NEEDLE LOSS IN BLACK SPRUCE: NUTRIENT CONCENTRATION DURING SHOOT EXTENSION

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ABSTRACT

Needle loss in black spruce (*Picea mariana* (Mill.) B.P.S.) plantations growing on very well-drained acid podsols was pursued as a nutrient problem. Sampling during the period of bud burst and shoot extension, followed by foliar nutrient analysis, highlighted boron deficiency as a possible cause. Black spruce rapidly took up fertiliser boron. A speculative explanation for 1-year-old foliage mortality in the spring following drought in the previous summer involved the role of boron in regulating carbohydrate metabolism and winter dormancy.

Keywords: foliage loss; aluminium toxicity; boron deficiency; drought; *Picea mariana*.

INTRODUCTION

Large areas of mixed species uplands, owned by J.D.Irving Ltd, in northern New Brunswick have been harvested, crushed to facilitate movement of workers, and planted in conifer during the past 30 years. Volunteer hardwood competitors in these plantations were controlled by herbicide applications. Severe needle loss was first observed in 1985 in black spruce planted in the late 1960s and early 1970s and losses continued annually until 1988. More than 1000 ha of plantations were involved (Pelletier 1987). The incidence of this condition was predominantly on one soil type (Glassville) and was associated with plantations which had recently attained canopy closure. As much as 80% of 1-year-old foliage turned pink and was shed during the early summer as buds were swelling and new shoots were expanding. After several years of foliage loss, which was more serious in the lower crown than in the upper crown (Nitschke 1988), the plantation canopies had an unusually open appearance and shoot lengths were observed to be decreasing with time. Loss of apical dominance did not appear to be associated with this needle loss pathology. The seed for these plantations did not originate on Glassville soils and, although some of the seed was of New Brunswick origin, much of it came from northern Ontario some 1200 km distant.

The needle loss symptoms consisted of a rapid colour change on 1-year-old needles from green to pink as current foliage buds started to swell. The discoloration was complete by mid-June when 1-year-old needles started to fall. These symptoms were thought initially to be due to needle-cast and needle-rust fungi; however, microscopic inspection of discoloured needles ruled out fungal agents. The possibility of a viral disease has not been completely

ruled out, but the lack of spread of the needle loss symptoms to soil types other than Glassville may argue against a viral agent.

Possible Predisposing Factors

Rainfall was below normal from mid summer onwards in both 1984 and 1985 and the first half of the 1986 growing season was also dry. Glassville soils are coarse-textured, well-drained glacial tills that have low available calcium and high available aluminium (White 1992).

Nutritional problems may arise when trees that have evolved on certain soils with specific nutrient availabilities are planted on soils where their uptake patterns and defence mechanisms against deficiencies and toxicities are inappropriate (Salonius *et al.* 1988).

The rooting patterns of black spruce are much shallower than those of the hardwoods which previously formed a substantial part of the stand structure on these acid, coarse, former mixedwood sites. Structural and growth rate abnormalities were observed for black spruce roots on Glassville soils (White 1992). Calcium:aluminium molar ratios of fine black spruce roots in unhealthy plantations were found to be less than 0.3, while ratios in healthy plantations were over 0.7 (A 1991).

Preliminary one-time foliar sampling and chemical analysis during the autumn of 1987 had not revealed any obvious foliar nutrient deficiencies. Carter *et al.* (1986) suggested that dormant season foliar sampling might not be a good indicator of nutrient supply during the growth season. In order to pursue the possibility of nutrient deficiency as a cause of needle loss on black spruce, a programme of sequential foliar sampling from healthy and unhealthy trees, during budbreak and shoot extension, was initiated; this methodology was similar to that used previously by Salonius (1977). The rationale for this period of sampling concerned the possibility of identifying nutrients in a low-supply situation when dilution is occurring because of rapid shoot extension.

METHODS

During 1988, regular samplings (five occasions) were made of healthy trees and those showing needle loss. The black spruce in the plantations sampled on Glassville soils were over 20 years old and canopies had been closed for several years. One-year-old foliage was displaying progressively increasing necrosis as buds were swelling and new shoots were extending during June and July; during this period samples were taken at about 14-day intervals, following a foliar sampling regime used previously (Salonius 1977).

Foliage from 88 healthy (H) trees was pooled into four shoot-length groups for analysis, based on shoot measurements taken at the third sampling (7 July). Foliage from 55 unhealthy (U) trees with moderate to severe foliage loss symptoms was pooled into three shoot-length groups. The same weight of foliage from each tree made up the pooled samples before the foliage was ground to pass through a 1-mm-mesh screen. This grouping produced pooled foliage samples from about 20 trees from each shoot-length group at each sampling date for chemical analysis. Concentrations of nutrients in foliage on both 1-year-old (YO) and current (C) expanding shoots were plotted over mean shoot length for pooled groups of trees. A spline function (SAS Institute Inc. 1985) was used to smooth curves through 20 (H) and

15 (U) analysis points for each element to show trends in nutrient concentration pattern during shoot extension. The nutrient concentration analyses are here presented graphically as trends in time without statistical analysis.

In early May 1989, based partly on our 1988 results, plots in a black spruce plantation on Glassville soil were treated with nitrogen, copper, boron, and molybdenum. Soil applications of urea at 200 kg/ha, copper sulphate at 50 kg/ha, sodium borate at 50 kg/ha, and sodium molybdate at 2 kg/ha were applied. There were no combined applications. Foliar sampling was again carried out during shoot extension in June-July 1989. The foliage from five trees on each plot was pooled for chemical analysis for each sampling date. Only the results of foliar analysis for nitrogen, copper, and boron in extending shoots, on control and treated plots during 1989, are presented here. Shoot length was not measured in 1989 and foliar analysis results were plotted by calendar day.

Current and 1-year-old shoots were dried at 60°C and foliage was shaken off the twigs while the material was still hot. Foliage was ground in a Wiley mill to pass through a 1-mm-mesh screen after pooled samples were produced by using the same amount of foliage from each tree. Foliage was dry ashed at 450°C for 2 hours and the ash was taken up in 8N hydrochloric acid and filtered; then potassium, calcium, magnesium, manganese, and zinc were determined by atomic adsorption spectrophotometry (Varian Spectr AA 400) while phosphorus was determined colorimetrically (trAAcs 800, Method 792-86T) by the standard ammonium molybdate method (Flannery & Markus 1980). Copper, aluminium, and molybdenum were determined by flameless atomic adsorption spectroscopy using a graphite furnace (Varian GTA 96). Boron was determined by the Azomethine H method of Gaines & Mitchell (1979).

Foliage was also wet ashed in a digestion block (Tecator) at 330°C for 2.25 hours using concentrated sulphuric acid and hydrogen peroxide. This digest was used for colorimetric determination (trAAcs 800, Method 786-86T) of nitrogen using the method of Bremner & Mulvaney (1982).

RESULTS AND DISCUSSION

Concentrations of foliar nitrogen, phosphorus, and potassium during shoot extension in 1988 are shown in Fig. 1. Smoothed trends in the concentrations of the three elements in both expanding current shoots and 1-year-old foliage showed nutrient levels in unhealthy trees to be somewhat higher than levels in healthy trees. Dilution of nutrient concentrations by rapid biomass accumulation in expanding shoots (current foliage) can be seen in Fig. 1. This dilution is similar to that seen in another sequential sampling study in black spruce during early summer (Salonius 1977). Foliar calcium and magnesium concentrations are presented in Fig. 2. Calcium levels were marginally higher for unhealthy trees and the normal accumulation of calcium in 1-year-old spruce foliage was evident. Magnesium levels in the 1-year-old foliage of unhealthy trees were somewhat lower than those in healthy trees; however, levels of magnesium were similar in expanding current foliage where magnesium deficiency (yellowing) is usually found.

Aluminium and manganese levels in the 1-year-old foliage of unhealthy trees were much higher than those in the foliage of healthy trees (Fig. 3). Glassville soils have high available aluminium and manganese levels (White 1992). The ability of roots to entrap aluminium
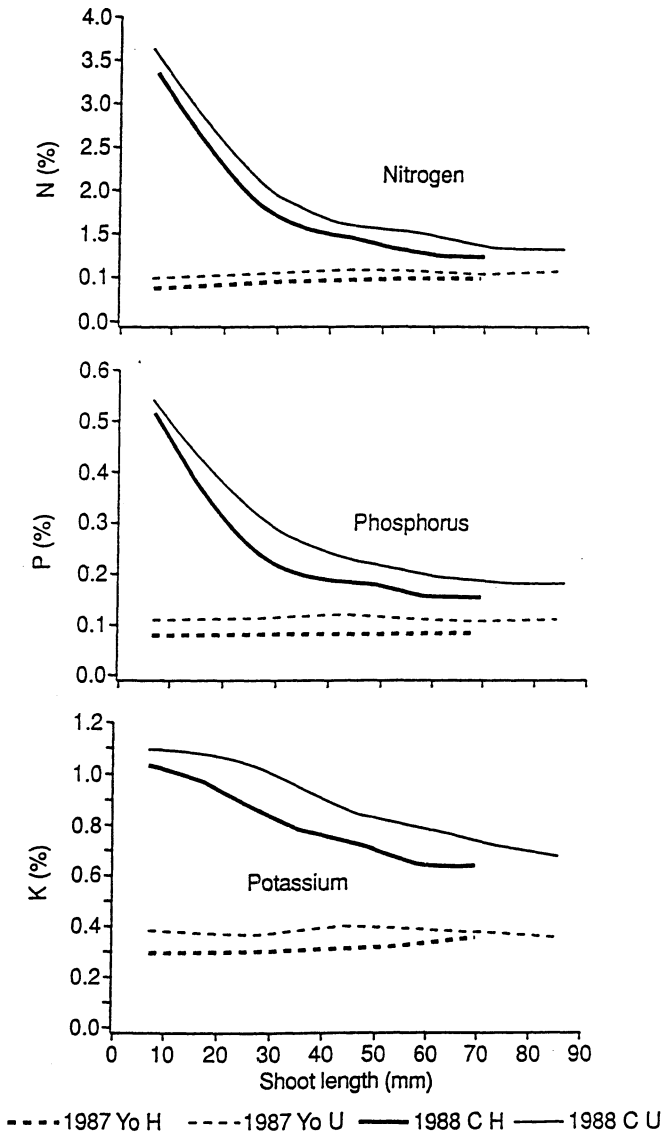
FIG. 1–Concentrations of nitrogen, phosphorus, and potassium in current (C) and 1-year-old
(YO) foliage of healthy (H) and unhealthy (U) black spruce.

(Foy *et al.* 1978) and possibly manganese may have acted to prevent much higher foliar
levels of these elements. Our experience with black spruce foliage from other areas in eastern
Canada suggests that the levels of aluminium and manganese in the unhealthy foliage
(Fig. 3) were not outside the normal range for healthy foliage; these levels would not be
expected to have produced primary toxicity (Salonius *et al.* 1988). Foy *et al.* (1978) and
others (McCormick & Steiner 1978) have suggested that there may be a genetic component
to the tolerance of high aluminium. The finding by A (1991) of low Ca:Al molar ratios in fine
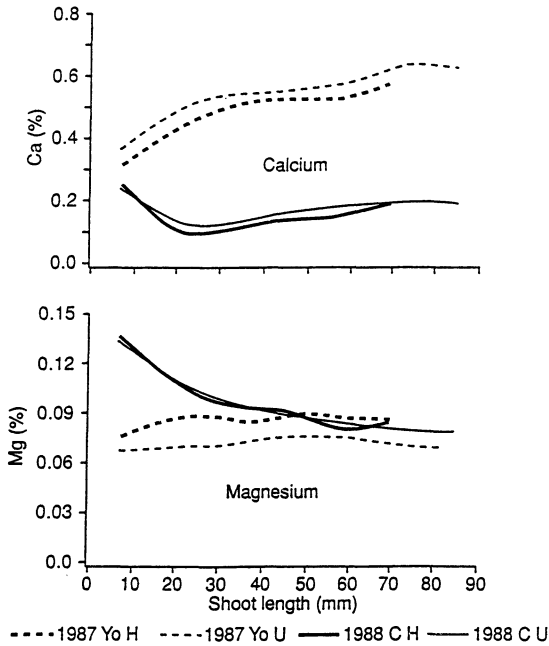
FIG. 2–Concentrations of calcium and magnesium in the current (C) and 1-year-old (YO) foliage of healthy (H) and unhealthy (U) black spruce.
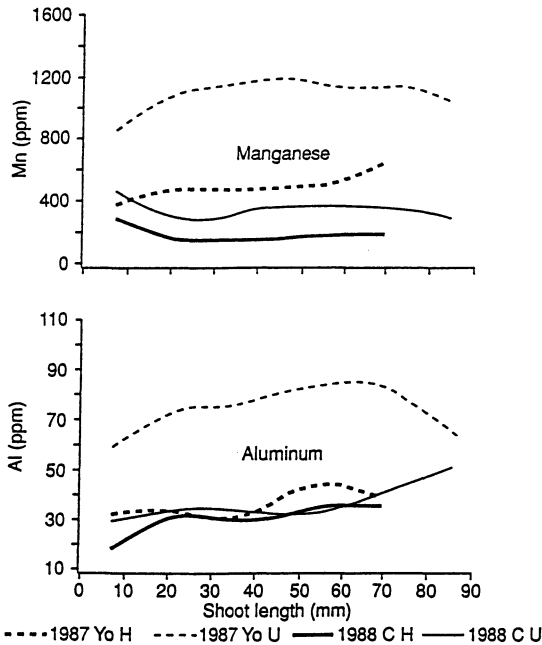

FIG. 3–Concentration (parts per million) of manganese and aluminium in the current (C) and 1-year-old (YO) foliage of healthy (H) and unhealthy (U) black spruce.

spruce roots on Glassville soils and higher ratios on soils where needle loss symptoms did not occur, as well as the fact that thickened discoloured roots are unable to expand rapidly into Glassville soils (White 1992), suggests that aluminium may play a secondary role in the needle loss pathology. The similarity of calcium concentrations in healthy and unhealthy foliage, however, may indicate that aluminium in these soils does not limit calcium availability in the manner described by Shortle & Smith (1988).

Even though copper levels were in the deficiency range, which is below 4 ppm for many tree species (Stone 1968), both current and 1-year-old foliage levels were higher in unhealthy trees than in healthy trees (Fig. 4). Zinc levels were not in the range commonly understood to produce deficiency (Carter *et al.* 1986) and unhealthy trees had higher zinc levels (Fig. 4). The boron levels in both current and 1-year-old foliage were higher in healthy trees (Fig. 4)

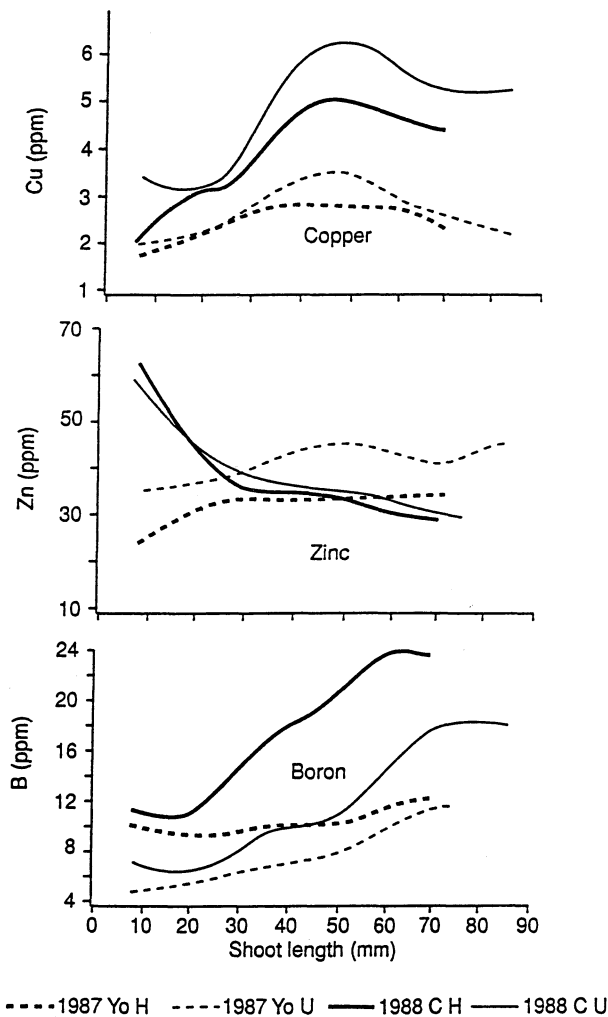- - - - 1987 Yo H   - - - - 1987 Yo U   ———— 1988 C H   ———— 1988 C U

FIG. 4—Concentration (parts per million) of copper, zinc, and boron in current (C) and 1-year-old (YO) foliage of healthy (H) and unhealthy (U) black spruce.

and the levels in older foliage of unhealthy trees were in the deficiency range for various tree species (Möller 1983; Aronsson 1983; Hopmans & Flinn 1984; Carter *et al*. 1984). Boron deficiency may explain the mortality of 1-year-old foliage in black spruce. However, this remains speculative in the absence of such typical boron deficiency symptoms as apical mortality (Braekke 1983; Silfverberg 1983; Brockley 1990).

Nitrogen was one of the elements applied to plots in 1989 because other work has indicated that nitrogen fertiliser can induce or exacerbate boron deficiency (Wikner 1983; Brockley 1990). Molybdenum was included in the fertiliser treatments because it had not been included in the analysis in 1988. Copper and boron had been observed to be at rather low levels in 1988.

Nitrogen concentrations decreased in foliage on expanding black spruce shoots as a result of dilution (Fig. 5). In this study nitrogen was applied as urea, which is taken out of the available soil nitrogen pool by microbial activity in greater proportions than nitrogen from ammonium salts (Salonius 1972). This greater incorporation of the applied nitrogen into the soil microbial population may explain the absence of such differences in nitrogen uptake between nitrogen-treated and untreated trees as were observed by Salonius (1977) when nitrogen salts were applied. Copper application did not influence foliar copper concentrations. Of the fertiliser nutrients applied to black spruce plots on Glassville soil, only boron (applied at about 5 kg/ha) produced definitive increases in foliar boron concentrations (Fig. 5). The marked uptake of boron may have produced some increase in needle size as was shown by White (1992) with similar applications; however, we did not measure needle size. The presence of considerable amounts of ammonium ion from the nitrogen fertiliser does not appear to have interfered with the boron levels of current foliage during 1989; Wikner (1983) has suggested that coprecipitation of boron by aluminium is exacerbated by an abundance of ammonium ions in soil.

The 1987 and 1988 growing seasons had more normal rainfall and there was no needle drop during 1989. The base foliar levels of boron in early 1989, before the uptake from added borate (Fig. 5), were considerably higher than they had been in previous low rainfall years.

Since 1988 there has been an absence of symptoms which might have shown differences between plots with and without added borate, and so a definitive explanation of boron deficiency cannot be made. If needle drop symptoms recur in black spruce plantations on Glassville soils, they are expected to follow a series of dry summers. If trees on plots treated with boron do not lose foliage, we can assume that boron deficiency is the causative agent (Hopmans & Flinn 1984). Boron deficiency has often been associated with drought (Silfverberg 1983; Will 1990; Hopmans & Clerehan 1991), especially on coarse-textured soils (Carter *et al*. 1986) which are very well drained. The hardwoods which occupied these Glassville soils in the former mixed stands, before black spruce was planted, were deeper rooted and less susceptible to drought. The hardwoods would be expected to have cycled considerably more basic cations from deep in the soil profile on to the soil surface, which would have decreased the tendency towards high aluminium availabilities on these acid mineral soils. Much of the rooting of the introduced black spruce is confined to the surface horizon of these podsol soils where some protection against the effects of high aluminium may be provided by organic material (Bloom *et al*. 1979); however, this shallow rooting must exaggerate the effects of drought as black spruce has access to a very limited soil volume. The conversion from mixed species to black spruce on these Glassville soils has probably
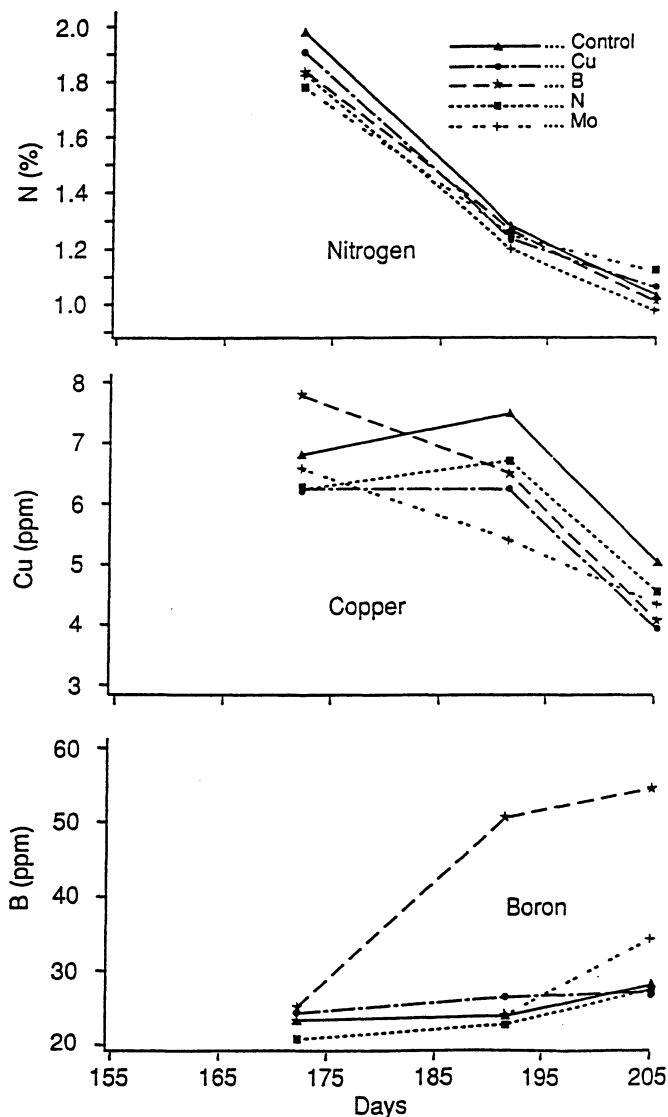
FIG. 5–Concentrations of nitrogen, copper, and boron in current foliage of black spruce on
control and treated plots during 1989.

not changed mineral soil chemistry in a major way, but it has produced stands which depend
on water supplies in the shallow surface soil layers.

High aluminium levels have been shown to interfere with water uptake (Foy *et al.* 1978)
and root elongation (McCormick & Steiner 1978; Schier 1985; Meiwes *et al.* 1986).
Inhibited root elongation, when it occurs, may be due to the interference by aluminium with
boron uptake (Wikner 1983). In this study, when large amounts of boron were available in
a year with normal precipitation, the ability of aluminium to coprecipitate boron (Wikner
1983) may have been exceeded.

Boron is instrumental in controlling the stiffening of cell walls of growing root tips so as to facilitate root elongation. Root elongation is inhibited in the relative absence of boron (Torssell 1956). Structural abnormalities of black spruce roots on Glassville soils were observed by White (1992) and similar aberrant structures have been found to be associated with boron deficiency (Raitio & Rantala 1977). Root damage and growth abnormalities would have exacerbated the effects of drought which may have induced the boron deficiency (Carter *et al.* 1986). The needle loss symptoms on these Glassville soils occurred near the time of plantation canopy closure when nutrient accumulation rate in the spruce (the ratio of uptake:return of nutrients in litterfall) would be expected to be higher than at any other time in the rotation (MacLean & Wein 1977). This may explain why occurrence of drought at this time resulted in visible deficiency symptoms.

The narrow margin between boron deficiency and toxicity influences plants to control their boron uptake, sometimes by a single gene (Brown & Jones 1971). The black spruce plantations in this study have seed sources on other soils where drainage characteristics, rooting restrictions, available aluminium levels, and nutrient availability are different from those on Glassville soil. Natural selection can be expected to have produced mechanisms in specific races of trees to allow them to deal with exigencies of their specific sites (Salonius *et al.* 1988). These mechanisms may not serve specific races of trees at all well on other sites. By fortunate circumstance, a black spruce provenance trial had been situated on Glassville soil. Both local and non-local seed sources showed needle loss symptoms; however, the severity of the needle loss became more pronounced as seed originated from further west in central Canada and the northern lake states of the U.S.A. (Nitschke 1988).

Typical symptoms of boron deficiency such as bushy crowns with multiple leaders and loss of apical dominance (Braekke 1983; Hopmans & Flinn 1984; Carter *et al.* 1984) were not seen in this study. Tissue damage in black spruce on Glassville soil was observed in the 1-year-old foliage which had the lowest boron levels. Lee & Aronoff (1967) and Pietiläinen (1983) described abnormalities in carbohydrate metabolism in foliage that were caused by a deficiency of boron which moderates the level of activity of certain enzymes. In the relative absence of boron these authors observed an excessive production of phenolic acids. They suggested that these phenolic acids complex more actively with boron than the enzymes which boron normally moderates, and thus an autocatalytic system for phenolic acids production is established. Metabolic aberrations can cause structural damage in photosynthetic tissue before visual boron deficiency symptoms become apparent (Lee & Aronoff 1966).

Braekke (1983) observed that damage to conifers which were deficient in boron was associated with severe frost and drought. Carbohydrate metabolism, which is normally inhibited by boron during winter, may increase abruptly during warm periods if boron is deficient; this improper dormancy control may result in frost damage to the actively metabolising exposed needles, which have low boron levels, when normal winter temperatures recur (Pietiläinen 1984). This scenario presents a speculatively plausible argument to explain why obvious 1-year-old needle mortality was not observed on Glassville soil until the early part of the growing season when damaged needles recommenced physiological activity and then died. Conifer needles often take considerable time to turn color and drop after mortality has occurred. The rising current foliage appears (Fig. 4) not to have been so deficient in boron and these needle primordia were protected against injury inside the bud during winter.

CONCLUSION

In view of the production of a growth response by foliar application of boron to black spruce plantations on Glassville soils in a year without foliage loss symptoms (White 1992) and the finding by others of sublethal effects of boron deficiency (Stone & Will 1965; Lee & Aronoff 1966), a recommendation for application of boron to these plantations will be appropriate if future needle loss episodes spare experimental plots with previous boron amendments. This recommendation will be especially pertinent if treatment with nitrogen fertiliser is contemplated during the plantation rotation. Sodium calcium borate (Ulexite), which is coarsely ground, has been found to provide a prophylactic, slowly soluble, boron source on deficiency-prone soils (Hunter *et al.* 1990).

ACKNOWLEDGMENTS

REFERENCES

A, H. 1991: Fine root distribution in selected black spruce plantations in northwestern New Brunswick. M.Sc. Thesis, Faculty of Forestry, University of New Brunswick.

ARONSSON, A. 1983: Growth disturbances caused by boron deficiency in some fertilized pine and spruce stands on mineral soils. *Communicationes Instituti Forestalis Fenniae 116*: 116–22.

BLOOM, P.R.; McBRIDE, M.B.; WEAVER, R.M. 1979: Aluminum organic matter in acid soils: Buffering and solution aluminum activity. *Soil Science Society of America Journal 43*: 488–93.

BRAEKKE, F.H. 1983: Micronutrient—prophylactic use and cure of forest growth disturbances. *Communicationes Instituti Forestalis Fenniae 116*: 159–69.

BREMNER, J.M.; MULVANEY, C.S. 1982: Nitrogen - total. Pp.595–624 *in* Page, A.L.; Miller, R.H.; Keeney, D.R. (Ed.) "Methods of Soil Analysis. Part 2, Agronomy 9". American Society of Agronomy, Madison, Wisconsin.

BROCKLEY, R.P. 1990: Response of thinned, immature lodgepole pine to nitrogen and boron fertilization. *Canadian Journal of Forest Research 20*: 579–85.

BROWN, J.C.; JONES, W.E. 1971: Differential transport of boron in tomato (*Lycopersicon esculentum* Mill.). *Physiologia Plantarum 25*: 279–82.

CARTER, R.E.; OTCHERE-BOATENG, J.; KLINKA, K. 1984: Dieback of a 30-year-old Douglas-fir plantation in Brittain River valley, British Columbia: Symptoms and diagnosis. *Forest Ecology and Management 7*: 249–63.

CARTER, R.E.; SCAGEL, A.M.; KLINKA, K. 1986: Nutritional aspects of distorted growth in immature forest stands of southwestern coastal British Columbia. *Canadian Journal of Forest Research 16*: 36-41.

FLANNERY, R.L.; MARKUS, D.K. 1980: Automated analysis of soil extracts for phosphorus, calcium and magnesium. *Journal of Association of Official Analytical Chemists 63*: 779–87.

FOY, C.D.; CHANEY, R.L.; WHITE, M.C. 1978: The physiology of metal toxicity in plants. *Annual Review of Plant Physiology 29*: 511–66.

GAINES, T.P.; MITCHELL, G.A. 1979: Boron determination in plant tissue by the Azomethine H method. *Communications in Soil Science and Plant Analysis 10*: 1099–108.

HOPMANS, P.; CLEREHAN, S. 1991: Growth and uptake of N, P, K, and B by *Pinus radiata* D. Don in response to application of borax. *Plant and Soil 131*: 115–27.

HOPMANS, P.; FLINN, D.W. 1984: Boron deficiency in *Pinus radiata* D. Don and the effect of applied boron on height growth and nutrient uptake. *Plant and Soil 79*: 295–8.

HUNTER, I.R.; WILL, G.M.; SKINNER, M.F. 1990: A strategy for the correction of boron deficiency in radiata pine plantations in New Zealand. *Forest Ecology and Management 37*: 77–82.

LEE, S.; ARONOFF, S. 1966: Investigations on the role of boron in plants. III. Anatomical observations. *Plant Physiology 41*: 1570–7.

———1967: Boron in plants: A biochemical role. *Science 158*: 798–9.

MacLEAN, D.A.; WEIN, R.W. 1977: Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. *Canadian Journal of Forest Research 7*: 562–78.

McCORMICK, L.H.; STEINER, K.C. 1978: Variation in aluminum tolerance among six genera of trees. *Forest Science 24*: 565–8.

MEIWES, K.J.; KHANNA, P.K.; ULRICH, B. 1986: Parameters for describing soil acidification and their relevance to the stability of forest ecosystems. *Forest Ecology and Management 15*: 161–79.

MÖLLER, G. 1983: Variation of boron concentration in pine needles from trees growing on mineral soil in Sweden and response to nitrogen fertilization. *Communicationes Instituti Forestalis Fenniae 116*: 111–5.

NITSCHKE, P. 1988: Foliage loss of black spruce in a rangewide provenance test. J.D.Irving Ltd, Report.

PELLETIER, G. 1987: 1987 black spruce foliage loss problem—Black Brook. J.D.Irving Ltd, Report.

PIETILÄINEN, P. 1983: 6-phosphogluconate dehydrogenase activity in Scots pine vegetative buds on a growth disturbance area. *Communicationes Instituti Forestalis Fenniae 116*: 141–7.

———1984: Foliar nutrient content and 6-phosphogluconate dehydrogenase activity in vegetative buds of Scots pine on a growth disturbance area. *Communicationes Instituti Forestalis Fenniae 123*: 1–18.

RAITIO, H.; RANTALA, E.M. 1977: Macroscopic and microscopic symptoms of a growth disturbance in Scots pine: Description and interpretation. *Communicationes Instituti Forestalis Fenniae 81*: 1–29.

SALONIUS, P.O. 1972: Microbial response to fertilizer treatments in organic forest soils. *Soil Science 114*: 12–19.

———1977: Nutrient concentration in black spruce foliage immediately following fertilization. *Soil Science Society of America Journal 41*: 136–9.

SALONIUS, P.O.; BEATON, K.P.; VAN RAALTE, G.D.; MAHENDRAPPA, M.K.; GLEN, W.M. 1988: Mortality in semi-mature white spruce on Prince Edward Island: age related foliar nutrient studies. *Forestry Canada, Maritimes, Fredericton, New Brunswick, Information Report M -X-172*.

SAS INSTITUTE INC. 1985: "SAS User's Guide, Version 5". SAS Institute Inc., Cary, N.C.

SCHIER, G.A. 1985: Response of red spruce and balsam fir seedlings to aluminum toxicity in nutrient solutions. *Canadian Journal of Forest Research 15*: 29–33.

SHORTLE, W.C.; SMITH, K.T. 1988: Aluminum-induced calcium deficiency syndrome in declining red spruce. *Science 240*: 1017–8.

SILFVERBERG, K. 1983: Development of growth disturbance in Scots pine. *Communicationes Instituti Forestalis Fenniae 116*: 31–5.

STONE, E.L. 1968: Microelement nutrition of forest trees: A review. Pp.132–75 *in* "Symposium on Forest Fertilization". Gainsville, Florida, April 1967 Tennessee Valley Authority, Muscle Shoals, Alabama.

STONE, E.; WILL, G.M. 1965: Boron deficiency in *Pinus radiata* and *P. pinaster*. *Forest Science 11*: 425–33.

TORSSELL, K. 1956: Chemistry of arylboric acids. VI. Effects of arylboric acids on wheat roots and the role of boron in plants. *Physiologia Plantarum 9*: 652–64.

WHITE, B. 1992: A study of root growth and mineral nutrition relating to early needle loss in black spruce plantations. M.Sc. Thesis, Faculty of Forestry, University of New Brunswick.

WIKNER, B. 1983: Distribution and mobility of boron in forest ecosystems. *Communicationes Instituti Forestalis Fenniae 116*: 131–41.

WILL, G.M. 1990: Influence of trace-element deficiencies on plantation forestry in New Zealand. *Forest Ecology and Management 37*: 1–6.