Boron, Phosphorus and Nitrogen Fertilization in Norway Spruce Stands Suffering from Growth Disturbances

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Growth disturbance symptoms typical of B deficiency have been reported on Norway spruce (*Picea abies* (L.) Karst.) trees in many parts of eastern Finland. In order to test the B deficiency hypothesis and explore the possibilities of curing the disturbed trees with B fertilization, three experiments were established in October 1999 in young Norway spruce stands growing on fertile sites in eastern Finland. All the stands contained healthy, slightly and severely damaged trees with growth disturbances typical of B deficiency (B < 5 mg kg^{-1}). 40 healthy, 40 slightly damaged, and 40 severely damaged trees were selected as sample trees in each stand. In May 2000, the trees were fertilized with 2.0 kg B ha^{-1} as borax (B), 2.0 kg B ha^{-1} and 40 kg P ha^{-1} as superphosphate (B+P) or 200 kg N ha^{-1} as urea (N). The control trees were not fertilized (0).

The needle response to B fertilization was rapid, relatively high B concentrations being achieved already after one growing season. Boron fertilization cured the growth disorders and increased height growth within four years, but had no effect on diameter growth. The trees also recovered without B fertilization, but to a lesser extent compared to the B fertilized trees. Compared to the control, boron fertilization increased the height growth in all the disorder classes, i.e. 5, 17 and 19 cm yr^{-1} for healthy, slightly and severely damaged trees, respectively. As the healthy trees also seemed to benefit from B fertilization, this indicates that B deficiency in fact retards height growth before any disorder symptoms become apparent in individual trees. Compared with B alone, the application of P together with B gave no additional benefit. Nitrogen fertilization alone appeared to have a detrimental effect on height growth in the severely disturbed trees.

1 Introduction

Boron deficiency has been reported in coniferous forests worldwide (Stone 1990, Shorrocks 1997), especially on trees growing on abandoned fields and pastures (Ferm et al. 1992, Hytönen and Ekola 1993) and on ditched peatlands treated with macronutrient fertilizers (Brække 1983a). In Finland, B deficiency and growth disorders have been observed especially in young spruce stands in parts of eastern Finland where slash-and-burn agriculture was practiced up until the beginning of the 20th century (Hynönen et al. 1999, Hynönen and Makkonen 2002, Tamminen and Saarsalmi 2004). Soils with minimum maritime influence seem to be susceptible to B deficiency (Wikner 1983, Stone 1990, Shorrocks 1997).

Boron deficiency results in growth defects caused by leader dieback when apical dominance is disturbed. Subsequent regeneration of shoots below the apex results in multiple leaders, and repeated leader dieback gives the tree a bushy appearance (Hopmans and Clerehan 1991). Chronic deficiency causes stunting, poor survival and stand irregularities (Stone 1990). Even single episodes of deficiency cause severe stem defects and loss of future saw-timber or even pulp wood. Despite a considerable loss of vitality, the trees usually retain their recovery potential for some time (Brække 1983a).

Boron deficiency is known to decrease shoot height growth in many coniferous species (Hopmans and Flinn 1984, Stone 1990, Hopmans and Clerehan 1991). Lipas (1990) demonstrated the limiting effect of B deficiency on the height growth of 50-year-old Norway spruces, even in cases where no visible symptoms occurred. Boron deficient stands have been reported to respond to B fertilization by increasing B uptake, and the growth of trees with a recovery potential has returned to normal (Brække 1983b).

A strong dependence has been found between the growth disturbance frequency in a stand and needle B concentrations, when the B concentration decreases to below 5 mg kg^{-1} (Aronsson 1983, Lipas 1990, Hytönen and Ekola 1993). Typical symptoms of B deficiency are often triggered indirectly by physiological stress factors related to climate and soil (Brække 1983b, Hop-

mans and Flinn 1984, Hopmans and Clerehan 1991). In fact, shifts from severe damage due to low B uptake in one year to normal development and growth some years later, frequently occur (Brække 1983b). This could be due to variations in B availability in the root zone over time, and the fact that susceptible plant tissue with a low B concentration can avoid irreversible damage at moderate or low stress (Brække 1983b). The limiting effect of water shortage on B uptake by plants is well known (Mengel and Kirkby 1982). In fact, the limiting effects of B deficiency on both height and volume growth have been demonstrated for radiata pine (*Pinus radiata* D. Don.) in south-eastern Australia during dry years (Hopmans and Flinn 1984, Hopmans and Clerehan 1991). Similarly, in a growth chamber experiment, drought reduced the height growth of Norway spruce seedlings at a low B supply rate (Möttönen et al. 2001).

Nitrogen is the only nutrient that has increased tree growth on upland forest soils in Finland when added alone (e.g. Kukkola and Saramäki 1983). The N/P ratio in the soil decreases with increasing site fertility (Tamminen and Mälkönen 2003). In fact, P fertilization has increased growth in Norway spruce (*Picea abies* (L.) Karst.) stands when applied together with N, and the effect of P has become proportionally more important as the fertility of the site increases (Kukkola and Saramäki 1983). Repeated N fertilization results in similar symptoms as B deficiency in both Scots pine (*Pinus sylvestris* L.) and Norway spruce in those parts of Scandinavia where B deposition is low (Aronsson 1983, Möller 1983, Mälkönen et al. 1990).

The aim of this study is to test whether B deficiency alone is the cause of the disturbances observed in Norway spruce stands. The possibilities of curing the growth disturbance with B fertilization are also investigated.
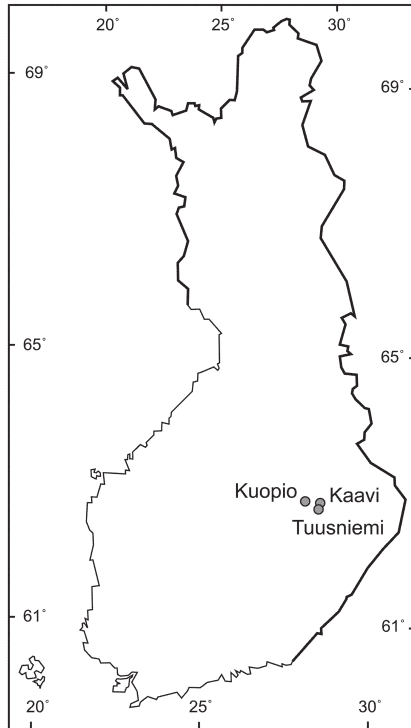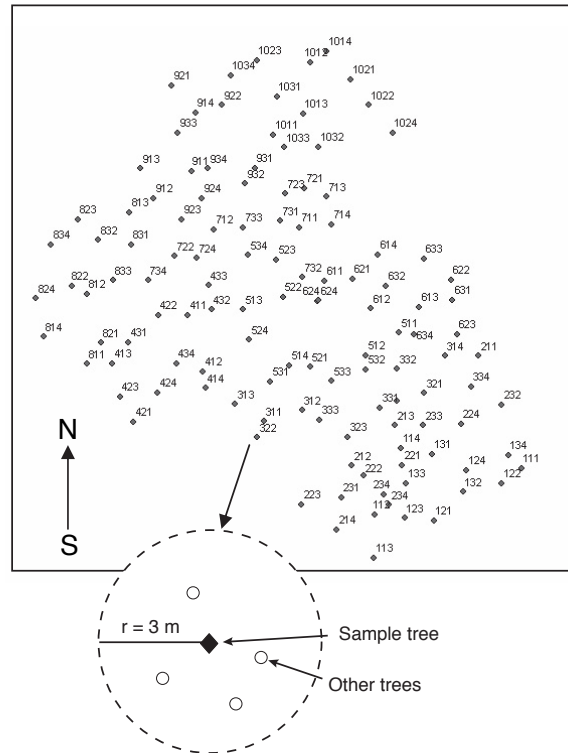
Fig. 1. Location of the experiments.

Experimental plot (single tree plot)

Fig. 2. Experimental design. The Kaavi experiment as an example. In the figure, all the 120 sample trees have been numbered. The number of the repetition or the block is indicated by the first number (1 to 10), the second number indicates the disorder class (1, 2 and 3), and the last number the treatment (1, 2, 3 and 4 for the treatments control 0, B, B+P and N, respectively). Treatments: 0 = control, B = 2 kg B ha^{-1} as borax, B + P = 2 kg B ha^{-1} as borax and 40 kg P ha^{-1} as superphosphate, N = 200 kg N ha^{-1} as urea.

2 Material and Methods

2.1 Establishment of the Experiments

The fertilizer experiments were established in three Norway spruce stands in Kuopio, Tuusniemi and Kaavi (Fig. 1) in October 1999. The stands were growing on fertile *Oxalis acetosella-Vaccinium myrtillus* (OMT) sites (Cajander 1949), and had been planted about 30 years earlier. All the experimental sites have been utilised for slash-and-burn farming at least during the 19th century, and since then also for pasturing. As a result of these activities the sites were dominated by *Alnus incana* and *Betula pendula* and *B. pubescens* before spruces were planted under the broadleaved stand. All the stands included healthy and slightly and severely damaged trees with growth disturbances typical of B deficiency (cf. Kolari 1979, Hynönen et al. 1999) (see below). The soil on two of the sites was a haplic podzol with a mor layer (FAO-UNESCO 1988), and the

Tuusniemi site a cambic podzol with a very thin mull or moder layer.

In each stand, sample trees of different disorder status (1, 2, 3) were picked at random. The trees were located at least 7 m apart from each other and the relatively adjacent repetitions or blocks (10/experiment) contained 12 spruces, four of each disorder class, i.e. 4 × 3 (Fig. 2). Trees representing healthy trees (disorder class 1) had one distinct leader shoot with normal growth. Slightly damaged trees (disorder class 2) had 3–4 leader

Fig 3. Norway spruce trees suffering from growth disturbances.

Table 1. Number, mean breast height diameter and basal area of spruces and other tree species and disorder class distribution of the spruces in the individual experiments, based on the measurements of all the trees on the single tree plots (n = 120/experiment; r = 3 m) before fertilization.

Experiment	n		$\bar{D}_g$, mm[1]		BA, m² ha⁻¹		Disorder class, %			Total
	S[2]	O[2]	S	O	S	O	1	2	3	
Kuopio	394	129	172	94	21.9	1.9	31.8	34.1	34.1	100.0
Tuusniemi	508	564	153	66	19.8	4.2	25.2	35.9	38.9	100.0
Kaavi	524	1316	160	50	25.1	4.5	20.6	39.6	39.8	100.0

[1] Mean breast height diameter weighted by basal area.
[2] S – spruce, O – other tree species.

shoots with normal growth and of equal length. Severely damaged trees (disorder class 3) had bushy crowns with several leader shoots, and a number of shoots that were possibly dead (Fig. 3). Each experiment consisted of 120 experimental plots (single tree plots) with a sample tree in its centre and other trees within a radius of 3 m. After all the trees in the experimental plots had been measured, the treatments were randomized for the sample trees in each block.

In May 2000, the trees were fertilized with 2.0 kg B ha⁻¹ as borax (B), 2.0 kg B ha⁻¹ and 40 kg P ha⁻¹ as superphosphate (B+P) or 200 kg N ha⁻¹ as urea (N). The control trees were not fertilized (0). The fertilizers were applied manually around the sample trees (r = 3 m). A buffer zone of at least 1 m was left between the experimental plots.

The sample trees were measured before fertilization and again in September 2003, i.e. four growing seasons after fertilization. Recovery of the sample trees was estimated at the same time. The diameter at breast height of the sample trees was measured to an accuracy of 1 mm in two directions, and tree height to an accuracy of 0.1 m. The other trees inside a circle (r = 3 m) around the sample tree were also tallied before fertilization.

The trees in the Kuopio experiment had the largest mean breast height diameter (Table 1) and the stand had already been thinned for the first time. The other two stands were younger and approaching the commercial thinning stage. More than one third of the spruces in all the stands were severely damaged (Table 1).

2.2 Soil Samples

Soil samples were collected from 21 single tree plots in May 2000 before fertilization in all the experiments. These plots were selected subjectively in order to cover evenly each experimental stand. A composite sample of the organic layer (LFH) consisted of 10 sub-samples taken with a steel cylinder (d=58 mm), and a composite sample of the 0–10 cm mineral soil layer consisted of 10 sub-samples taken with a spade. All the sub-samples were collected within a maximum distance of 1.5 m around the sample tree. In the Tuusniemi experiment the organic layer was too thin to be sampled and only mineral soil samples were therefore collected. Soil sampling was repeated in the Kaavi experiment in October 2002, i.e. three growing seasons after fertilization. The samples were taken from 12 single tree plots: from 6 control plots and 6 plots fertilized with B.

The soil samples were air-dried at 40°C. The organic layer samples were then ground in a mill fitted with a 2 mm bottom sieve, and the mineral soil samples were sieved and the <2 mm fraction retained. All the analyses were performed on the ground or sieved samples.

The total element concentrations in the organic samples were determined by dry digestion (3 h/550°C) and, following extraction of the ash with HCl (Halonen et. al 1983), by inductively coupled plasma atomic emission spectrometry (ICP/AES, ARL 3580). The total nitrogen concentration was determined on the organic layer samples with a CHN analyser (Leco 1000) and on the mineral soil samples with a modification of the Kjeldahl method (Kubin 1978, Kubin and Siira 1980). pH was determined by adding 25 ml of distilled water to 10 ml of sample, stirring, leaving to stand for 2 hours, followed by measurement with a calibrated pH meter. Soil boron was determined by the most common method for available boron, i.e. hot water extraction (Keren 1996). Hot water extractable B was determined on the organic layer and the mineral soil samples as follows: 5 ml of the organic layer sample or 10 ml of the mineral soil sample was weighed into a Teflon-PFA vessel, and 25 ml of distilled water was added to the organic layer sample and 20 ml to the mineral soil sample in batches of 5 ml to wet the sample thoroughly. The samples were heated in a micro-wave-oven at full power (800 W) for 5 minutes, and then kept in the oven for a further 5 minutes. The samples were placed in a freezer for 15 to 30 minutes to cool down, and then filtered into 50 ml bottles, which were filled to the mark. The B concentrations were determined by ICP/AES.

2.3 Needle Samples

The needle samples were taken from current shoots in the third to fifth branch whorl from the top, on the southern side of the crown. Sampling was performed on each sample tree before fertilization in November 1999, and on every second sample tree in December 2000 and in October 2002, i.e. one and three growing seasons after fertilization. In the Kuopio experiment, in addition to current needles (C), also one (C+1) and two-year-old (C+2) needles were sampled in 1999 and 2002.

The needle samples were dried (40°C, 48 h), ground and analyzed separately for each tree. Needle unit mass (mg/needle) was determined separately for each tree. The concentrations of Ca, K, Mg, P, B, Cu, Fe, Mn, and Zn were determined by dry digestion (550°C for 3 h) and extraction with HCl (Halonen et al. 1983), and the filtered solutions analysed by ICP/AES. Total N concentration was determined with a CHN analyser.

2.4 Calculation of the Results

In the statistical tests the significance level was set to $p \leq 0.05$. t tests, analysis of variance (ANOVA), Pearson's correlations and regression analysis were used for interval scale variables. Mann-Whitney's test, Kruskall-Wallis analysis of variance and Spearman's rank correlations were

Table 2. Properties of the soil in the experiments before fertilization. B_w = hot water extractable boron concentration, $_{tot}$ = total concentration.

	Kuopio	Experiment Tuusniemi	Kaavi	Reference [1]
Organic layer	n=21		n=21	n=100
pH_w	4.6	–	4.3	4.5 (3.6–5.5)
B_{tot}, mg kg^{-1}	2.2	–	1.2	2.2 (0.5–5.3)
B_w, mg kg^{-1}	0.98	–	0.70	1.6 (0.6–4.5)
C, %	38.5	–	29.5	35.1 (7–53)
N_{tot}, g kg^{-1}	19.9	–	16.4	16.4 (4–32)
C/N	19	–	18	21 (15–30)
Mineral 0–10 cm	n=21	n=21	n=21	n=100
pH_w	4.1	4.2	4.2	4.6 (4.1–5.5)
B_w, mg kg^{-1}	0.079	0.054	0.076	0.17 (0.03–1.12)
N_{tot}, g kg^{-1}	0.22	0.27	0.22	0.27 (0.05–1.08)
Texture class	sandy loam	silt loam	loamy sand	

[1] Material from 102 sample plots of the 9th National Forest Inventory in southern Finland (Tamminen and Saarsalmi 2004).

Table 3. Hot water extractable boron concentrations (mg kg^{-1}) on the control and boron fertilized plots in the Kaavi experiment in 2002.

	Fertilization Control	B, 2 kg ha^{-1}	t value	p value
Organic layer	1.05	2.26	–6.08	0.000
Range	0.94–1.22	1.47–2.85		
Mineral soil 0–10 cm	0.10	0.34	–6.80	0.000
Range	0.07–0.15	0.24–0.47		
n	6	6		

applied for ordinal scale variables. Bonferroni's test was used for post hoc pairwise comparisons between class means.

3 Results

3.1 Soil

The soil properties of the experiments were average and representative for the *Oxalis acetosella–Vaccinium myrtillus* site type in southern Finland, except for a low C/N ratio in the organic layer, low extractable B concentrations, and low mineral soil pH (Table 2).

In the Kaavi experiment only extractable B concentrations were affected by fertilization (Table 3). The increase in B concentrations due to fertilization was distinct, but not as large as in

the case of the needles (cf. Table 5). However, the concentration ranges of the treatments did not overlap (Table 3).

3.2 Needles

The needles of the trees in all the experiments, irrespective of the disorder stage, showed severe B deficiency (<5 mg kg^{-1}), and in the Kaavi experiment also a deficiency of P (<1.4 g kg^{-1}) (cf. Jukka 1988) (Table 4). Nitrogen concentrations corresponded to the average level for the site type in southern Finland, i.e. 14 to 16 g kg^{-1} (Tamminen and Saarsalmi 2004), in all the experiments.

In all the experiments, the trees with severe disorder symptoms had significantly lower needle B concentrations than the healthy trees (Fig. 4). A significant negative correlation was found

Table 4. Average nutrient concentrations in the needles before fertilization. Lower row: standard error of mean. All three disorder classes combined. Needle mass (Mass) is expressed as g/1000 needles.

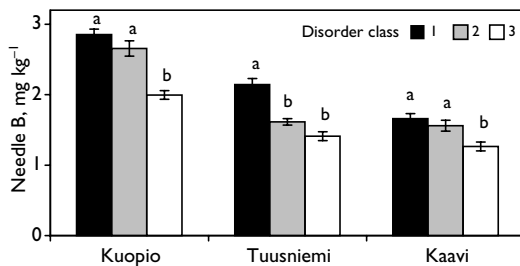| Experiment	Ca	K	Mg g kg^{-1}	N	P	B	Cu	Fe mg kg^{-1}	Mn	Zn	Mass g
Kuopio	4.66	6.15	1.04	14.45	1.57	2.50	2.99	25.9	731	37.0	4.01
n = 120	0.10	0.12	0.02	0.17	0.02	0.06	0.04	0.23	20	0.81	0.08
Tuusniemi	3.42	5.22	1.10	14.29	1.55	1.72	3.07	27.7	706	26.5	4.32
n = 120	0.08	0.11	0.02	0.18	0.02	0.05	0.04	0.37	25	0.69	0.08
Kaavi	4.24	5.52	0.90	15.59	1.19	1.50	3.46	24.8	860	32.0	3.84
n = 120	0.09	0.11	0.01	0.14	0.01	0.04	0.05	0.24	23	0.64	0.09

Fig. 4. Boron concentrations in current needles of the trees representing different disorder classes in the Kuopio, Tuusniemi and Kaavi experiments before fertilization. Standard error of the mean is marked on the columns by bars. Disorder classes: 1 = healthy, 2 = slightly damaged, 3 = severely damaged. Mean values with the same letter do not differ significantly from each other (p < 0.05). For each experiment n = 120, i.e. 40/disorder class.

between the needle B concentrations and the disorder class in all the experiments (Kuopio: r = –0.60***, Tuusniemi: r = –0.52***, Kaavi: r = –0.44***), i.e. the lower the B concentration, the more likely that the tree showed deficiency symptoms (* p < 0,05, ** p < 0,01, *** p < 0,001).

A positive correlation was found between the needle P concentrations and the disorder class in the Tuusniemi (r = 0.23*) and in the Kaavi (r = 0.23*) experiments, as well as in the combined material (r = 0.13*). In the Tuusniemi experiment (p = 0.03) and in the combined material (p = 0.008), the trees with severe disorder symptoms had significantly higher needle P concentrations than the healthy trees. No significant correlations were found between the concentrations of other nutrients and the disorder class of the sample trees.

In the Kuopio experiment, the average B concentrations before fertilization were 2.48, 1.41 and 1.59 mg kg^{-1} in the C, C + 1 and C + 2 needles, respectively (data not shown). In the youngest needles, irrespective of the disorder class, the concentrations of N, P and K were also significantly higher, but those of Ca lower than in the older needles.

According to the rapid increase in the needle B concentrations irrespective of the disorder class of the tree, boron application resulted in the immediate uptake of B (Table 5). After one growing season (in 2000), the needle B concentrations reached maximum values of ca. 43, 39 and 50 mg kg^{-1} in the Kuopio, Tuusniemi and Kaavi experiments, respectively. This was followed by a decline to a level of 17 to 22 mg kg^{-1} by the year 2002.

In the Kuopio experiment, the needle B concentrations of the B fertilized trees were, three years after fertilization (in 2002), highest in the C + 2 needles (Fig. 5), i.e. in the needles that developed in the year the fertilizer was applied (in 2000). The differences in B concentrations between the needles of different ages were, however, not significant. When the B concentrations of the C needles in 2000 (38 mg kg^{-1}) and of the same needles (at that time C + 2 needles) in 2002 (21 mg kg^{-1}) were compared, the B concentrations appeared to have halved (Table 5 and Fig. 5). This difference in B concentrations between the same needles after one and three growing seasons on the B treated trees, 17 mg kg^{-1} or 45 %, is an approximate measure of B redistribution within the tree canopy.

After one growing season, N fertilization had resulted in significantly elevated needle N con-

Table 5. Average P, N and B concentrations in current needles in the Kuopio, Tuusniemi and Kaavi experiments one (in 2000) and three (in 2002) growing seasons after fertilization. Disorder classes combined. n = 60 for each experiment in both years studied. See Fig. 2 for explanation of the treatments. Mean values for the same letter within a nutrient in the same year do not differ significantly from each other (p < 0.05).

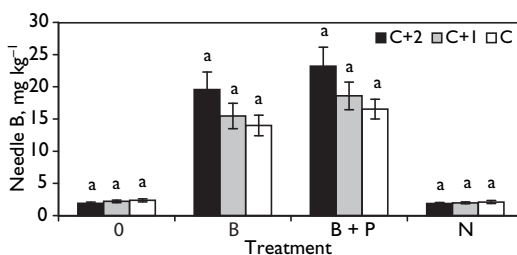|	Treatment	Kuopio		Tuusniemi		Kaavi	
		2000	2002	2000	2002	2000	2002
P,	0	1.45 a	1.31 a	1.69 a	1.81	1.24 a	1.31 a
g kg^{-1}	B	1.43 a	1.28 a	1.65 a	1.71	1.20 a	1.27 a
	B+P	1.92 b	1.61 b	2.06 b	1.91	1.67 b	1.67 b
	N	1.48 a	1.35 a	1.53 a	1.60	1.17 a	1.30 a
N,	0	13.3 a	12.1	15.8	14.6	16.1	14.5
g kg^{-1}	B	13.4 a	12.1	15.5	14.9	16.1	14.3
	B+P	14.2 a	12.0	16.8	14.6	16.8	14.3
	N	15.7 b	12.2	17.5	13.5	17.8	14.3
B,	0	2.6 a	2.4 a	2.5 a	2.2 a	2.2 a	2.7 a
mg kg^{-1}	B	32.6 b	14.0 b	39.4 b	22.3 b	41.2 b	18.9 b
	B+P	42.5 b	16.5 b	33.0 b	21.3 b	50.4 b	18.4 b
	N	2.4 a	2.1 a	2.8 a	2.5 a	2.5 a	2.5 a

Fig. 5. Boron concentrations in needles of different ages three years after fertilization (in 2002) in the Kuopio experiment. Trees of all disorder classes combined. Mean values with the same letter do not differ significantly from each other (p < 0.05). See Fig. 2 for explanation of the treatments. For each experiment n = 60, i.e. 15/treatment.

centrations in the Kuopio experiment (Table 5). Two years later, there was no longer any response in the N concentrations of the C needles in any of the experiments. In the Kuopio experiment, however, B fertilizer had, according to one-way ANOVA, decreased the N concentrations in the C+2 needles (p<0.012) and to a slight extent also in the C+1 needles (p<0.10) (data not shown).

Significantly elevated needle P concentrations were found in all the experiments one growing season after B+P fertilization, and in Kuopio and Kaavi also two years later (Table 5).

3.3 Proportion of Damaged Spruces

Four growing seasons after fertilization a high proportion of the disturbed spruces had recovered irrespective of the fertilizer treatment (Table 6). However, B fertilization appeared to have cured more damaged trees than the control or N treatments. In the Kaavi experiment there was no statistical difference between the treatments in this respect. The disorder class distributions of the treatment pairs 0 and N and B and B+P were similar, but 0 and N differed from B and B+P (Table 7).

3.4 Growth Response to the Treatments

Growth disturbances had affected the spruces for some time before the treatments, as can be seen from the differences in the H/D$_{1.3}$ ratios between the trees representing different disorder classes (Table 8). There was a negative correlation (–0.74, p<0.001) between the disorder class and the H/D$_{1.3}$ ratio. This ratio could be a good indicator for estimating the long-term or cumulative effects of the growth disturbance on spruces. Boron fertilization had a significant effect on the H/D$_{1.3}$ ratio only in the case of severely damaged trees; in 2003 the ratio was 0.57 for B fertilized trees and 0.52 for non-fertilized trees (t=3.30,

Table 6. Relative frequencies of the spruces in 2003 by disorder class and treatment. Before fertilization all cell frequencies were 33.3 % (n = 10). Similarity of disorder class distributions by treatment were tested with the Kruskall-Wallis one-way analysis of variance. See Fig. 2 for explanation of the treatments.

Treatment	Disorder class[1]	Experiment Kuopio	Tuusniemi	Kaavi	Total
0	1	70.0	70.0	60.0	66.7
	2	20.0	23.3	36.7	26.7
	3	10.0	6.7	3.3	6.7
B	1	93.3	93.3	80.0	88.9
	2	6.7	6.7	20.0	11.1
	3	0.0	0.0	0.0	0.0
B + P	1	90.0	93.4	63.3	82.2
	2	6.7	3.3	36.7	15.6
	3	3.3	3.3	0.0	2.2
N	1	60.0	76.6	66.7	67.8
	2	20.0	16.7	30.0	22.2
	3	20.0	6.7	3.3	10.0
X^2		14.15	8.95	3.26	19.25
p		0.003	0.030	0.354	0.000

[1] 1 = healthy, 2 = slightly damaged, 3 = severely damaged.

Table 7. Similarity of the disorder class distributions of the treatments in 2003 tested pair-wise with the Mann-Whitney test [1]. A lower value of the mean rank (MR) based on disorder classes 1–3 indicates healthier trees. See Fig. 2 for explanation of the treatments.

	n	MR					
Treatment 1	90	0 100.8	0 97.7	0 90.5	B 87.4	B 80.5	BP 83.5
Treatment 2	90	B 80.2	BP 83.3	N 90.5	BP 93.6	N 100.5	N 97.6
z [1]		–3.68	–2.44	–0.01	–1.31	–3.59	–2.38
p		0.000	0.015	0.992	0.189	0.000	0.017

Table 8. $H/D_{1.3}$ (m/cm) ratio by disorder class and experiment before fertilization. The marginal means of experiment and disorder class variables marked with the same letter are equal.

Experiment	n	Disorder class 1	2	3	Total
Kuopio	120	0.788	0.657	0.512	0.652a
Tuusniemi	120	0.679	0.589	0.472	0.580c
Kaavi	120	0.714	0.665	0.514	0.631b
Total	360	0.727a	0.637b	0.499c	0.621

Two-way ANOVA with the covariate $D_{1.3}$

Source	F value	p value
Experiment	20.6	0.000
Disorder class	90.0	0.000
Exp × Disord	3.11	0.016
$D_{1.3 (1999)}$	242.5	0.000

Table 9. Effect of disorder class and treatment (0, B and B+P, N) on the height growth (cm yr^{-1}) of spruces during four growing seasons after fertilization in the individual experiments. Multiple comparisons (Bonferroni) were made in the vertical direction, both by treatment in each experiment and together, i.e. within the treatment sections of the columns (0–B/BP–N) and by disorder class within the total section of the columns. The marginal means marked with the same letter are equal. See Fig. 2 for explanation of the treatments.

Treatment	Disorder class	n	Kuopio	Tuusniemi	Kaavi	Total
0	1	10	52	53	47	51
	2	10	45	40	35	40
	3	10	20	43	40	34
	Total	30	39a	45a	40a	42b
B and B+P	1	20	55	56	59	56
	2	20	58	57	54	57
	3	20	54	54	50	53
	Total	60	56b	56b	54b	55c
N	1	10	46	50	39	45
	2	10	39	42	37	39
	3	10	22	16	28	22
	Total	30	36a	36a	35a	35a
Total	1	40	52b	53b	51b	52b
	2	40	50b	49b	45ab	48b
	3	40	38a	41a	42a	40a
	Total	120	47	48	46	47

Two-way ANOVA

Source	Kuopio		Tuusniemi		Kaavi		Total	
	F	p	F	p	F	p	F	p
Treatment	23.5	0.000	15.9	0.000	21.8	0.000	58.0	0.000
Disorder class	16.6	0.000	8.4	0.000	3.8	0.026	24.7	0.000
Treat × Disord	4.6	0.002	4.3	0.003	0.7	0.625	5.1	0.001

p = 0.001), the average ratio in 1999 being 0.50 (Table 8).

The height growth was, on the average, 47, 48 and 46 cm yr^{-1} in the Kuopio, Tuusniemi and Kaavi experiments, respectively, during the four-year study period (Table 9). The effects of treatment (0, B and B + P, N) and disorder class on height increment were statistically significant in all the experiments separately and combined (Table 9). Height growth was lowest in the N treatment and highest in the B treatments (B and B + P). Trees that were severely damaged at the beginning of the study had the lowest height growth, and trees that were healthy looking at the beginning of the study had the highest height growth (Table 9). Compared to the control, B fertilization (B and B + P) increased height growth in all the disorder classes, i.e. 5, 17 and 19 cm yr^{-1} for healthy, slightly and severely damaged trees,

respectively, during the four-year study period (Table 9). Boron fertilization equalized the height growth between the disorder classes. Compared to the control, N seemed to have no, or in the case of severely damaged trees a decreasing effect on height growth, t = 2.60, p = 0.012 (Table 9).

Expectedly, the height growth also correlated positively with B fertilization (0.45***), but negatively with N fertilization (–0.37***), when all the material was combined.

Regression equations were calculated to estimate the effects of all potential variables on height growth at the same time. Height growth was best explained by B fertilization (0/1), but also to some extent by N fertilization, disorder class 3 (0/1), i.e. severely damaged, and needle B concentration before fertilization (Table 10).

Height growth was more strongly correlated with needle B concentration in 2002 (r = 0.44***)

Table 10. Annual height growth (cm yr^{-1}) during the period 2000–2003 as a function of fertilization, disorder class and needle B concentration in the whole material.

Variable	b	t value	p value
Constant	39.55	12.84	0.000
B fertilization (0/1)	13.41	6.61	0.000
Disorder class 3 (0/1)	–8.47	–4.52	0.000
N fertilization (0/1)	–6.44	–2.75	0.006
B$_{needles\ 1999}$	2.82	2.06	0.040

$R^2 = 0.28$, $s_f = 15.7$ cm; n = 360.

than with that in 1999 (r = 0.22**) or in 2000 (r = 0.38***). In every case the relationship between the needle B concentration and the height growth was, however, weak.

The treatments had no effects on diameter growth. Diameter growth, however, differed between the experiments (4.8, 5.4 and 6.4 mm yr^{-1} for the Kuopio, Tuusniemi and Kaavi experiments, respectively) and between the disorder classes (6.6, 5.9 and 4.2 mm yr^{-1} for disorder classes 1, 2 and 3, respectively).

4 Discussion

The experimental sites were typical growth disorder sites, i.e. very fertile, with a slash-and-burn and pasturing history and spruce planted under a deciduous cover (cf. Tamminen and Saarsalmi 2004). At the beginning of the study the needle B concentrations were, irrespective of the disorder class, clearly lower than the B concentrations in the C needles of 102 young Norway spruce stands in southern Finland (mean value of 8.9 mg/kg), except for some stands close to the studied stands in eastern Finland in an area classified as suffering from B deficiency and disorders (Tamminen and Saarsalmi 2004). The B concentrations were also lower than the deficiency limit of 5 mg kg^{-1} earlier reported for Norway spruce (Aronsson 1983, Brække 1983b, Jukka 1988, Lipas 1990). A highly significant negative correlation was found between the needle B concentrations and the disorder class of the trees in all three experiments at the beginning of the study, i.e. the lower the B concentration, the more likely a tree had defi-

ciency symptoms. The symptoms were expressed as stunted height growth and bush-like tops.

Although there were statistical differences between the disorder classes in the needle B concentrations, the disorder classes could not be discriminated on the basis of the B concentrations. The growth disturbance frequency of a stand seems to be a function of the average needle B concentration (Hytönen and Ekola 1993), but this relationship does not hold true for individual trees. For instance, in this material the needle B concentrations were very low in all the experiments, but in all the stands 21 to 32 % of the spruces were healthy at the beginning of the study (Table 1). Manifestation of the disturbance in a specific tree seems to depend on the inherited capacity of a tree to adapt to low B concentration. Another question is how well do needle samples taken during the dormant period describe B availability during the vital phases of bud development in each tree.

There appeared to be a shortage of B also in the soil. However, identifying B deficient sites solely on the basis of soil B determinations appears to be difficult, because only a relatively weak correlation has been reported between soil and needle B concentrations (Tamminen and Saarsalmi 2004).

According to earlier studies, B deficient stands have responded to B fertilization by increasing their uptake of B (e.g. Brække 1983b, Lehto and Mälkönen 1994, White and Krause 2001, Möttönen et al. 2003). An initial fast uptake seems to be followed by a rapid decline to a lower but more stable level (Hopmans and Clerehan 1991). The B concentrations are likely to remain at a level sufficient for normal growth for the next 8–10 years at least (Aronsson 1983, Hopmans and Clerehan 1991, Möttönen et al. 2003). In our study, the needle response to B fertilization was rapid: relatively high B concentrations were observed already after one growing season. Following this initial high uptake, the B concentrations declined to about 20 mg kg^{-1} after three growing seasons.

Although N application has been reported to lower needle B concentrations as a result of a dilution effect (Aronsson 1983), this was not the case in our study. This may be due to the fact that, in contrast to earlier findings (cf. Kukkola and

Saramäki 1983), there was no growth response to N probably due to a very good N status in soil (C/N < 20). A similar decreasing effect of B application on the N concentrations in the C+1 and C+2 needles, as found in the Kuopio experiment after three years, has also been reported by Lehto and Mälkönen (1994).

The stands showed marked recovery with or without the treatments during the four-year study period. However, B fertilization significantly accelerated this positive development. The proportion of severely damaged trees amongst the B-fertilized trees was almost zero. The reasons for the recovery of the trees that were not treated with B remained, however, unclear. Hynönen et al. (1999) reported that stands suffering growth disorders due to B deficiency also seem to have temporary recovery periods, and this variation between phases of damage and recovery can be seen along their stems as crooks, increased branching density and vertical branches or forks. The height development of severely damaged trees may also clearly fall behind that of taller trees. It is known that symptoms typical of B deficiency are often triggered indirectly by physiological stress factors related to climate and soil, and trees can grow almost normally at low B uptake when climatic or edaphic stress is low (Brække 1983b, Hopmans and Flinn 1984, Hopmans and Clerehan 1991). However, in this material the recovery of the spruces not treated with B could not be explained by an increase in needle B concentrations, because the concentrations remained at the same low level throughout the study period.

Boron fertilization increased the height growth in the damaged trees, i.e. B fertilization normalized height growth. Healthy trees also seemed to benefit from B fertilization, which means that B deficiency may in fact retard height growth before any disorder symptoms appear on individual trees (cf. Brække 1983b, Lipas 1990). Height growth development seemed to be a better recovery indicator than estimates of the disorder class because of its objectivity and very logical behaviour. Although the results showed that there is correlation between height growth and the needle B concentration, it was not possible to investigate this relationship in detail because the needle B concentrations were in most cases either very low (<5 mg kg^{-1}) or relatively high

(>10 mg kg^{-1}). Also Lipas (1990) reported a significant positive correlation between height growth and the needle B concentrations in a 37-year-old Norway spruce stand with low needle B concentrations (2.9–8.5 mg kg^{-1}) in south-eastern Finland. The dependence between height growth and needle B obtained by Lipas (1990) was even higher when needle B concentrations over 5 mg kg^{-1} were excluded.

Boron fertilization had no effects on diameter growth, which is in agreement with the results obtained by Lipas (1990). Neither did White and Krause (2000) detect any B effect on radial growth four years after B fertilization in a 21-year-old black spruce plantation suffering from a mild B deficiency (B < 6 mg kg^{-1}). According to Möttönen et al. (2003), the slight positive effect of B fertilization on the mean annual volume growth in a mature Norway spruce stand was non-significant.

5 Conclusions

In B deficient stands a high proportion of the trees may be damaged to a varying extent, and almost all the trees may suffer from retarded height growth. Boron fertilization increases needle B concentrations already during the first growing season following fertilization, and cures growth disorders, i.e. a lack of apical dominance and poor height growth, within four years. Shifts from severe damage in one year to normal development and growth some years later if climatic and edaphic stress is low, frequently occur. Hence, the trees may recover without B fertilization. The application of B will, however, ensure that they do in fact recover. Boron fertilization will also cure trees that have been suffering from growth disorders for a long period of time. However, owing to stem defects in severely damaged trees and their dominated position below taller trees, fertilization may not be very viable in the case of advanced growth disorders. Prophylactic measures seem to be the best way to handle a B deficiency problem, i.e. to prevent growth disorders with B fertilization in advance.

There are areas, especially in eastern Finland, where B application is recommended in young

spruce stands (see Tamminen and Saarsalmi 2004). Nitrogen fertilization alone can have a detrimental effect on height growth in disturbed spruce stands. Compared with B fertilization alone, applying P together with B gave negligible results.

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