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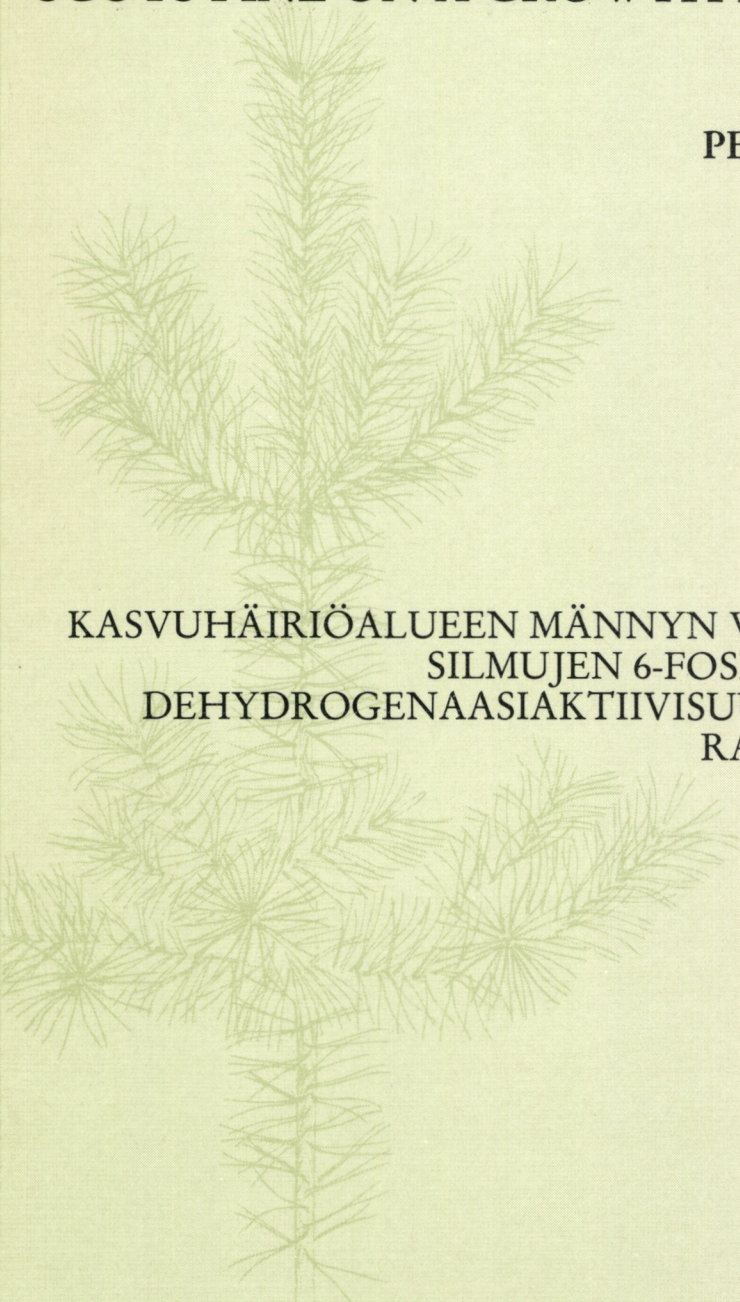
FOLIAR NUTRIENT CONTENT AND
6-PHOSPHOGLUCONATE DEHYDROGENASE
ACTIVITY IN VEGETATIVE BUDS OF
SCOTS PINE ON A GROWTH DISTURBANCE
AREA

PEKKA PIETILÄINEN

SELOSTE

KASVUHÄIRIÖALUEEN MÄNNYN VEGETATIIVISTEN
SILMUJEN 6-FOSFOGLUKONAATTI
DEHYDROGENAASIAKTIIVISUUS JA NEULASTEN
RAVINNEPITOISUUS

HELSINKI 1984



COMMUNICATIONES INSTITUTI FORESTALIS FENNIAE



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Cover (front & back): Scots pine (*Pinus sylvestris* L.) is the most important tree species in Finland. Pine dominated forest covers about 60 per cent of forest land and its total volume is nearly 700 mil. cu.m. The front cover shows a young Scots pine and the back cover a 30-metre-high, 140-year-old tree.

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Approved on 31.1.1984

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PIETILÄINEN, P. 1984. Foliar nutrient content and 6-phosphogluconate dehydrogenase activity in vegetative buds of Scots Pine on a growth disturbance area. Seloste: Kasvuhäiriöalueen männyn vegetatiivisten silmujen 6-fosfoglukaatti dehydrogenaasiaktiivisuus ja neulasten ravinnepitoisuus. Commun. Inst. For. Fenn. 123: 1—18.

The study was carried out to see if boron effects 6-phosphogluconate dehydrogenase activity in the regulation of pentose phosphate shunt of Scots pine (*Pinus sylvestris* L.) vegetative buds. The experimental material consisted of vegetative buds from NPK-fertilized phenotypically normal and growth disturbance pines and ash fertilized pines.

The dry weight and nutritional contents of the vegetative buds were determined. The seasonal 6-phosphogluconate dehydrogenase activity was measured from the monthly collected buds. An attempt was made to determine the interaction of boron on 6-phosphogluconate dehydrogenase activity in the crude enzyme fraction of the buds.

The dry weight of the buds was rather constant throughout the research period. The 6-phosphogluconate dehydrogenase activity of the buds was highest in autumn and lowest during the winter months. A significant gain of activity occurred in spring. The enzyme activities of the buds from phenotypically normal and growth disturbance pines were higher than that of the buds from ash fertilized pines. The enzyme activity of phenotypical normal and growth disturbance pines rose after a warm period in January during the dormancy period.

The interaction of boron on the 6-phosphogluconate dehydrogenase activity was studied with the crude enzyme fraction of the buds that were collected in September. Physiological concentrations of 5 ppm, 10 ppm and 15 ppm of boric acid showed marked inhibitory effects on the 6-phosphogluconate dehydrogenase activity of the crude enzyme fraction.

The study showed that there is some changes in the water content of the growth disturbance area pine buds. Also it is evident that the state of dormancy of the buds was broken in the growth disturbance area trees. Physiological concentrations of boron inhibited the activity of 6-phosphogluconate dehydrogenase in the crude enzyme fraction.

On the basis of the present results the cause of the disturbance can not be specified to anyone nutrient. More likely the results indicated that the disturbance results from a disorder of several nutrients.

Tutkimuksen tarkoituksena oli selvittää boorin ja 6-fosfoglukaattidehydrogenaasin osuutta pentoosifosfaattireitin säätelyssä männyn vegetatiivisissa silmuissa. Tutkimusmateriaali koostui Muhoksella (65°52'N, 26°07'E) kerätystä NPK-lannoitettujen ilmiänsuhtaan normaalien ja kasvuhäiriöpuiden sekä tuhkalannoitettujen puiden vegetatiivisista silmuista.

Vegetatiivisten silmujen kuivapainot ja ravinnepitoisuudet määritettiin. Vuotuinen 6-fosfoglukaattidehydrogenaasin aktiivisuus sekä 6-fosfoglukaattidehydrogenaasin ja boorin keskinäinen vaikutus mitattiin silmujen raakaentsyymifraktiosta.

Silmujen kuivapainot olivat jokseenkin vakaat tutkimusjakson aikana, vain kahden kuukauden aikana ilmeni tilastollinen ero.

Tuhkalannoitetuissa puissa entsyymiaktiivisuus oli korkein syksyllä, alhaisin talvella, ja merkittävä aktiivisuuden nousu tapahtui keväällä. Ilmiänsuhtaan normaalien ja kasvuhäiriöpuiden entsyymiaktiivisuus oli tuhkalannoitettuja korkeampi ja entsyymiaktiivisuus näissä puissa nousi tammikuussa lämpimän jakson jälkeen.

Fysiologiset 5 ppm:n, 10 ppm:n ja 15 ppm:n ortoboorihappokonsentraatiot vaikuttivat raakaentsyymifraktioon selvästi inhiboiden 6-fosfoglukaattidehydrogenaasiensyymien aktiivisuutta.

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1. INTRODUCTION

Tree growth on drained peatlands is stimulated by applying macronutrients (N = nitrogen, P = phosphorus and K = potassium) to sites originally poor in nutrients (Lukkala 1955, Kaila 1956, Huikari and Paarlahti 1967, Huikari and Paavilainen 1972, Kurki 1972, Paavilainen 1979). The amount of the applied nutrients depends on the nutritional status of the site (Huikari 1952, 1961, Heikurainen 1971, Paavilainen 1979). However, sooner or later micronutrients may become a factor limiting tree growth (Hearman 1938, Prevot and Ollagnier 1961, Paavilainen 1969, 1980, Bussler 1974, Huikari 1974, Tolonen 1974, Sillanpää 1975, Veijalainen 1977, Kolari 1979) and result into growth disturbances (Veijalainen 1975, Raitio and Rantala 1977, Kolari 1979).

Most of the growth disturbances in Scots pines appear on deserted agricultural peatlands, on naturally leached acidic soils and especially on mire centre effect peatlands after forest improvement measures (Veijalainen 1978, Kolari 1979, Silfverberg 1979). The first visible signs of growth disturbance are the malformation of the buds, which result into retardation of growth and shoot dieback in the apical portions of the pines. After repeated shoot dieback the appearance of the Scots pine becomes bushy (Veijalainen 1975, Raitio and Rantala 1977, Kolari 1979).

Needle analyses (Stoate 1950, Smith 1962, Paarlahti ym. 1971, Driessche 1974) have revealed that macronutrient fertilization induces a micronutrient dilution effect (Prevot and Ollagnier 1961, Veijalainen 1977) which can continue without visible growth disturbances (Bussler 1974, Raitio and Rantala 1977). It is noteworthy that the macronutrient (N, P, PK and NPK) fertilization treatments have interactions with the micronutrients and lower the foliar micronutrient contents in plants. For example PK- and NPK-fertilization combinations decrease the Scots pine's foliar boron (B)

content even to such an extent that the effect of NPK combination fertilization differed significantly from that of mere phosphorus (P) or mere potassium (K) fertilizations (Bingham et al. 1958, Schütte 1959, Bingham and Garber 1960, Appleton and Slow 1966, Bradford 1966, Albrektson et al. 1977, Veijalainen 1977, Braekke 1979).

The antagonistic effect on micronutrients i.e. the decrease of the foliar micronutrient content, resulting from macronutrient fertilization may occur in the soil (Hatcher et al. 1967), in the root (nutrient absorption) (Puustjärvi 1956, 1973) and in the plant (distribution of the nutrients to functional sites and nutrient mobility within the plant) (Olsen 1972, Oertli 1963, Epstein 1973). Nevertheless it is evident that plain macronutrient fertilization induces nutritional changes in plants and enhances nutritional disorders which result in susceptibility of abiotic and biotic damages that arise from unbalanced metabolic activities (Kurkela 1976, Epstein 1972, Gauch 1972, Levitt 1972, Keller 1973, Bussler 1974, Nicholas and Egan 1975, Veijalainen 1977, Braekke 1979, Aronsson 1980).

11. Foliar nutrient analysis of Scots pine

Different plant species have their own characteristic optimum nutrient requirements. The optimum and deficiency levels of mineral nutrition concentrations of Scots pine foliage are shown in Table 1.

The needle sample for nutrient analysis is taken from the last years lateral macroshoot from the southern side of the tree. The foliar nutrient analysis gives a general view of the tree's nutritional status. One must bear in mind that various nutrients have interactions. Thus it has become necessary to compare the ratios of various nutrients eg. N/P ratios to detect abnormalities.

Table 1. Optimum and deficiency levels of Scots pine foliar nutrient contents.

Taulukko 1. Männyn neulasten ravinnepitoisuuksien optimi- ja puutostasot. (Puustjärvi 1965, Paarlanti ym. 1971, Veijalainen 1977, Paavilainen 1979, Pietiläinen 1980).

	N	P	K	Mg	Mn	Fe	Zn	Cu	B
	%	mg/g	mg/g	mg/g	µg/g	µg/g	µg/g	µg/g	µg/g
optimum <i>optimi</i>	>1,4	1,8—2,1	4,5—6,0	—	—	—	—	3—6	8—35
critical range* <i>krüittinen raja</i>	1,2—1,4	1,4—1,8	3,5—4,5	0,8	70—400	40—100	25—40	2—3	3—8
deficiency** <i>puutos</i>	<1,2	<1,4	<3,5	—	—	—	—	<2	<3

* critical range = retardation of growth, fertilization recommended
*krüittinen raja kasvun hidastunut, lannoitus suositeltava*** deficiency = nutrient deficiency
puutos = nutritional disorders, fertilization required
= *ravinnepuutos, vaatii lannoituksen*— numeric value not available
numeerinen arvo puuttuu

Furthermore it is always suggestable to check to environmental conditions such as growth site, drainage, flooding etc., which effect the nutrient absorbtion in the roots. The nutrient uptake may be hindered by an change of the ionization state of compounds or by slowed metabolic activities of the root.

12. Mineral nutrient disorders in Scots pine

Nutritional deficiencies show some characteristic symptoms in the phenotype of the pine. Most of the deficiency symptoms are actually a combination of several interactions that result from a basic nutritional disorder. In the following a few of the common phenotypic features of nutrient disorders in Scots pine are encountered.

Nitrogen (N) deficiency is common in pines growing on peatlands with naturally low nitrogen and phosphorus levels. The pines are stunted. The needles are short and pale yellow. Yellowing is equally strong in all of the shoot's needles. High nitrogen levels induce large, dark blue-green needles. The tissues are improperly lignified and the cold resistance is poor. The growth of the trees continue into late autumn, when the apical shoots freeze easily (Reinikainen 1968, Huikari and Paavilainen 1972).

The phosphorus (P) content is usually low in peatlands and the natural phosphorus is strongly combined organically and to iron and aluminum as complex molecules, which results in very scarce usable phosphorus.

Phosphorus deficiency appears as slender shoots, varying degrees of necrosis in the tips of the needles and abscission of the last year's needles, and twisted stems and branches. Severe deficiency result in freezing damages of the apical shoots (Reinikainen 1968, Huikari and Paavilainen 1972).

Optimum potassium (K) levels improve frost hardiness and resistance towards fungal diseases (Kurkela 1976). Potassium contents are low in thick layered and nitrogen rich peatlands.

A potassium deficient pine's new needles are green and the old needles are yellow (chlorotic) from their tips. As the deficiency becomes more severe the older needles become necrotic from their tips and tip dieback of apical shoot becomes frequent (Reinikainen 1968, Huikari and Paavilainen 1972).

Magnesium (Mg) deficiency appears somewhat like that of potassium: (the tips of) the needles are yellowish or orange (Jamalainen 1968).

Manganese (Mn) deficiencies are extremely rare on Finnish peatlands. The deficiency retards elongation and in severe cases it results in shoot dieback. Younger needles are chlorotic, light green, and the older needles are brown and necrotic (Stone 1968).

In Finnish peatland pine stands iron (Fe) deficiency cases have not been encountered. The deficiency symptoms are the following: apical growth is retarded, the young needles are chlorotic, short twisted and necrotic, whereas older needles are green or grey green (Stone 1968).

Zinc (Zn) deficiency results in retarded growth and shoot dieback. Rosetting and chlorosis of the needles are common symptoms. Some of the deficiencies in pines have been suspected to be caused by the lack of zinc (Stoate 1950, Stone 1968).

In copper (Cu) deficient trees crooked and down bent pendulous leaders are common. Growth retards and tip dieback is frequently encountered. Needles have tip burns and chlorotic tips. Some of the needles may be fused and twisted at the shoot apex. The general appearance of the tree is branchy. This far in Finland it has not been demonstrated that copper alone has caused a deficiency state (Will 1972, Veijalainen 1980, 1981).

Boron (B) deficiency results in shoot and tip dieback. Bud dieback and disorders are frequent. Height growth is strongly retarded. Repeated dieback results in a bushy appearance of the tree. The needles are short and immature at the shoot apex and necrotic at their tips. Needles are commonly thick and distorted and may be fused. Rosetting results from retarded intercalary elongation. Boron deficiency has been encountered in Finnish peatland forest stands (Huikari 1974, Braekke 1977, Veijalainen 1980, 1981).

There is rather little information on molybdenum (Mo) deficiency symptoms. There are no cited symptoms on the apical leaders. Needles are blue green and long. Chlorotic needles are also encountered (Stone 1968).

As the previous macroscopic deficiency symptom review indicates it is rather difficult to distinguish the symptoms caused by one nutrient from those of the other nutrients. Microscopical studies have been carried out to find some specific symptoms but equally confusing result have turned out (Raitio and Rantala 1977, Raitio 1981). Nitrogen, phosphorus and potassium deficiencies have been shown with fertilization experiments (eg. Huikari 1952). In addition boron deficiencies have been clearly demonstrated with fertilization experiments (Braekke 1977, 1979, Veijalainen 1981). Copper and manganese have had a positive effect on growth disturbance. Zinc has shown no effect on growth or phenotypical deficiency symptoms (Veijalainen 1981).

13. Effect of boron on carbohydrate metabolism

The pentose phosphate shunt generates NADPH+H⁺ and ribose 5-phosphate in the cytosol. NADPH+H⁺ is used in reductive biosynthesis and ribose-5-phosphate used in RNA, DNA, and nucleotide coenzymes. Erythrose-4-phosphate is used to synthesize shikimic acid which is an important intermediate in the synthesis of aromatic aminoacids and other aromatic compounds such as phenol derivatives, lignins, indolacetic acid etc. (Gibbs 1959).

Lee and Arnoff (1967) have postulated that boron affects the activity of 6-phosphogluconate dehydrogenase by forming esters with the substrate 6-phosphogluconate. Boron thus interferes with the activity of the pentose phosphate shunt and affects significantly the carbohydrate metabolism (Weiser et al. 1964).

The effect of boron on the activity of 6-phosphogluconate dehydrogenase should be detectable in the end products which utilize intermediates of the pentose phosphate shunt in their synthesis. Rather extensive work has been done on the end products during the 1960s' and again during the recent years. Johnson and Albert (1967) noted that the first symptoms in boron deficiency were the decrease in RNA content and cessation of tomato root growth. Shkolnik et al. (1961), Shkolnik and Solojova (1961), Albert (1965), Shkolnik (1974), Timashov (1966), Johnson and Albert (1967) also noticed a decrease of RNA in boron deficient plants. Robertson and Loughman (1974) showed that boron deficiency reduced the rate of incorporation of phosphate into the nucleotides (Figure 3). Hundt et al. (1970) demonstrated the effect of boron deficiency on nucleic acid metabolism protein synthesis. Coke and Whittington (1968) as well as Shkolnik (1974) suggested that necrosis in the growing points of boron deficient plants is caused by auxin accumulation. Rajaratnam and Lowry (1974) also noticed increased auxin in boron deficient plants.

One of the most common features in boron deficient plants is the accumulation of phenol derivatives. Perkins and Arnoff (1956) identified chlorogenic acid and caffeic acid from several plants whereas coumarine,

vanilinic acid and ferulic acid were identified by Watanabe et al. (1964) and Rajaratnam and Lowry (1974). Lee and Arnoff (1967) and Walker (1973) suggested, that boron may form complexes not only with 6-phosphogluconate but also with the phenolic acids that result from the accelerated pentose phosphate shunt activity. An autocatalytic system may be formed as boron is combined into phenolic compounds to form phenol boric acids. Thus there is less boron for the inhibition of 6-phosphogluconate dehydrogenase and this results into a build up of phenolic compounds through the further accelerated phosphate shunt. Phenol boric acids that are formed from this kind of autocatalytic system form complexes with sugars easier than sugars with boric acid but phenylboric acid can only form a monodiol ester complex bond. Torssell (1956) obtained results that supported this postulation. Torssell (1956) has also suggested that arylboric acids are very active compounds and that the lipophilic group allows the complex to penetrate the cell membrane.

The results achieved from the metabolism of a number of boron deficient plants are similar and it is not difficult to correlate their anatomical and phenotypic deficiency symptoms with the known metabolic disorders. This far very little work has been done on the metabolism of boron deficient pines. The phenotypic and anatomic boron deficiency symptoms (Kolari 1979) are analogical with those of other plants. The most frequently encountered macrosymptoms in Scots pines are 1) shoot or tip dieback, 2) bud dieback or disorders, 3) resin flow from shoots or buds, 4) secondary leading shoots, 5) retarded growth, 6) repeated dieback and bushiness, 7) fascicle or lateral bud proliferation, 8) needles are often short or immature at the shoot apices, 9) necrotic at their tips, 10) yellow and shed at apex, 11) thick and distorted. The roots are reduced in size and number (Kolari 1979).

The microscopic deficiency symptoms in conifers are as follows (de Lanuza 1966 and Raitio and Rantala 1977). 1) The apical meristems are abnormal and cavities may be located in the growing points. 2) Hypotrophic

cells and cavities are encountered in the transfusion tissue of the needles. 3) The root's primary xylem fails to differentiate and 4) the break down of the central cylinder may occur resulting into cavities.

14. Purpose

Boron deficiency has been claimed to cause growth disturbances in Scots pine (Huikari 1974, Veijalainen 1975, Kolari 1979). The metabolic role of boron has not been studied in Scots pine. The scheme that was proposed by Lee and Arnoff (1967) was taken as the basic hypothesis in this work. It postulates that boron complexes with 6-phosphogluconate forming boric esters (Gauch and Dugger 1954). These boric esters can not be utilized by 6-phosphogluconate dehydrogenase as the unesterified 6-phosphogluconate is. Thus the enzyme activity is depressed and the pentose phosphate shunt activity is regulated by the inhibition of 6-phosphogluconate dehydrogenase. In boron deficient plants that enzyme activity is uncontrolled because boric ester complexes are not formed. At optimum boron concentrations 6-phosphogluconate dehydrogenase activity is controlled.

The purpose of this study was to elucidate the seasonal activity and the role of boron on 6-phosphogluconate dehydrogenase activity in the vegetative buds of phenotypically normal and growth disturbance Scots pines. The foliar nutrient contents were also studied.

Growth disturbances of various trees have been studied since 1976 in the Finnish Forest Research Institute in a special project.

The project has been studying the relations between forest trees and micronutrients. The Department of Peatland Forestry, the Department of Forests Protection and the Department of Forest Inventory and Yield of the Research Institute have participated in the growth disturbance project. Prof. Olavi Huikari (chairman), Ph.Lic. Antti Reinikainen and Bsc Heikki Veijalainen have directed the research of the project. This study was carried out at the Department of Botany, University of Oulu under the direction of Prof. Sirkka Kupila-Ahvenniemi. The manuscript was read by Prof. Sirkka Kupila-Ahvenniemi, Prof. Eero Paavilainen and Ph.D. Veikko Koski.

2. MATERIAL AND METHODS

21. Vegetative buds

Vegetative buds of Scots pine were collected from a forest fertilization experiment at Muhos (65°52'; 26°07'E). The small sedge open peatland was drained in 1933 and the pine seeds were sown in 1934. The stand was fertilized with 200 kg/ha Urea (46 %) and 500 kg/ha of Peatland Forest Fertilizer (10 % P—12 % K) in 1971. The ash fertilization 10 000 kg/ha was carried out in 1972. The height of the stand was 3—5 m in 1978.

The collections were made monthly on the following dates: 4th of September 1978, 4th of October 1978, 2nd of November 1978, 20th of January 1979, 9th of February 1979, 5th of March 1979, 4th of April 1979 and 2nd of May 1979. Each time buds were taken from the upper two thirds of the crown of three ash fertilized, three NPK-fertilized phenotypical normal and three NPK-fertilized growth disturbance pines (all together from 72 pines). The scales of the buds were removed in the laboratory. The remaining tissue was stored at -21 °C in small plastic bags and used later for enzyme activity measurements.

The stored frozen vegetative buds were thawed and 0,5 g of buds were weighed and ground for 10 min in a mortar with 1,0 g of sea sand and 10 ml of tris- HCl buffer of pH 7,6 in an ice bath. The obtained homogenates was pressed through a gauze. The turbid solution thus obtained was centrifuged at 12 000 g for 15 min at 4°C. The supernatant was tested for enzyme activity as was the resuspended and recentrifuged (12 000 g) pellet. The 6-phosphogluconate dehydrogenase activity was high in the supernatant and very low in the pellet. The grinding time of the buds was determined by measuring activities of the recentrifuged pellet supernatants. After 10 min grinding the 6-phosphogluconate dehydrogenase activity was negligible (modified from Sagisaka 1972, 1974).

22. Enzyme activity measurements

Three parallel 6-phosphogluconate activity measurements were done from each tree's bud sample. The 6-phosphogluconate dehydrogenase assay was carried out by conventional spectrophotometric methods as follows: The reaction mixture contained 2,6 μmoles of NADP⁺, 30 μmoles of MgCl₂ and 0,5 μmoles of 6-phosphogluconate, 150 μmoles of tris-HCl buffer of pH 7,6 and the bud supernatant (crude enzyme) 0,5 ml,

in a total volume of 4,0 ml. The absorbance of the crude enzyme was measured in a Hitachi spectrophotometer 100—40 at wavelength 340 nm against a blank, which was composed of the same reagents except for the crude enzyme (modified from Sagisaka 1972, 1974).

The relative enzyme activity in the crude enzyme was expressed as the evolution of NADPH+H⁺, which has an absorption change after reduction at wavelength 340 nm.

The crude enzyme of the buds that were collected in September was tested for boron and 6-phosphogluconate dehydrogenase interaction in the previously described reaction mixture with 5 ppm, 10 ppm and 15 ppm boron concentrations. All experiments were carried out in triplicates.

23. Needle analysis

The needle samples were collected in February 1980 from the same stands as the buds. The foliar sample was taken from the last years lateral growth from the southern side of the tree.

Needles were taken from six trees and mixed to obtain an average nutritional status of the fertilization stands (Veijalainen 1978).

The needles were dried at 108 °C to determine the dry weight (Dickmann and Kozłowski 1969b). Nitrogen (N) was analysed by the micro-Kjedahl method, phosphorus (P) and boron (B) spectrophotometrically. Potassium (K), magnesium (Mg), calcium (Ca), manganese (Mn), zinc (Zn) and copper (Cu) were measured with an atomic absorption spectrophotometer. The specific analytical methods were carried out as described in the Finnish Forest Research Institute nutrient analyses which are combined in Halonen and Tulkki (1981).

24. Deficiency symptoms

Boron deficiency symptoms (Kolari 1979) were encountered in the study area. Because of the difficulties in the interpretation of the symptoms their relative frequencies were not studied throughly. Rather the symptoms were used to locate on area of boron deficiency. The deficiency was confirmed with the foliar analysis.

3. RESULTS

31. Dry weight of the vegetative buds

The dry weight of the buds was rather constant through out the research period. The dry weight of the vegetative buds of the NPK-fertilized growth disturbance pines differed significantly from the other two classes in October. Also the dry weight of the vegetative buds of the NPK-fertilized phenotypically normal pines differed significantly from those of the other classes in May (Figures 1 a, 1 b and 1 c).

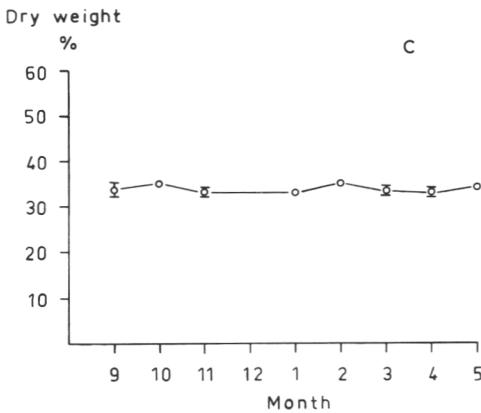
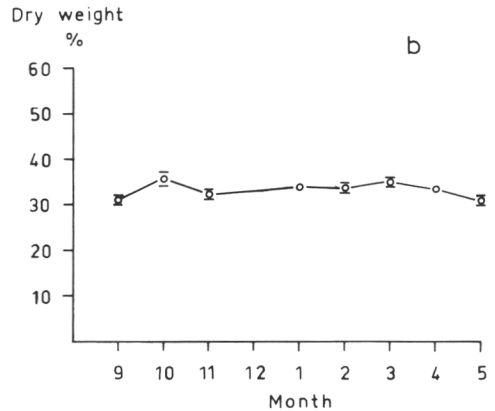
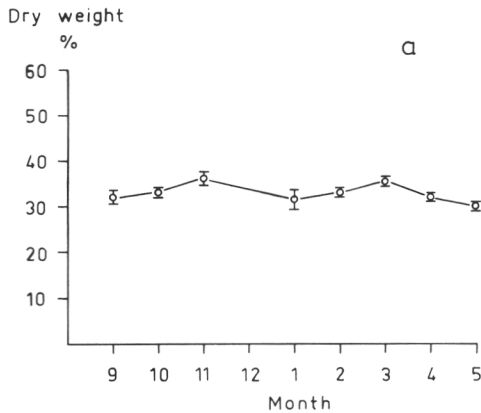


Figure 1. a) Dry matter content of the vegetative buds from ash fertilized pines. b) Dry matter content of the vegetative buds from NPK-fertilized growth disturbance pines. c) Dry matter content of the vegetative buds from NPK-fertilized phenotypical normal pines ($t_{05} \cdot S\bar{x} = 95\%$ confidence level).

Kuva 1. a) Tubkalla lannoitetun puuston vegetatiivisten silmujen kuiva-ainepitoisuus. b) NPK-lannoitetun kasvuhäiriöpuuston vegetatiivisten silmujen kuiva-ainepitoisuus. c) NPK-lannoitetun ilmasultaan normaalin puuston vegetatiivisten silmujen kuiva-ainepitoisuus ($t_{05} \cdot S\bar{x} = 95\%$ luotettavuustaso).

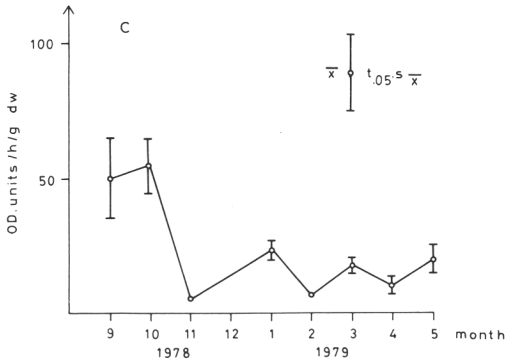
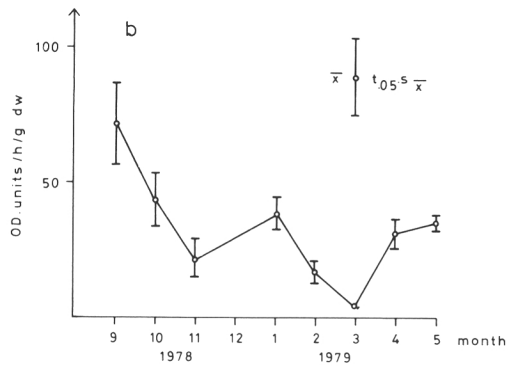
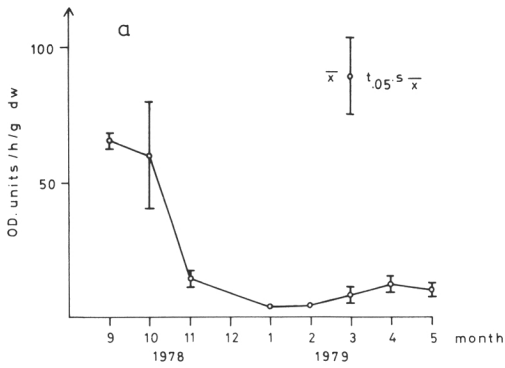


Figure 2. a) Seasonal 6-phosphogluconate dehydrogenase activity of the vegetative buds from ash fertilized pines. b) Seasonal 6-phosphogluconate dehydrogenase activity of the vegetative buds from NPK-fertilized phenotypical normal pines. c) Seasonal 6-phosphogluconate dehydrogenase activity of the vegetative buds from NPK-fertilized growth disturbance pines ($t_{0.05} \cdot \bar{S}x = 95\%$ confidence level).

Kuva 2. a) Tuhkalla lannoitetun puuston vegetatiivisten silmujen 6-fosfoglukonaatti dehydrogenaasiaktiivisuuden vuotuinen vaihtelu. b) NPK-lannoitetun ilmi-asultaan normaalin puuston vegetatiivisten silmujen 6-fosfoglukonaatti dehydrogenaasiaktiivisuuden vuotuinen vaihtelu. c) NPK-lannoitetun kasvuhäiriöpuuston vegetatiivisten silmujen 6-fosfoglukonaatti dehydrogenaasiaktiivisuuden vuotuinen vaihtelu ($t_{0.05} \cdot \bar{S}x = 95\%$ luotettavuustaso).

trees contained very high levels of dehydrogenase activity in September and in October. The dehydrogenase activity decreased sharply in October as hardening occurred and remained low through the wintering phase. In March the dehydrogenase activity started to rise. The first statistical difference between wintering buds (February) and the buds that had commenced growth occurred in March. In newly grown shoot the enzyme activities were not measured (Figure 2 a).

In the phenotypical normal NPK-fertilized pine buds the dehydrogenase activity was high during the early autumn. During the wintering period and onset of growth it diverged from that of the buds of ash fertilized pines by remaining rather high. The activity was at its minimum in March and subsequently as the buds resumed their growth the dehydrogenase activity was three times higher than that of the ash fertilized trees (Figure 2 b).

The buds of NPK-fertilized growth disturbance pines had dehydrogenase activities that resembled those of the NPK-fertilized phenotypical normal trees though the level of the activities during midwinter and spring were not as high (Figure 2 c).

33. Crude enzyme and boron interaction

As boron was added to the reaction mixtures containing bud extracts from the ash fertilized trees there was an inhibitory effect on the enzyme activity. The inhibitory effect was stronger with higher boron concentrations (Figure 3 a).

When boron was added to the bud extracts of the NPK-fertilized phenotypical normal trees an inhibitory effect also occurred. It was noteworthy that the enzyme

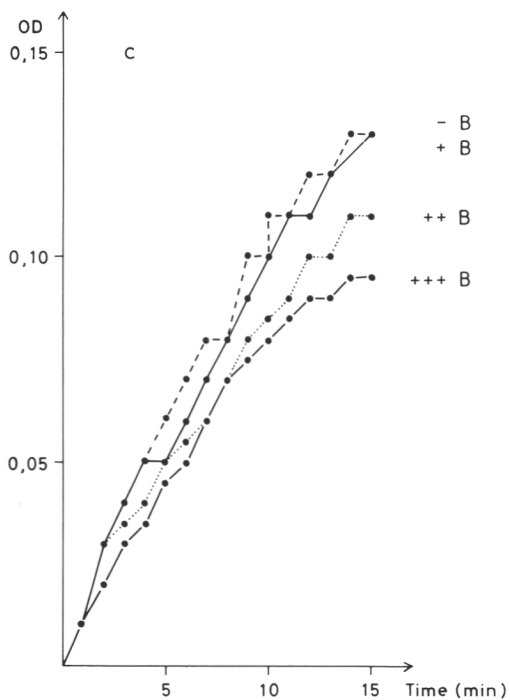
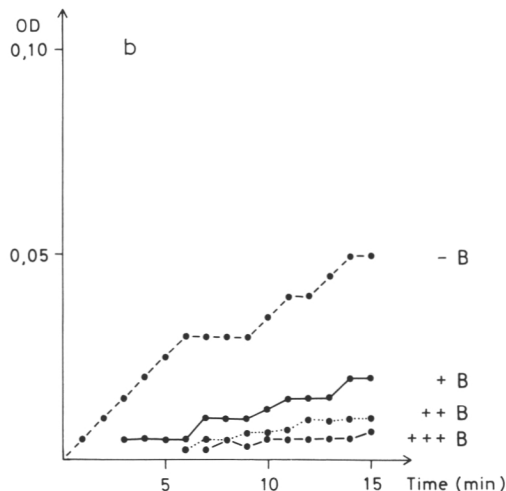
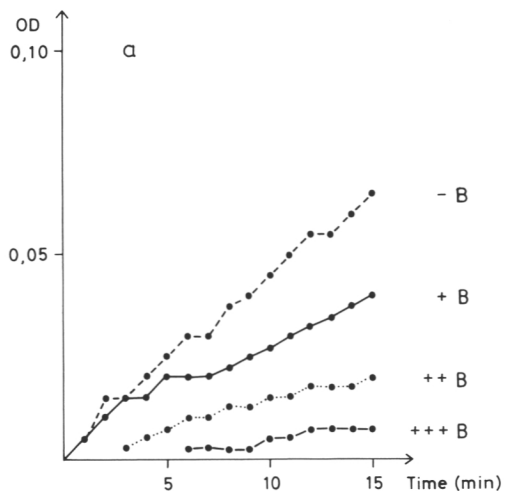


Figure 3. a) Effect of boron on 6-phosphogluconate dehydrogenase activity of the vegetative buds of ash fertilized pines in September. The foliar boron content was $38,06 \mu\text{g/g}$ dry weight ($-B$ = no boron added, $+B$ = 5 ppm of boron, $++B$ = 10 ppm boron, $+++B$ = 15 ppm of boron in reaction mixture). b) Effect of boron on 6-phosphogluconate dehydrogenase activity of the vegetative buds of growth disturbance pines in September. The foliar boron content was $2,13 \mu\text{g/g}$ dry weight. ($-B$ = no boron added, $+B$ = 5 ppm of boron, $++B$ = 10 ppm of boron and $+++B$ = 15 ppm of boron in the reaction mixture). c) Effect of boron on 6-phosphogluconate dehydrogenase activity of the vegetative buds of phenotypical normal pines in September. The foliar boron content was $2,90 \mu\text{g/g}$ dry weight. ($-B$ = no boron added, $+B$ = 5 ppm of boron, $++B$ = 10 ppm of boron and $+++B$ = 15 ppm of boron in the reaction mixture).

Kuva 3. a) Boorin vaikutus tuhkalla lannoitetun puuston vegetatiivisten silmujen 6-fosfoglukonaatti dehydrogenaasiaktiivisuuteen syyskuussa. Neulasten booripitoisuus oli $38,06 \mu\text{g/g}$ kuiva-ainetta ($-B$ = reaktioseokseen ei lisätty booria, $+B$ = reaktioseokseen lisättiin 5 ppm booria, $++B$ = lisättiin 10 ppm booria ja $+++B$ = lisättiin 15 ppm booria). b) Boorin vaikutus NPK-lannoitetun kasvuhäiriöpuuston vegetatiivisten silmujen 6-fosfoglukonaatti dehydrogenaasiaktiivisuuteen syyskuussa. Neulasten booripitoisuus oli $2,13 \mu\text{g/g}$ kuiva-ainetta ($-B$ = reaktioseokseen ei lisätty booria, $+B$ = reaktioseokseen lisättiin 5 ppm booria, $++B$ = lisättiin 10 ppm booria ja $+++B$ = lisättiin 15 ppm booria). c) Boorin vaikutus ilmasultaan normaalin puuston vegetatiivisten silmujen 6-fosfoglukonaatti dehydrogenaasiaktiivisuuteen syyskuussa. Neulasten booripitoisuus oli $38,06 \mu\text{g/g}$ kuiva-ainetta ($-B$ = reaktioseokseen ei lisätty booria, $+B$ = reaktioseokseen lisättiin 5 ppm booria, $++B$ = lisättiin 10 ppm booria ja $+++B$ = lisättiin 15 ppm booria).

Table 2. Average foliar nutrient contents from the Scots pine stands used in the study.
 Taulukko 2. Tutkimuksessa käytettyjen puustojen neulasten keskimääräiset ravinnepitoisuudet.

	N %	P mg/g	K mg/g	Ca mg/g	Mg mg/g	Cu µg/g	B µg/g	Si mg/g	N/P	N/K
Control <i>Kontrolli</i>	1,37	0,86	2,32	1,39	1,21	3,44	8,09	1,76	15,9	5,9
$t_{0,05} s_x$	0,098	0,045	0,235	0,096	0,111	0,546	2,011	0,123		
Control disturbance <i>Kontrolli häiriö</i>	1,35	0,90	2,37	1,94	1,14	3,45	7,76	0,53	15,0	5,7
$t_{0,05} s_x$	0,145	0,076	0,384	0,232	0,073	0,556	3,572	0,085		
NPK normal <i>NPK normaali</i>	1,25	1,30	3,51	1,70	1,21	2,86	2,90	1,60	9,6	3,6
$t_{0,05} s_x$	0,098	0,090	0,506	0,217	0,116	1,164	0,588	0,493		
NPK disturbance <i>NPK häiriö</i>	1,21	1,33	3,44	2,10	1,04	3,21	2,13	0,94	9,0	3,5
$t_{0,05} s_x$	0,062	0,178	0,463	0,327	0,179	1,810	0,229	0,458		
Ash <i>Tubka</i>	1,26	1,41	4,33	2,34	1,71	2,43	38,06	1,50	8,9	2,9

activity of the buds was twice as high as that of the ash fertilized trees and that 10 ppm of boron had to be added before a notable inhibition took place (Figure 3 c).

The enzyme activity of the bud extract of the NPK-fertilized growth disturbance pine was somewhat lower than in the ash fertilized tree buds. The inhibitory effect of boron was strong (Figure 3 b).

The high enzyme activity of the vegetative buds from the phenotypically normal trees suggested that there was more pentose phosphate shunt activity than in the other groups. This also implied that the substrate ie. 6-phosphogluconate concentration was higher than in the other.

34. Foliar nutrient contents

The average foliar nutrient content of ash fertilized, NPK-fertilized growth disturbance and phenotypically normal trees are shown in Table 2.

When comparing the unfertilized and NPK-fertilized trees it was evident that the fertilization had caused significant rises in the levels of the foliar phosphorus (P) and potassium (K). The most drastic change resulting from fertilization had occurred in the foliar boron (B) levels which had decreased approximately 5 µg/g dry weight. The nitrogen content of the fertilized trees had also dropped somewhat.

One the unfertilized and fertilized plots the silicon content of the phenotypically normal trees was higher than in the growth disturbance trees.

The main differences between the ash- and NPK-fertilized trees were in the foliar phosphorus (P), potassium (K) and boron (B) contents (Table 1).

4. DISCUSSION

The study on the seasonal variation of 6-phosphogluconate dehydrogenase of the buds of the Scots pine revealed that the enzyme activity was highest in September and lowest during midwinter. In October as the temperature sank and the onset of dormancy occurred the enzyme activity decreased and was low through out the winter. The first notable increase in the activity occurred in March.

The high activity in autumn coincided with the period of lignification (Dickmann and Kozlowski 1969). The following steep decrease in the enzyme activity occurred at the onset of dormancy (Kupila-Ahvenniemi 1966, Kupila-Ahvenniemi and Pihakaski 1966) and coincided with a number of changes at the subcellular level (Kupila-Ahvenniemi and Hohtola 1980). During dormancy the enzyme activity was uniformly low. It was also noteworthy that there was some enzyme activity through out dormancy as was also observed by Kupila-Ahvenniemi et al. (1978) in the case of RNase activity. The first signs of regained enzyme activity occurred in March.

The 6-phosphogluconate dehydrogenase activity of the NPK-fertilized phenotypical normal, as well as growth disturbance pine buds behaved as those of the ash fertilized pine buds during autumn and the onset of dormancy. In midwinter the enzyme activity rose very abruptly after the warm period in January (Meteorological yearbook 1979). The rise in the enzyme activity could be attributed to improper dormancy. Samples from the phenotypical normal trees showed a drop in March. The final break of dormancy occurred in April. In the growth disturbance trees the enzyme activity fluctuated from month to month.

The level of the enzyme activity differed in the three types of the trees. It was lowest in the ash fertilized pine buds and highest in the NPK-fertilized phenotypical normal pine buds. The study on the seasonal changes of the enzyme activity gave some

evidence that the wintering processes of the growth disturbance area pines were not properly regulated. This may result in frost damages at cellular levels during the winter, especially if the cold period is broken by a warm spell and in spring as the pines enter the growth phase.

When it was established that the enzyme activities were highest in autumn 6-phosphogluconate and boron interaction was studied in crude enzyme supernatants of the three pine classes. The results obtained were in accordance with those of Lee and Arnoff (1967) (Figure 3 a, b and c). In the ash fertilized and the growth disturbance Scots pine buds the enzyme activity was of the same magnitude. The inhibitory effect that was achieved with 5 ppm boron concentration was approximately the same in both cases (Figure 3 a and 3 b).

The enzyme activity of the buds from phenotypical normal Scots pine was 2–5 times higher than in the others. A clear inhibition was obtained with 10 ppm boron concentration (Figure 3 c).

It could be speculated that the differences in the level of enzyme activities resulted either from the substrate (6-phosphogluconate) and/or the boron concentration (Lee and Arnoff 1967). The difference in the enzyme activity could not be correlated to foliar boron concentrations.

It should be stressed that care should be taken with the interpretation of the results since the enzymatic activity studies were done with crude enzyme fractions and the scatter between samples was immense.

The nutrient analysis revealed that the N/P and N/K ratios of the unfertilized trees were too high and the pines suffered from a phosphorus and potassium deficiency (Puustjärvi 1965, Paarlahti et al. 1971). This deficiency was overcome by the NPK-fertilization. The NPK-fertilization induced a boron dilution effect (compare Veijalainen 1977), which has been suggested to be the main cause of growth disturbances. The

cases where boron fertilization has cured a growth disturbance are reported by Braekke 1979 and Veijalainen 1980. It was also interesting that the silicon contents of the unfertilized and fertilized growth disturbance trees were significantly lower than in the others. The NPK-fertilization had improved the silicon content of the fertilized growth disturbance pines.

It was obvious that the growth disturbance area trees do not winter properly and the inadequate dormancy enhanced frost damage (compare Aronsson 1980). It also seems evident that the poor hardening is

caused by improper enzymatic regulation. Possibly this allows a build up of phenolic or some other compounds, which enhance necrosis of the buds. Apparently boron through its effect on the 6-phosphogluconate dehydrogenase and pentose phosphate shunt activity is one of the factors causing growth disturbances in pine.

On the basis of the present results the cause of the disturbance can not be specified to anyone nutrient. More likely the results indicated that the disturbance results from a disorder of several nutrients.

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SELOSTE

Kasvuhäiriöalueen männyn vegetatiivisten silmujen 6-fosfoglukonaattidehydrogenaasiaktiivisuus ja neulasten ravinnepitoisuus

Tutkimuksessa oli tarkoitus selvittää boorin ja 6-fosfoglukonaattidehydrogenaasin osuutta pentosifosfaattireitin säätelyssä männyn vegetatiivisissa silmuissa. Tutkimusmateriaali koostui NPK-lannoitettujen ilmiäsultaan normaalien ja kasvuhäiriöpuiden sekä tuhkalannoitettujen puiden vegetatiivisista silmuista.

Silmujen kuivapainot ja ravinnepitoisuudet määritettiin. Vuotuinen 6-fosfoglukonaattidehydrogenaasiaktiivisuus sekä 6-fosfoglukonaattidehydrogenaasin ja boorin keskinäinen vaikutus mitattiin silmujen raakaentsyymifaktiosta.

Silmujen kuivapainoissa oli vähäisiä muutoksia jakson aikana. Tilastolliset erot sattuivat loka-kuulle NPK-lannoitetuissa fenotyypiltään normaaleissa ja kasvuhäiriöpuissa huhtikuulle verrattuna tuhkalannoitettujen puiden silmuihin (kuva 1 a, 1 b ja 1 c).

Silmujen 6-fosfoglukonaattidehydrogenaasi, aktiivisuus oli korkeimmillaan syksyllä ja alhaisin talvella lepokauden aikana. Merkittävä aktiivisuuden nousi tapahtui keväällä kasvukauden alussa. Merkittävää oli, että ilmiäsultaan normaalien ja kasvuhäiriöpuiden entsyymiaktiivisuus oli kor-

keampi kuin tuhkalannoitettujen puiden. Ilmasultaan normaalien ja kasvuhäiriöpuiden aktiivisuus nousi lepokauden aikana tammikuussa olleen lämpimän jakson jälkeen (kuva 2 a, 2 b ja 2 c).

Boorin ja 6-fosfoglukonaattidehydrogenaasin keskinäistä vaikutusta tutkittiin syyskuussa kerättyjen silmujen raakaentsyymifraktiosta. Fysiologisilla booripitoisuuksilla (5 ppm, 10 ppm ja 15 ppm) oli inhiboiva vaikutus 6-fosfoglukonaattidehydrogenaasin aktiivisuuteen raakanetsyymifraktiossa (kuva 3 a, 3 b ja 3 c).

Tutkimuksesta kävi ilmi, että silmujen vesipitoisuuksissa tapahtuu muutoksia. Talvilepo keskeytyi kasvuhäiriöalueen puissa. Fysiologiset booripitoisuudet inhiboivat 6-fosfoglukonaattidehydrogenaasiaktiivisuutta. Ravinnepitoisuudet ovat samanlaiset kuin Veijalaisen 1977 esittämässä tutkimustuloksissa (taulukko 2).

Tulosten perusteella ei voi nimetä yhtä ravinnetta kasvuhäiriön syyksi, vaan pikemminkin tulokset viittaavat, että häiriöt johtuvat usean ravintein epäsuhteista.

PIETILÄINEN, P. 1984. Foliar nutrient content and 6-phosphogluconate dehydrogenase activity in vegetative buds of Scots pine on a growth disturbance area. Seloste: Kasvuhäiriöalueen männyn vegetatiivisten silmujen 6-fosfoglukonaatti dehydrogenaasiaktiivisuus ja neulasten ravinnepitoisuus. Commun. Inst. For. Fenn. 123: 1—18.

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A study on the seasonal activity and the role of boron on 6-phosphogluconate dehydrogenase activity in the vegetative buds of ash fertilized and NPK-fertilized growth disturbance Scots pines (*Pinus sylvestris*). The foliar nutrient contents were also studied.

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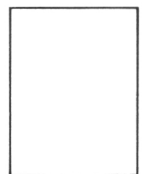
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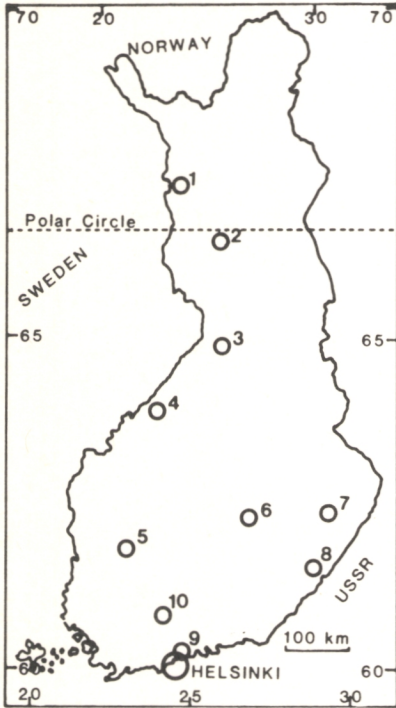
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FACTS ABOUT FINLAND

Total land area: 304 642 km² of which 60—70 per cent is forest land.

Mean temperature, °C:	Helsinki	Joensuu	Rovaniemi
January	-6,8	-10,2	-11,0
July	17,1	17,1	15,3
annual	4,4	2,9	0,8

Thermal winter (mean temp. < 0°C):	Helsinki	Joensuu	Rovaniemi
	20.11.—4.4.	5.11.—10.4.	18.10.—21.4.

Most common tree species: *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Betula pubescens*



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- 123 Pietiläinen, P. Foliar nutrient content and 6-phosphogluconate dehydrogenase activity in vegetative buds of Scots pine on a growth disturbance area. Seloste: Kasvuhäiriöalueen männyn vegetatiivisten silmujen 6-fusoglukonaatti dehydrogenaasiaktiivisuus ja neulasten ravinnepitoisuus.

