remained between 4 and 7 mg/kg throughout the 9-year study period. Visual symptoms of B deficiency have been reported within this range for many species (Stone and Will 1965; Lambert and Turner 1977; Braekke 1983*b*; Hopmans and Flinn 1984; Carter et al. 1984). However, typical B deficiency symptoms were not evident at this

Fig. 3. The effect of various fertilizer treatments on foliar boron concentration over 9 years at Blackwater Creek. For each treatment and year, plotted values represent the mean of five composite samples (10 trees/composite). For each year, error bars represent the least significant difference (p = 0.05).

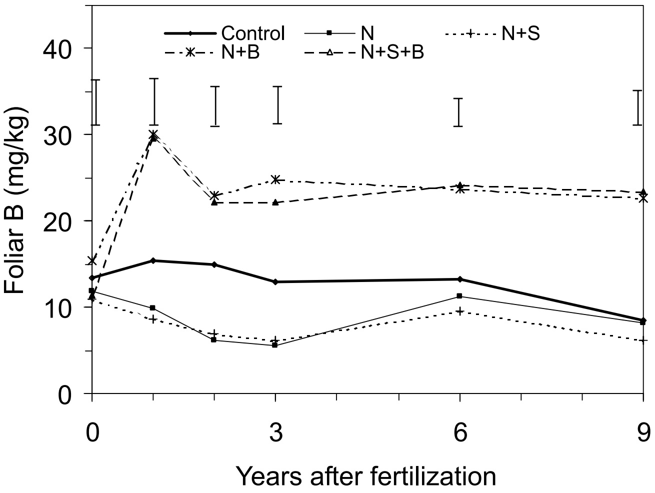
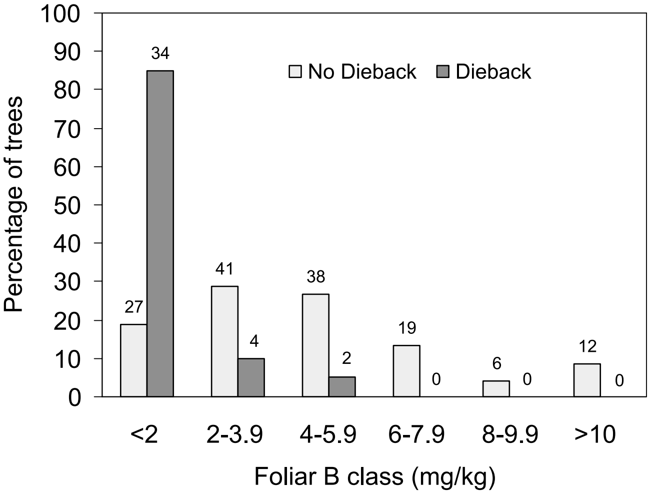


Fig. 4. Distribution of tip or shoot dieback of the terminal leader in year 3 by foliar boron class in N and N + S fertilized trees at Blackwater Creek. The total number of damaged and undamaged trees in each boron class is located above the bars.



site. This observation is consistent with that of Aronsson (1983), who reported that symptoms in Scots pine and Norway spruce are unusual above foliar B levels of 4–5 mg/kg.

Interestingly, the significant top damage that was readily observed and documented at Blackwater Creek occurred at higher mean foliar B levels than were measured in the undamaged trees at Lord Lake. Mean foliar B concentrations in N and N + S fertilized trees ranged from 5.5 to 11.5 mg/kg throughout the 9-year study period. The same laboratory, using the same analytical methodology, was used to determine B levels in the composite foliage samples from each site. However, field observations indicated that virtually all of the top damage in the N and N + S fertilized treatments occurred during the second and third years, when foliar B levels were at the very low end of this range. Also, the two study sites are geographically distinct, and foliar B levels, and likely damage susceptibility, are strongly controlled by genotype (Stone 1990).

At Blackwater Creek, the foliar B levels in the third-year individual-tree samples were considerably lower than the mean foliar B levels reported for the third-year composite samples. Differences in analytical methodology likely account for these differences. Following dry ashing of the composite samples, B was determined by the azomethine H colorimetric method (Gaines and Mitchell 1979). For individual samples, B was determined with an inductively coupled plasma spectrophotometer (ICP) following wet digestion with nitric acid. Two separate comparisons of these two techniques, each using 25 individual foliage samples, were recently undertaken by the author (data not shown). In both cases, the relationship between the two methods was very strong (R^2 > 0.97). However, within the foliar B range reported in this study, foliar B levels determined with ICP were 2–3 mg/kg lower than those of the azomethine colorimetric method.

Uptake of B is primarily through mass flow of water to roots and is, therefore, strongly influenced by soil moisture (Mengel and Kirkby 1987). As such, year-to-year differences in available soil water would likely cause fluctuations in foliar B concentration. For example, Hopmans and Clerehan (1991) reported that large fluctuations in foliar B levels were strongly correlated with rainfall during the preceding spring and summer. Considerable year-to-year variation in foliar B of unfertilized trees has also been reported in other studies (Knight et al. 1983; Brockley 1989). At Blackwater Creek, foliar B fluctuations between 8.5 and 15.5 mg/kg in control trees possibly reflect differences in soil water availability during the 9-year study period. As already noted, however, foliar B concentrations in unfertilized trees at Lord Lake remained within a very narrow range (4–7 mg/kg) throughout the study. Although not specifically measured, year-to-year differences in soil water availability at Lord Lake likely occurred over the 9-year study period. Therefore, the small fluctuation in foliar B levels may indicate an inherently low soil B supply at this site, even in periods of favourable soil moisture supply. At Lord Lake, B uptake may also have been partially controlled by soil temperature. Root activity and the decomposition of surface organic material (a major source of available B) are depressed in cold soils (Brady and Weil 1998).

At both study sites, the lower B levels measured in N and N + S fertilized foliage relative to controls are consistent with previously reported studies (Aronsson 1983; Moller 1983; Wikner 1983; White and Krause 2001). Lower B levels can probably be largely attributed to dilution caused by increased leaf area, tree growth, and metabolic demands. Although Wikner (1983) described possible antagonistic effects of N fertilization on B uptake, it is difficult to understand how antagonism could account for the prolonged reduction in foliar B in the N and N + S treatments at Blackwater Creek.

Applied B was readily and rapidly taken up by lodgepole pine at both sites. Favourable uptake of applied B has commonly been reported, regardless of the tree species or source of fertilizer B (Stone 1990). Of particular interest, however, is the longevity, and consistency, of foliar B response at both study sites. Similar results were reported by Hopmans and Clerehan (1991), who found that foliar B levels in radiata pine remained higher than control values 6 years after fertilization. In Scots pine, two applications of B at 5 kg/ha rapidly increased foliar B to 100 mg/kg followed by a rapid decline and stabilization at about 20 mg/kg after 3 years (Aronsson 1983). Foliar B remained considerably higher than pre-fertilization levels (4 mg/kg) for another 7 years. However, these results are in contrast to other studies in which higher foliar B levels have not been sustained for lengthy periods. For example, higher foliar B levels were maintained for only 5 years following B fertilization of radiata pine in New Zealand (Knight et al. 1983). Similarly, Will (1985) reported that a single application of B increased foliar concentrations in radiata pine for only 4 years.

Hopmans and Clerehan (1991) attributed the longevity of foliar B response in radiata pine to a combination of factors, including (*i*) enhanced availability of soil B, (*ii*) improved root growth of B-fertilized trees, (*iii*) efficient recycling of B through litter decomposition, and (*iv*) redistribution of B from old to new tissues in tree crowns. It is not possible to evaluate the relative importance of these factors in sustaining foliar B responses of lodgepole pine in the present studies. However, the long-term increases in soil B availability reported by Knight et al. (1983) following application of 22 kg B/ha are presumably less likely at Lord Lake and Blackwater Creek, given the low B application rates (1.5–3 kg/ha). Because borate is easily lost in leaching (Mengel and Kirkby 1987), long-term increases in soil B availability would be especially unlikely in the coarse-textured, glacial outwash soil at Blackwater Creek. Wikner (1983) reported a good correlation between soluble B in the organic layer and foliar B concentration, indicating the importance of the release of B from needle litter. However, the thinned lodgepole pine at Lord Lake and Blackwater Creek are only beginning to close the canopy. As such, it is seems unlikely that litterfall has progressed to the point where litter decomposition is a major factor in prolonging foliar B response. Also, as noted previously, low soil temperature may retard litter decomposition at Lord Lake. Of particular interest is the possible role of B retranslocation from old to new tissues in maintaining higher foliar B levels in current-year's foliage. Stone (1990) indicated that B is immobile in foliage, with little movement from old to new tissue. However, evidence provided by Hopmans and Clerehan (1991) suggests that B is retranslocated in the foliage of radiata pine, at least under conditions of high B availability. Therefore, efficient retranslocation of foliar B may offer the most likely explanation for the longevity of foliar B response in the present studies.

Foliar analysis can be an effective tool for identifying stands that are either B deficient or at risk from N-induced B deficiencies following fertilizer operations. However, foliar analysis has certain limitations when used to diagnose B deficiency (Stone 1990). Near the minimum range, concentrations of trees without symptoms may be less than in visibly deficient trees. As noted earlier, there may be a strong genetic component to foliar B concentration and the level at which visible damage occurs. Foliar B levels, and the occurrence of deficiency symptoms, may also fluctuate from year to year in response to soil moisture and soil supplies of available B. Finally, the diagnosis of B deficiency may be affected by differences in analytical methodology. Despite these weaknesses, the results from the Lord Lake and Blackwater Creek studies indicate that significant visible symptoms of B deficiency are unlikely to occur in lodgepole pine at foliar levels >6 mg/kg. However, results also strongly indicate that subacute B deficiency may suppress height development in the absence of deficiency symptoms. The results also indicate that leader dieback can occur following N fertilization in lodgepole pine stands where foliar B concentrations in unfertilized trees are at, or slightly above, 12 mg/kg. To avoid height suppression, and to provide a "buffer" against acute or subacute problems that may rapidly develop during periods of restricted B uptake, 12 mg/kg may be the lowest acceptable limit for foliar B when evaluating candidate stands for fertilizer operations. Where foliar B levels are below this threshold, stands can either be eliminated as candidates for fertilization, or a small amount of B can easily be added to the fertilizer prescription. When combined with nitrogenous fertilizers, B applications of 1.5–3.0 kg/ha are likely sufficient to achieve, and maintain, favourable B status and healthy growth of trees over a prolonged period, without risk of significant dieback.

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