Boron and Manganese Nutrition of Birch Seedlings in Nutrient Solutions

Inverkan av varierad bor- och mangangiva på björkplantor i näringslösningar

by

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I. Introduction

The importance of the micro-nutrients boron and manganese to the normal development and growth of plants has been known for a long time (24, 39, 43, 44). However, interest in the requirements for these elements in different forest tree species has only recently appeared and it has often been stated that they are only exceptionally of importance to productivity in forestry even if they are recognized as essential in small amounts. Hence, the available literature on boron and manganese nutrition of forest tree species is very small (*cf.* 17, 18, 45). For forest trees in the field, reports on evident deficiency of these elements are almost lacking, but in culture experiments boron as well as manganese deficiency has been demonstrated in pine seedlings (19, 20, 35). In these cases, however, the concentrations of the elements in the seedlings were not determined. In birch and spruce manganese deficiency was found in a stand on a lime-rich fen and percentage contents in the leaves of trees with deficiency symptoms and limited growth were determined (14).

The purpose of the present investigation was to study the influence of a varied supply of boron and manganese on the development, growth, and nutrient uptake of birch seedlings (*Betula verrucosa*, Ehrh.) under controlled growth conditions and with otherwise optimal nutrition. The main problem was to determine whether the concentrations of boron and manganese within the seedlings were as decisive for the seedlings, as the macro-nutrients (15), and, thus, whether the boron and manganese status of birch may be diagnosed on the basis of the leaf analysis data. Analysis of plant parts for diagnosis of the micro-nutrient status of plants has been shown to imply certain difficulties (*e.g.* 12, 38) because the analytical values are not always univocally related to growth.

II. Technique

The seedlings were grown for 71 days in nutrient solutions in a room with controlled temperature and artificial light as described earlier (13, 15). The number of seedlings per vessel was reduced after 48 days so that 4 seedlings usually remained at harvest (Table 3). In the low nutrient treatments a greater number was left to promote a better utilization of the nutrient supply and a more rapid development of deficiency in the seedlings.

Within the boron series the growth method was changed to some extent to avoid impurities. In the sub-optimal treatments polyethylene beakers were used as culture vessels instead of pyrex glass. Furthermore, for these treatments the pyrex-glass-distilled water was redistilled twice in a quartz still. The composition of the nutrient solutions is shown in Table 1 and the variations in boron and manganese supply are given in Table 3. This solution contains nearly optimal concentrations of all macro-nutrients under the experimental conditions used (15).

Table 1. The nutrient solutions. Dilution of the basic solutions 1 : 100 gives control concentrations.
Näringslösningar. Utspädning av förrådslösningarna med 1: 100 ger kontrollkoncentrationerna

Compound Salt	g/litre in basic solutions g/liter i förrådslösningar	Supplied element Tillfört element	ppm of element in control solution mg element per liter i kontrollen
NH_4NO_3	40.0	N	140
KH_2PO_4	43.9	K	126
		P	100
$CaCl_2$, $6H_2O$	65.7	Ca	120
$MgSO_4$, $7H_2O$	49.2	Mg	48
		S	64
$FeCl_3$, $6H_2O$	1.4	Fe	2.8
$CuCl_2$, $2H_2O$	0.015	Cu	0.06
$ZnCl_2$	0.012	Zn	0.06
Na_2MoO_4, $2H_2O$	0.0022	Mo	0.009
H_3BO_3	0.29	B	0.5
$MnCl_2$, $4H_2O$	0.18	Mn	0.5

The analytical methods have been described earlier: macro-nutrients (15), iron (13), and manganese (14). The boron analyses have been carried out with quinalizarin as reagent according to the method described by PORTER and SHUBERT (28). These workers indicated that among available micro-methods this is one of the most reliable. The samples were weighed in quartz tubes in which all treatments and reactions up to the time of the photometric measurement were carried out.

The statistical treatment of the results is similar to that used earlier (15). In this investigation all treatments have been carried out in four replications. Percentile experimental errors of the means for four vessels are given for some measurements in Table 2.

Table 2. Percentile standard errors in the means for four treatments.
Procentuella medelfel i medeltalen av fyra bestämningar.

Dry weight of Torrvikt av	$\pm \varepsilon$ %	ppm boron in mg bor per kg i	$\pm \varepsilon$ %	ppm manganese in mg mangan per kg i	$\pm \varepsilon$ %
Leaves Blad	17	Leaves Blad	10	Leaves Blad	10
Shoots Skott	17	Stems Stammar	17	Stems Stammar	22
Seedlings Plantor	18	Roots Rötter	13	Roots Rötter	28

III. Results and Discussions

1. *Relations between Supply and Seedling Dry Weight*

Though the relations between supply and growth or nutrient uptake are dependent on the particular conditions of the experiments (15), it is of interest to compare the micro-nutrient relations with earlier results. The various

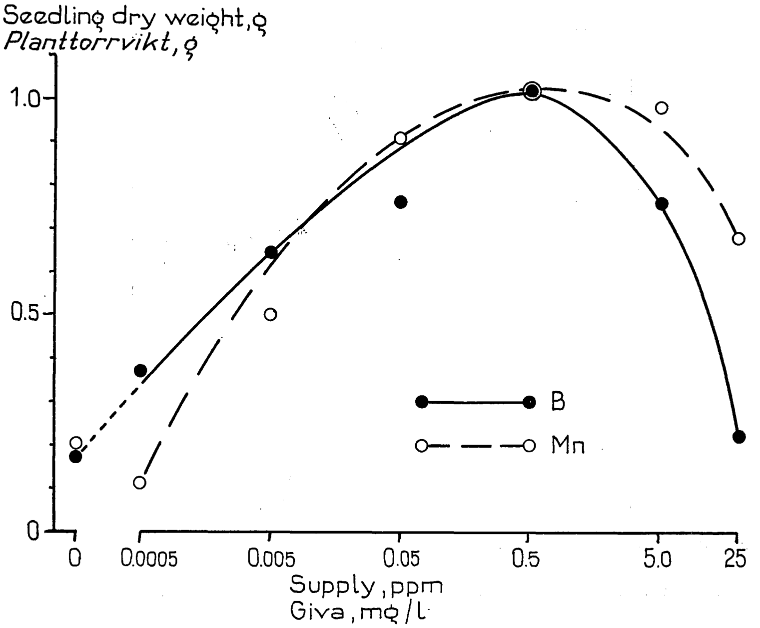

Figure 1. Relation between supply of boron and manganese and seedling dry weight.
Sambandet mellan bor- och mangangiva och planttorrvikt.

Table 3. Growth results. Control figures in italic type.
Tillväxtresultat. Kontrollvärdena kursiverade.

Element Element	Supply, ppm Giva, mg/l	Average number of seedlings per vessel Genomsnittligt antal plantor per kärl	Growth values per seedling Tillväxtvärden per planta					
			Seedling fresh weight, g Plantfriskvikt, g	Dry weight, g Torrvikt, g			Length, cm Längd, cm	
				Leaves Blad	Shoot Skott	Seedling Planta	Stem Stam	Root Rot
B	0	6.25	0.83	0.12	0.16	0.17	11	5.5
	0.0005	5.5	1.62	0.22	0.33	0.37	15	8.1
	0.005	4	2.74	0.38	0.57	0.64	21	8.3
	0.05	4	3.56	0.42	0.68	0.76	26	10.3
	0.50	*4*	*4.89*	*0.55*	*0.90*	*1.02*	*30*	*10.8*
	5.0	4	3.64	0.42	0.67	0.76	26	10.6
	25*	4	1.28	0.14	0.20	0.22	15	9.5
Mn	0	4	1.10	0.13	0.18	0.20	14	13.0
	0.0005	9.75	0.71	0.07	0.10	0.11	14	10.5
	0.005	4	2.61	0.30	0.44	0.50	22	10.6
	0.05	4	4.36	0.50	0.81	0.91	28	9.9
	0.50	*4*	*4.89*	*0.55*	*0.90*	*1.02*	*30*	*10.8*
	5.0	4	4.51	0.52	0.88	0.98	31	9.4
	25*	4	3.34	0.37	0.60	0.68	26	10.1

* The first 20 days 50 ppm was used.
De första 20 dagarna användes 50 mg/l.

Figure 2. Leaves with boron deficiency symptoms. To the left a leaf with a large chlorotic spot is seen.
Blad med borbristsymptom. Till vänster ses ett blad med en stor, gul fläck.

growth results are compiled in Table 3, and in Figure 1 the relation between the element supply and seedling dry weight is shown graphically. It is seen that the relationship is represented by an optimum curve for both boron and manganese. The seedlings have about the same sensitivity or tolerance to variations in the concentration (supply per time unit) of boron and manganese.

The growth of the seedlings is about the same in the boron and manganese series for equal, low concentrations (expressed as ppm) in the solutions (Figure 1). The requirement of the seedlings for 50 per cent of maximum growth (about 0.0015—0.0040 ppm boron or manganese in the solution) is much lower than for the macro-nutrients (about 1—10 ppm). A growth of 90 per cent of maximum is attained on the sub-optimal side with a supply of 0.06 ppm boron or manganese, whereas the corresponding values for the macro-nutrients range between about 3 and 75 ppm (15).

The supra-optimal effects of boron and manganese on growth are probably entirely associated with toxic effects of the elements as such, since the properties of the solutions otherwise are changed only to a very small extent, in contrary to what was the case when the macro-nutrients were varied (15). In the region of change from optimal to supra-optimal supplies the internal concentrations of boron and manganese increase very rapidly (Table 7) as does also the absorption of the elements (Table 5) and it seems as if the toxicity may be attributed to the high internal concentrations. That toxic effects appear at high boron or manganese supplies has been reported by many workers (*e.g.* 22, 39, 42, 46).

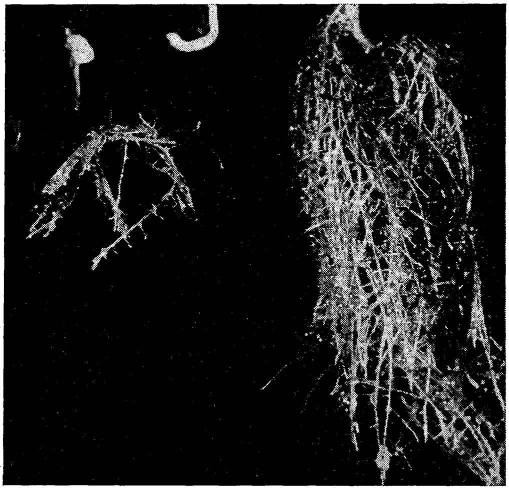

Figure 3. Left, a root at the lowest boron supply; right, a control root.
Till vänster ses en rot vid den lägsta borgivan; till höger en kontrollrot.

2. *Morphological Effects*

Visual Deficiency Symptoms

Boron. Symptoms of boron deficiency appeared regularly in the leaves at the three lowest supplies but also in some seedlings at the supply of 0.05 ppm. As has been reported for other plants (*cf.* 39, 44) boron deficiency in birch was connected with injuries in the meristems. The lateral growth of the leaves at the shoot apices was inhibited. On account of uneven growth of the mesophyll, these leaves, but also older ones, had a blistery surface (Figure 2). The leaves were dark green in colour but in some of the older leaves a few large chlorotic and necrotic spots appeared in the mesophyll (Figure 2). The root meristems also were injured by boron deficiency, leading to the formation of very short lateral roots (Figure 3). The marked effect of boron deficiency on root development has been described by many workers (*e.g.* 26, 27, 39). Effects of boron deficiency on root cell elongation have been demonstrated by Albert and Wilson (1) and Odhnoff (26).

Manganese. Symptoms of manganese deficiency were found in the leaves at the three lowest supplies. The symptoms are of the same type as reported for other plants (*e.g.* 39, 44). There was chlorosis in the mesophyll, especially in the older leaves. Necrosis appeared, beginning at the leaf margins and in spots in the chlorotic parts.

Visual Toxicity Symptoms

Boron. At the two highest supplies of boron visible toxicity symptoms developed. The symptoms consisted of mottled chlorosis in the leaves, especially in the leaf margins, just as reported by, for example, SCOTT (32) in Helianthus. Later the chlorosis developed to necrosis around the whole leaf margin and in spots in the mesophyll.

Manganese. No specific symptoms of manganese toxicity occurred in the experiments, though there was increased anthocyanin colouring of the leaves at the highest manganese supply.

Other Morphological Effects

The root/shoot ratio was influenced only slightly at the varied levels of boron and manganese (Table 4). The ratio of leaf to seedling dry weights had a

Table 4. Morphological effects. Control figures in italic type.
Morfologiska effekter. Kontrollvärdena kursiverade.

Element Element	Supply, ppm Giva mg/l	Dry weights Torrvikter		Dry weight/length, mg/mm Torrvikt/längd, mg/mm	
		Root/shoot Rot/skott	Leaves/ seedling Blad/planta	Stem Stam	Root Rot
B	0	0.10	0.71	2.5	1.8
	0.0005	0.11	0.59	3.9	2.5
	0.005	0.12	0.59	3.6	3.2
	0.05	0.12	0.55	3.9	3.3
	0.50	*0.13*	*0.54*	*4.6*	*4.4*
	5.0	0.13	0.55	3.8	3.4
	25	0.11	0.64	1.7	1.0
Mn	0	0.11	0.65	1.3	0.6
	0.0005	0.11	0.64	2.1	1.0
	0.005	0.12	0.60	2.5	2.1
	0.05	0.13	0.55	4.5	4.1
	0.50	*0.13*	*0.54*	*4.6*	*4.4*
	5.0	0.13	0.53	4.6	4.8
	25	0.13	0.54	3.6	3.2

tendency to high values at deficiency levels of both boron and manganese (Table 4). The ratio of stem to leaf dry weights, which varied very little with the macro-element nutrition of the seedlings (15), was affected by boron and manganese. This distribution of the dry matter indicates disturbances of carbohydrate translocation from the leaves at boron and manganese deficiency. Such effects have also been demonstrated to occur in boron-deficient plants of certain species (*e.g.* 8, 34).

The dry weight/length ratios for the stems and roots were very clearly affected by the boron and manganese supply with a maximum in the optimum range (Table 4). The quotient for the roots reflects the importance of the boron and manganese nutrition for the root branching, which was also noticed in the macro-element nutrition (15).

3. Nutrient Uptake

Uptake of Boron and Manganese

From Table 5 it is seen that the total uptake of boron and manganese increased with increasing supply at almost all levels, both when the uptake is expressed per vessel and per seedling. However, in the manganese series the uptake of manganese per seedling was somewhat lower in the 0.0005 ppm treatment than in the 0 ppm treatment. This depends on the fact that the number of seedlings per vessel was higher for the former. The uptake per vessel increased throughout the series.

The total element content in the seedlings per vessel was, at the lowest supply, higher than the total amounts added to the solutions and, thus, it is obvious that impurities interfered in these treatments.

Table 5. Boron and manganese uptake and the distribution of the amounts taken up.
Bor- och manganupptagningen samt fördelningen av de upptagna mängderna.

Element Element	Supply, ppm Giva, mg/l	Supply, mg/vessel Giva, mg/kärl	Content in seedlings, mg Innehåll i plantorna, mg				
			Per vessel Per kärl	Per seedling Per planta			
				Whole seedlings Hela plantor	Leaves Blad	Stem Stam	Root Rot
B	0	0	0.049	0.0078	0.0058	0.0013	0.0006
	0.0005	0.0022	0.070	0.012	0.0089	0.0026	0.0009
	0.005	0.0225	0.098	0.024	0.017	0.0069	0.0010
	0.05	0.225	0.16	0.040	0.034	0.0041	0.0018
	0.5	*2.25*	*0.26*	*0.067*	*0.057*	*0.0066*	*0.0030*
	5.0	22.5	1.20	0.29	0.26	0.024	0.0058
	25	125	1.42	0.32	0.31	0.0067	0.0045
Mn	0	0	0.012	0.0021	0.0010	0.0001	0.0010
	0.0005	0.0022	0.013	0.0014	0.0008	0.0002	0.0004
	0.005	0.0225	0.021	0.0052	0.0035	0.0006	0.0011
	0.05	0.225	0.099	0.024	0.020	0.0029	0.0011
	0.5	*2.25*	*0.54*	*0.13*	*0.11*	*0.017*	*0.0032*
	5.0	22.5	2.09	0.52	0.44	0.071	0.012
	25	125	3.04	0.76	0.63	0.10	0.024

Uptake of Other Elements

In general the internal concentrations of the unvaried elements vary only slightly with varied supply of boron or manganese (Table 6). There is no indication from the leaf contents of the unvaried nutrients that they have influenced growth. However, in the boron series there was a comparatively high percentage of nitrogen and potassium in the leaves at the highest supply.

Table 6. Contents in leaves and roots of the unvaried elements. Control figures in italic type.

Halter i blad och rötter av de ovarierade elementen. Kontrollvärdena kursiverade.

Element Element	Supply, ppm Giva, mg/l	Content in leaves, % of dry weight Halt i blad, % av torrvikt						Content in roots, % of dry weight Halt i rötter, % av torrvikt					
		N	P	K	Ca	Mg	Fe	N	P	K	Ca	Mg	Fe
B	0	3.20	0.39	2.40	0.32	0.43		3.32	0.77	2.80	0.14	0.13	
	0.0005	3.30	0.42	2.33	0.28	0.42		3.19	0.70	2.60	0.17	0.12	
	0.005	3.30	0.42	2.46	0.29	0.39		3.00	0.52	1.88	0.14	0.10	
	0.05	3.83	0.46	2.54	0.32	0.45		2.97	0.44	2.33	0.15	0.11	
	0.50	*3.80*	*0.48*	*2.47*	*0.36*	*0.39*		*2.66*	*0.76*	*2.16*	*0.13*	*0.07*	
	5.0	3.73	0.65	2.88	0.48	0.50		2.83	0.57	2.27	0.17	0.09	
	25	4.01	0.64	3.50	0.30	0.48		2.84	0.84	4.14	0.17	0.11	
Mn	0	4.29	0.45	2.59	0.36	0.55	0.010	2.55	1.15	3.99	0.32	0.06	2.47
	0.0005	4.54	0.50	2.96	0.41	0.57	0.014	2.51	1.22	3.03	0.25	0.09	2.68
	0.005	3.71	0.42	2.68	0.36	0.48	0.009	2.61	0.90	2.76	0.18	0.11	1.33
	0.05	3.68	0.52	2.24	0.43	0.44	0.012	2.79	0.90	2.02	0.13	0.08	0.78
	0.50	*3.80*	*0.48*	*2.47*	*0.36*	*0.39*	*0.012*	*2.66*	*0.76*	*2.16*	*0.13*	*0.07*	*0.95*
	5.0	3.62	0.50	2.26	0.40	0.39	0.012	3.32	0.76	1.66	0.12	0.09	0.84
	25	3.71	0.51	2.17	0.43	0.44	0.010	2.85	0.85	2.03	0.15	0.10	1.28

In the roots, on the other hand, the nitrogen percentage was highest at the lowest supply, whereas the potassium percentage was high both at the lowest and the highest supply. In the manganese series the nitrogen percentage in the leaves was comparatively high at the lowest supplies. There was a similar tendency for magnesium. In the roots the percentages of phosphorus, potassium, calcium, and iron were relatively high at the lower manganese supplies.

Many workers have found antagonistic effects between iron and manganese (*e.g.* 4, 9, 31, 36, 37, 40). However, TWYMAN (41) found that at low manganese supplies an increase in the supply increased the iron uptake. In the present experiments the contents of iron in the leaves were not influenced by the manganese supply (Table 6), but the root analysis results show high iron values at low manganese supplies. The iron analysis, however, is somewhat unreliable for the roots because a large amount of iron may remain on the root surface despite the washing at harvest.

It is seen that variations in the boron or manganese supplies did not significantly affect the capacity of the seedlings for uptake of other elements, but that the rate of uptake is mainly determined by the rate of growth. Many workers have reported effects on the uptake of the macro-nutrients (*cf.* 8, 39). In the present study, however, the unvaried nutrients were supplied in nearly optimal amounts.

4. *Transport and Distribution of Boron and Manganese*

Amounts in the Various Organs

In Table 5 the quantitative distribution of the elements in the various parts of the seedlings is shown. The amounts in the leaves were much greater than in the stems and roots. Consequently, most of the elements taken up are translocated to the leaves, but the distribution pattern depends on the supply. Thus, in the boron series the boron content in the stems and roots does not increase with supply as rapidly as in the leaves. In the manganese series there is about the same manganese content in the roots at all sub--optimum treatment levels, with the exception of the 0.0005 ppm treatment. Thus, the seedlings retained a certain amount of the elements in the roots independent of the supply. The reason for this distribution pattern may be a time trend in the fixation of boron and manganese in the roots. In the beginning of the experiments the boron and manganese concentrations have probably been comparatively high, as was found for the macro-nutrients (15). Later they have been "diluted" by growth and redistributed within the seedlings. In the low supply treatments the redistribution may have been restricted because of fixation of the elements in the roots during the earlier stages. In the treatment 0.0005 ppm manganese a greater number of seedlings was present, deficiency was developed earlier, and because then less manganese may have been fixed a more even distribution would be the result, just as was experimentally found.

Concentrations in the Various Organs

The results in Table 7 show that the concentrations of boron and manganese in the leaves increased with the supply, at first very slowly or not at all and then more rapidly. In the boron series the concentrations of boron in the

Table 7. Contents in leaves, stems, and roots of boron within the boron series and manganese within the manganese series. Control figures in italic type.

Halter i blad, stammar och rötter av bor inom borserien och mangan inom manganserien. Kontrollvärdena kursiverade.

Supply, ppm Giva, mg/l	B contents, ppm of dry weight Borhalt, mg/kg torrvikt			Mn contents, ppm of dry weight Manganhalt, mg/kg torrvikt		
	Leaves Blad	Stems Stammar	Roots Rötter	Leaves Blad	Stems Stammar	Roots Rötter
0	51	30	40	9	3	80
0.0005	41	24	25	10	7	33
0.005	45	36	15	12	4	20
0.05	82	16	22	41	10	11
0.50	*100*	*20*	*26*	*210*	*50*	*28*
5.*0*	640	93	70	850	200	100
25	2,500	110	230	1,700	460	290

stems and roots decreased with increasing supply within the sub-optimum region. This phenomenon was still more pronounced in the roots of seedlings in the manganese series where a distinct minimum manganese concentration was recorded for the 0.05 ppm treatment. However, in the stems the manganese concentration increased with supply throughout the series. It is seen that the concentrations are usually highest in the leaves and lowest in the stems.

Conclusions

It has been demonstrated that the transport of the elements to the leaves proceeds readily when the amount absorbed exceeds a certain minimum. For boron this is in agreement with the results of SCOTT and SCHRADER (31), for example, who found a greater correspondence between the boron concentrations in leaves and stems at low boron supply than at high. Similar results were reported for many species by EATON (6). Within a single leaf or from mature (but not senescent) leaves to younger ones the boron mobility is apparently high (2, 16, 32). The downward transport of boron in the phloem, however, is small according to KOHL and OERTLI (16), as also is the transport of boron from a root in a boron-containing solution to a root of the same seedling in a boron-free solution (1). The mobility of the bulk of the boron absorbed seems, thus, to be rather high, but a certain amount seems to be relatively immobile, at least in the lower parts of the seedlings.

Available reports for manganese are more conflicting. ROMNEY and TOTH (30) found that ^{54}Mn-labelled manganese sulphate, which was applied on the leaves, was mainly translocated upwards. Similar results were obtained (14) when manganese was supplied to a spruce tree through a bored hole in the stem 1½ meter above the ground. The deficiency symptoms disappeared in the branches above the level of injection and the manganese concentrations in the leaves were increased, whereas no effects could be detected in the lower branches during a period of several years. However, BOKEN (3) found that the application of manganese on the leaves caused increased manganese concentrations in the roots. It seems as if manganese is relatively easily translocated upwards to the leaves, but that, as for boron, a certain amount tends to remain in the roots.

5. The Significance of the Internal Boron and Manganese Concentrations

Concentrations in the Leaves Corresponding to Visual Symptoms

The concentrations of boron and manganese in the leaves when deficiency or toxicity symptoms have appeared are given in Table 8. Comparative values for birch are practically lacking in the literature, but it was found in the field

Table 8. Approximate boron and manganese concentrations in the leaves corresponding to visual symptoms and various growth levels.

Approximativa bor- och manganhalter i bladen motsvarande visuella symptom samt olika tillväxtnivåer.

Element Element	Symptom strength Symptom-styrka	ppm of dry weight at symptoms of mg/kg torrvikt vid symptom på		ppm of dry weight at a growth in relation to maximum of mg/kg torrvikt vid en tillväxt relativt maximum på		
		Deficiency Brist	Toxicity Giftverkan	50—90 % (sub- -optimum)	90—100—90 % (optimum)	90—50 % (supra- -optimum)
B	None Inga		100			
	Weak Svaga	82	640	50—70	70—300	300—1,200
	Strong Starka	51				
Mn	None Inga	41	1,700	13—25	25—1,000	1,000—2,200
	Strong Starka	12				

that birch leaves had slight manganese symptoms when the manganese content was 17 ppm and that there was no symptoms to toxicity at contents of 590—1,520 ppm (14). Thus, there is good agreement between the field and the laboratory results, and together they indicate that symptoms of deficiency are to be expected when the leaf manganese content is between 17 and 41 ppm.

In Table 9 values found in the literature for various species are compiled. It is seen that manganese deficiency symptoms correspond to very similar concentrations in the leaves in various species (see also 10). Toxic effects of manganese have been reported in Phaseolus when the manganese content in the leaves was about 1,200 ppm (22). Similar and higher values have been reported for other plants (10). The sensitivity of birch to high manganese contents in the leaves seems to be comparatively low.

For boron deficiency symptoms have been reported to appear at quite varying internal boron concentrations in different species (Table 9, *cf.* Goodall and Gregory, 10). The birch seedlings seem to be comparatively sensitive to boron deficiency and the symptoms developed at contents that are close to the highest reported for other plants. Toxicity symptoms have also been reported to develop at very different leaf contents of boron (6, 10) and values down to 70 ppm have been found in connection with toxicity. It seems that most plants develop toxicity symptoms when the boron concentration in the leaves is between 200 and 500 ppm. This range also seems critical for birch.

Table 9. Analytical values of boron and manganese reported in the literature to correspond to some characteristics of various plant species.

Analysvärden av bor och mangan angivna i litteraturen vid några karakteristiska tillstånd hos olika växtslag.

Element Element	Reference Källa	Species Växtslag	Analyzed material Analyserat material	Contents, ppm of dry weight / Halt, mg/kg torrvikt — At symptoms of / Vid symptom på: Deficiency Brist	Toxicity Förgiftn.	Low Låg	Optimal Optimal	High Hög
B	2	Broccoli Broccoli	Leaves Blad				50	
	6	Grape vine Vinranka	»	86	926	38—86		926
	6	Blackberry Björnbär	»	9	210		9	210
	6	Turnip Kålrot	»		399	65	108	399
	6	Cherry Körsbär	»	14			104	182
	6	Common beat Foderbeta	»	52	637—822		25—1,263	
	6	Cotton Bomull	»	16	522	16	187—1,625	
	23	Millet Hirs	»				10—150	
	29	Orange Apelsin	»			21—40	50—150	160—210
	32	Sunflower Solros	»		807			
	33	Grape vine Vinranka	»				57—146	
	44	Various sp. Olika växter	Tops or leaves Skott eller blad	5—23				
Mn	5	Lucerne Luzern	Leaves Blad					184
	11	Oats Havre	Tops Skott	< 30				
	12	Tomato Tomat	Young leaves Unga blad				20—40	
	14	Birch Björk	Leaves Blad	17	> 1,520			
	14	Spruce Gran	»	< 20	> 374			
	22	Bean Böna	»		1,200			
	25	Cereals Sädeslag	Tops Skott				30—40	
	29	Orange Apelsin	Leaves Blad			16—24	25—200	300—500
	44	Various sp. Olika växter	Tops or leaves Skott eller blad	6—17				

Relations between Concentrations in the Leaves and Seedling Dry Weight

The optimum content of boron is about 100 ppm and of manganese about 50—750 ppm of the leaf dry weight. The minimum concentrations seem to be about 35 ppm boron and about 7 ppm manganese in the leaves. In Table 8 intervals of contents corresponding to some growth levels are compiled.

The birch seedlings were more sensitive to variations in the boron than in the manganese concentrations in the leaves and the requirement of boron within the seedlings is essentially higher than the manganese requirement within the whole sub-optimal region. When the requirement is expressed in atomic units (Figure 4) the difference between boron and manganese is very

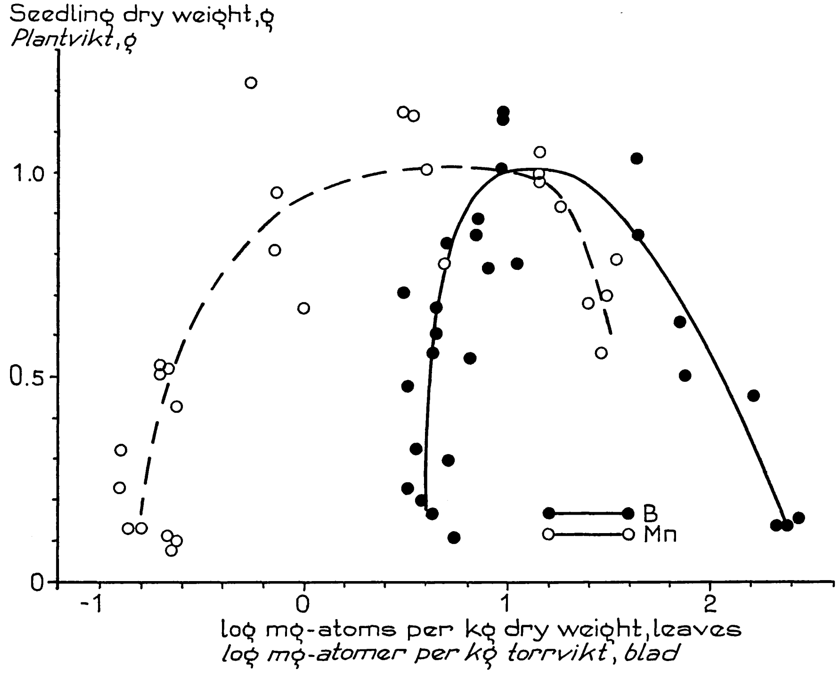

Figure 4. Relation between boron and manganese concentration in the leaves as mg-atoms per kg dry weight (logarithmic scale) and seedling dry weight.
Sambandet mellan bor- och manganhalten i bladen som mg-atomer per kg torrvikt (logaritmisk skala) och planttorrvikten.

pronounced in the optimal and sub-optimal ranges. In this relation the toxicity of manganese is greater than that of boron.

The authors know of no published values for birch which can be used for comparison and, therefore, further experiments are needed before the value of the leaf analysis method for these elements in birch can be fully assessed. However, it seems probable from the present results that the leaf analysis method is physiologically justified as a tool for diagnosis of the boron or manganese status of birch, at least in the main features. It seems possible to distinguish between contents corresponding with deficiency, maximum growth, and toxicity. Comparison with values for other species is of little value in this connection because of the very different requirements, especially for boron. EATON (6) found that grape vine, variety Sultania, attained about 53 per cent of maximum growth at a boron content of 86 ppm in the leaves. The variety Malaga attained 40 per cent of maximum at 38 ppm boron. These values correspond very closely with those found here for birch, as also some other values (Table 9). On the other hand, EATON found the best growth in many plants at very low boron contents and in some cases the optimum contents appear to have been below 10 ppm. It seems as if birch is a species with a comparatively high boron requirement and that it is also sensitive to variations in the internal boron concentration.

For manganese the similarity between the lowest contents in the leaves for maximum growth in various species is greater than for boron (Table 9). The upper limit of the optimum range, on the other hand, is for birch much higher than the corresponding values published for other species. The low sensitivity of the birch seedlings to comparatively high manganese contents in the leaves was also found in connection with the development of toxicity symptoms. The toxicity of manganese, however, has been reported by many workers to depend also on other nutrient factors (see 39) and it is possible that the comparatively low sensitivity of birch found here, may depend on the fact that the birch seedlings had nearly optimum status of the other nutrients.

Conclusions

The concentrations of boron and manganese in the leaves have within certain ranges a decisive influence on the growth of the birch seedlings. Analytical results from other parts of the seedlings are more difficult to interprete because after some time the mobility of the elements apparently becomes limited in the stems and, to a greater extent, in the roots. Thus, with increasing supply of boron and manganese the element concentration in the stems and roots at first tends to decrease down to a minimum value at intermediate supplies and then the concentration increases again (Table 7). Consequently, a comparatively high concentration in these organs or samples containing these organs may correspond to either a low or a relatively high growth rate within the sub-optimal region. In the leaves such phenomena seem to be of less importance (2, 7, 16, 32). Furthermore, the distribution of the dry matter within the seedlings found at the low supplies (Table 4) means a leaf growth and concomittantly "dilution" effect in the leaves that is not so obvious in the lower organs. The contents in the leaves, therefore, are quite univocally differentiated when supply is varied.

These relationships demonstrate the importance of using well-defined and morphologically uniform materials for analysis. The results of HEWITT (12), STEENBJERG (38), and others do not disprove the usefulness of the leaf analysis method, but emphasize the necessity for adequate sampling and for a knowledge of the mobility of the elements and their morphological effects.

IV. Summary

Birch seedlings were grown under controlled conditions in nutrient solutions with varied supplies of boron and manganese. Growth measurements and chemical analyses of the seedlings have been carried out. The main purpose of the investigation was to study the influences of boron and manganese on the development, growth, and nutrient uptake of birch and the significance of the internal concentrations of the varied elements in this species. The results may be summarized as follows.

1. The influences of the boron and manganese variations were studied under otherwise nearly optimum nutrition of the seedlings. The relationship between supply and growth is, however, related to the prevailing experimental conditions.

2. The variations in the boron or manganese supply did not influence the uptake of the other elements to any important extent.

3. Visual deficiency symptoms have been described for both boron and manganese. Discernible toxicity symptoms were found only for boron. The element concentrations in the leaves corresponding to symptoms are given in Table 8. Other morphological effects have also been recorded.

4. The translocation of boron and manganese upwards from the roots is limited at low supplies.

5. The results support the use of the leaf analysis method when diagnosing the boron or manganese status of birch. Leaf contents which correspond to some growth levels are given in Table 8. It is found to be essential to use a morphologically uniform material for the analysis and that the leaves are preferable because of an apparently low degree of fixation of boron and manganese in these organs.

6. The requirement of boron in birch is high in comparison to that reported for other plants. The manganese requirement, on the other hand, is intermediate.

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Sammanfattning

Inverkan av varierad bor- och mangangiva på björkplantor i näringslösningar

Mycket litet är känt om betydelsen av bor och mangan för skogsträdens tillväxt och utveckling (17, 18, 45). I föreliggande undersökning har reaktionerna hos unga björkplantor (*Betula verrucosa*, Ehrh.) studerats vid varierad koncentration av bor och mangan i näringslösningar. Som ett huvudproblem har frågan ställts, om halten av bor och mangan i bladen är lika avgörande för plantornas fysiologiska tillstånd, som fallet är för makroelementen (15), och sålunda, om bladanalysmetodiken är användbar som ett diagnostiskt hjälpmedel även för dessa element hos björk. Flera forskare har funnit svårigheter då det gäller att tolka analysvärden av spårämnena på grund av att sambandet mellan tillväxt och inre halt icke alltid är entydigt (se t. ex. 12, 38).

Försöksmetoderna har i stort sett varit desamma, som beskrivits tidigare (15), men vissa åtgärder har vidtagits för att minska inflytandet av föroreningar; vattnet har destillerats ytterligare två gånger i en kvartsglasapparat och polyetylen har använts i odlingskärlen vid låga borgivor. Näringslösningarnas sammansättning framgår av Tabell 1. Analysmetoderna utom för bor har beskrivits tidigare (13, 14, 15). Boranalyserna har utförts i stort sett enligt PORTER och SHUBERT (28).

Procentuella experimentella fel, beräknade liksom tidigare (15), återfinns för några mätresultat i Tabell 2. Felen gäller för medeltal från fyra kärl.

Tillväxtresultaten har samlats i Tabell 3 och relationen mellan giva och planttorrvikt återfinns i Fig. 1. Det framgår, att tillväxten varit starkt beroende av givan och att sambanden kan åskådliggöras med optimumkurvor. Detta samband är emellertid speciellt för dessa experiment (se 15).

Bristsymptom har registrerats vid de lägsta givorna. För borbrist var det typiskt, att meristemen påverkades i såväl skott (Fig. 2) som rötter (Fig. 3). Bladen var mörkt gröna och de yngre bladen verkade täckta med små blåsor. Enstaka, stora fläckar med gul färg och död vävnad uppträdde hos de äldre bladen. Manganbrist yttrade sig främst genom gula partier i bladskivan, speciellt hos de äldre bladen.

Förgiftningssymptom framkom vid de högsta borgivorna. Gula fläckar uppträdde i bladen och så småningom dog vävnaderna i bladkanterna och fläckvis i bladskivorna. I manganserierna saknades tydliga förgiftningssymptom.

Rot/skott-kvoten har påverkats i obetydlig grad (Tabell 4). Däremot har vikt/längd-kvoterna hos såväl stammar som rötter varierat med givan. Detta tyder för rötternas del på att bor- och mangantillståndet varit av betydelse för rötternas förgreningsgrad liksom makronäringstillståndet (15). Vikt/längd-kvoterna når också här maximum inom det optimala området (Tabell 4).

Bor- och manganupptagningen har starkt påverkats av givan (Tabell 5). Den inre koncentrationen av andra element än det varierade påverkas däremot ganska litet (Tabell 6). Det framgår, att den av plantorna upptagna bor- och manganmängden lätt transporteras upp till bladen, som innehåller större mängd än stammar eller rötter (Tabell 5). I borserien finner man emellertid att innehållet i stammar och rötter icke ökat så snabbt med givan som fallet är i bladen. I manganserien innehåller rötterna ungefär samma manganmängd vid alla de underoptimala givorna med undantag för behandlingen 0.0005 mg/liter, i vilket fall ett större antal plantor vuxit i kärlen. Plantorna har sålunda haft en tendens att hålla kvar en viss minsta mängd i rötterna oberoende av givan. Detta kan bero på att bor och mangan har fixerats i rötterna under tidigare utvecklingsstadier, då de inre halterna sannolikt varit högre enligt samma princip som visat sig gälla för makronäringsämnena (15).

Bor- och mangankoncentrationerna i olika organ framgår av Tabell 7. I bladen ökar halten med givan, långsamt eller inte alls vid låga givor och sedan allt hastigare. I stammar och rötter t. o. m. minskar halterna först, vilket är särskilt markant för manganhalten i rötterna från manganserien.

Genom att halten i bladen ökar med givan finns förutsättningar för en entydig tolkning av bladanalysvärdenas innebörd vid diagnos av plantornas bor- eller mangantillstånd (Fig. 4). I Tabell 8 ges approximativa halter motsvarande vissa tillväxtnivåer samt uppträdandet av symptom på brist eller förgiftning. I Tabell 9 redovisas liknande värden, som angivits för en rad olika växtslag i litteraturen. Vid analys av rötter eller stammar eller plantdelar, som innehåller dessa organ föreligger svårigheter att tolka värdena på grund av den fixering av elementen, som ägt rum i dessa organ vid låga givor. Resultaten tyder sålunda på att det är viktigt, att använda väldefinierade och morfologiskt enhetliga material för analys och att bladen är lämpliga vid diagnos av bor- och mangantillståndet på basis av de inre koncentrationerna.

Björkplantornas optimala halt av bor i bladen är högt i jämförelse med vad man finner hos de flesta andra växter. Björkens behov av bor synes därför vara jämförelsevis högt, manganbehovet däremot intermediärt.