SILVA FENNICA

Vol. 31(4), 1997

SILVA FENNICA
a quarterly journal of forest science

Publishers The Finnish Society of Forest Science
Finnish Forest Research Institute

Editors Editor-in-chief Eeva Korpilahti
Production editors Tommi Salonen, Seppo Oja

Editorial Office Unioninkatu 40 A, FIN-00170 Helsinki, Finland
Phone +358 9 857 051, Fax +358 9 625 308, E-mail silva.fennica@metla.fi,
WWW http://www.metla.fi/publish/silva/

Managing Board Erkki Annila (Finnish Forest Research Institute), Jyrki Kangas (Finnish Forest Research Institute), Esko Mikkonen (University of Helsinki), Lauri Valsta (Finnish Forest Research Institute), Harri Vasander (University of Helsinki), and Seppo Vehkamäki (University of Helsinki)

Editorial Board
Per Angelstam (Grimsö Wildlife Research Station, Sweden)
Julius Boutelje (Swedish University of Agricultural Sciences, Sweden)
Finn H. Brække (Swedish University of Agricultural Sciences, Sweden)
J. Douglas Brodie (Oregon State University, USA)
Raymond L. Czaplewski (USDA Forest Service, USA)
George Gertner (University of Illinois, USA)
Martin Hubbes (University of Toronto, Canada)
William F. Hyde (Virginia Polytechnic Institute and State University, USA)
Jochen Kleinschmit (Lower Saxony Forest Research Institute, Germany)
Michael Köhl (Dresden University of Technology, Germany)
Noel Lust (University of Gent, Belgium)
Bo Långström (Swedish University of Agricultural Sciences, Sweden)
William J. Mattson (USDA Forest Service, USA)
Robert Mendelsohn (Yale University, USA)
Hugh G. Miller (University of Aberdeen, United Kingdom)
John Pastor (University of Minnesota, USA)
John Sessions (Oregon State University, USA)
Jadwiga Sienkiewicz (Environment Protection Institute, Poland)
Richard Stephan (Federal Research Centre for Forestry and Forest Products, Germany)
Elon S. Verry (USDA Forest Service, USA)
A. Graham D. Whyte (University of Canterbury, New Zealand)
Claire G. Williams (Texas A&M University, USA)

Aim and Scope Silva Fennica publishes original research articles, critical review articles, research notes reporting preliminary or tentative results, and discussion papers. The journal covers all aspects of forest research, both basic and applied subjects. The scope includes forest environment and silviculture, physiology, ecology, soil science, entomology, pathology, and genetics related to forests, forest operations and techniques, inventory, growth, yield, quantitative and management sciences, forest products, as well as forestry-related social, economic, information and policy sciences.

SILVA FENNICA

a quarterly journal of forest science

Vol. 31(4), 1997

The Finnish Society of Forest Science

The Finnish Forest Research Institute

SILVA FENNICA
a quarterly journal of forest science

Publishers The Finnish Society of Forest Science
Finnish Forest Research Institute

Editors Editor-in-chief Eeva Korpilahti
Production editors Tommi Salonen, Seppo Oja

Editorial Office Unioninkatu 40 A, FIN-00170 Helsinki, Finland
Phone +358 9 857 051, Fax +358 9 625 308, E-mail silva.fennica@metla.fi,
WWW http://www.metla.fi/publish/silva/

Managing Board Erkki Annila (Finnish Forest Research Institute), Jyrki Kangas (Finnish Forest Research Institute), Esko Mikkonen (University of Helsinki), Lauri Valsta (Finnish Forest Research Institute), Harri Vasander (University of Helsinki), and Seppo Vehkamäki (University of Helsinki).

Editorial Board Per Angelstam (Grimsö Wildlife Research Station, Sweden)
Julius Boutelje (Swedish University of Agricultural Sciences, Sweden)
Finn H. Brække (Swedish University of Agricultural Sciences, Sweden)
J. Douglas Brodie (Oregon State University, USA)
Raymond L. Czaplewski (USDA Forest Service, USA)
George Gertner (University of Illinois, USA)
Martin Hubbes (University of Toronto, Canada)
William F. Hyde (Virginia Polytechnic Institute and State University, USA)
Jochen Kleinschmit (Lower Saxony Forest Research Institute, Germany)
Michael Köhl (Dresden University of Technology, Germany)
Noel Lust (University of Gent, Belgium)
Bo Långström (Swedish University of Agricultural Sciences, Sweden)
William J. Mattson (USDA Forest Service, USA)
Robert Mendelsohn (Yale University, USA)
Hugh G. Miller (University of Aberdeen, United Kingdom)
John Pastor (University of Minnesota, USA)
John Sessions (Oregon State University, USA)
Jadwiga Sienkiewicz (Environment Protection Institute, Poland)
Richard Stephan (Federal Research Centre for Forestry and Forest Products, Germany)
Elon S. Verry (USDA Forest Service, USA)
A. Graham D. Whyte (University of Canterbury, New Zealand)
Claire G. Williams (Texas A&M University, USA)

Aims and Scope Silva Fennica publishes original research articles, critical review articles, research notes reporting preliminary or tentative results, and discussion papers. The journal covers all aspects of forest research, both basic and applied subjects. The scope includes forest environment and ecology, physiology, biology, soil science, entomology, pathology, and genetics related to forests, forest operations and techniques, inventory, growth, yield, quantitative and management sciences, forest products, as well as forestry-related social, economic, information and policy

Critical Needle Potassium Concentrations Indicated by Diamine Putrescine in Norway Spruce Growing on Peat Soils

Seppo Kaunisto and Tytti Sarjala

Kaunisto, S. & Sarjala, T. 1997. Critical needle potassium concentrations indicated by diamine putrescine in Norway spruce growing on peat soils. Silva Fennica 31(4): 383–390.

Dormant needles from 129 Norway spruce trees from the 2nd and 3rd topmost whorls were collected from spruce stands locating fairly close to each other. Tree height varied from 8 to 25 metres. Trees with and without visual potassium deficiency symptoms in needles were selected and analyzed for nitrogen, phosphorus, potassium, magnesium, boron, copper, zinc, and 3 free polyamines putrescine, spermine and spermidine. The concentrations of all the analyzed nutrients ranged from deficient to satisfactory levels. Free putrescine, spermidine and spermine concentrations in the current needles had a wide variation between the trees. Spermidine had a positive and spermine a negative correlation with potassium. Putrescine had a strong negative correlation with potassium with statistically significant increase in putrescine starting at potassium concentrations below 5.4 mg/g dry weight. The regression between putrescine and potassium changed from a linear to a non-linear form at the potassium concentration of 4.2–4.6 mg/g dry weight representing a severe K deficiency limit. The corresponding K/P ratio was 2.6–2.7. Extremely low phosphorus concentrations ($P < 1.0$ mg/g) lowered putrescine concentrations, but otherwise the relationships between putrescine, spermidine or spermine and potassium concentrations were unaffected by tree nutrition. At adequate potassium levels the putrescine concentrations were only slightly lower in trees taller than 20 metres than in trees of 8–16 metres height. The results show that the needle putrescine concentration can be used quite reliably for describing potassium nutrition of Norway spruce in varying nutritional and tree size conditions.

Keywords potassium, *Picea abies*, nutrition, deficiency, free polyamines, stress, nutrient balance

Authors' address Finnish Forest Research Institute, Parkano Research Station, FIN-39700 Parkano, Finland **Fax** +358 3 443 5200 **E-mail** seppo.kaunisto@metla.fi

Received 29 November 1996 **Accepted** 19 May 1997

1 Introduction

Potassium is one of the nutrients often limiting tree growth on peatlands. Potassium deficiency may cause quite a sudden growth reduction and even lead to tree death (Kaunisto 1989). Therefore it would be most important to find methods for estimating the potassium nutrition status and the deficiency limit of trees growing on peat soils before the growth reduction and lethal consequences occur.

Foliar nutrient analysis as a means for estimating the nutritional status of spruce has been used since the 1940´s (Lundegårdh 1941, Leyton 1948, Aaltonen 1950). The published data is mostly from spruce stands on mineral soils and only few from peatland stands (Holmen 1964, Paavilainen 1975). The estimation of deficiency limits for spruce has mainly been based on results from different fertilization trials (Paavilainen 1975) and analyses comparing normal-looking trees and trees having different discoloration symptoms. Recently, also growth has been used as a deficiency indicator (Veijalainen personal communication).

Potassium deficiency limits for pine on peat soils have been well described (Paarlahti et al. 1971, Sarjala and Kaunisto 1993). The needle putrescine concentration has been used successfully for estimating potassium deficiency limits in Scots pine (acute potassium deficiency K < 3.5 mg/g dw) and has been shown to correlate negatively with the potassium concentrations in pine needles (Sarjala and Kaunisto 1993, Sarjala 1996, Sarjala and Kaunisto 1996). Putrescine is one of the polyamines which are polycationic ubiquitous molecules found in almost every cell compartment. They are involved in a whole series of cellular events concerned with growth and differentiation (Egea-Cortines and Mizrahi 1991). Putrescine is one of the common polyamines in plants and has been reported to respond to various stresses (Flores 1991). The accumulations of putrescine in Scots pine needles turned to non-linear when the potassium concentration approached the deficiency limit (Sarjala and Kaunisto 1993).

The aim of the study was to define the critical levels of the needle potassium concentration in Norway spruce by using the same method as earlier for Scots pine (Sarjala and Kaunisto 1993) by comparing the linear and non-linear regression between putrescine and potassium within a wide range of needle potassium concentrations. Because putrescine was found to indicate the potassium nutrition of Scots pine, the method was assumed to be applicable also to Norway spruce.

2 Material and Methods

2.1 Site Description and Sampling

The material was collected from an old drainage experiment area, Jaakkoinsuo, which was drained for the first time in 1909. Originally the sites represented sedge and herbrich pine and spruce mires, but have changed into transformed *Vaccinium myrtillus* sites and were growing pure spruce forests at the time of sampling. The sites had a fairly shallow peat layer; on six sampling points < 20 and on the others mainly 35–60 cm averaging 40 cm.

Originally, the needle samples were collected separately from 99 individual trees on six unfertilized permanent sample plots in January, 1994. Tree height varied mostly between 8–15 m (72 trees, age 35–50 years), but some were over 20 metres tall (27 trees, age 70–80 years). Because only six trees represented needle potassium concentrations of over 4 mg/g of dry weight, 30 additional samples from trees with no visible potassium deficiency symptoms were collected in February, 1995. Six of the trees were the same as in 1994. The trees in the 1995 material belonged to the height group of 8–15 metres. The tall trees were felled and sampled immediately. The smaller trees were sampled with a special sampling device. Current (C) and current+1-year-old (C+1) needles were collected from the 2nd and 3rd whorl facing the south.

2.2 Nutrient and Free Polyamine Analyses

The nutrient analyses were performed by the methods routinely used at the Finnish Forest Research Institute and described in detail by Halonen et al. (1983). The needles for polyamine analyses were stored at –80 °C and for nutrient analyses at –20 °C. The peat and needle samples for nutrient analyses were dried at +60 °C for 24 hours and ground before analyses. The analyses of K, Mg, Cu, and Zn were performed after the HCl extraction of dried and ground material with a flame atomic spectrophotometer (Varian AA-30). Boron and phosphorus were determined spectrophotometrically from dry ashed material. N was determined with the Kjeldahl method.

For polyamine analyses the needles were ground in liquid nitrogen and extracted in 5 % (v/v) $HClO_4$. Insoluble polyvinylpyrrolidone was added to the extract. The extract was centrifuged at 37,000 g for 15 min. at +4 °C and the supernatant fraction analyzed for free polyamines. The polyamines were dansylated and separated with HPLC (Merck-Hitachi) by a modification of the procedures of Flores and Galston (1982) and described in detail by Sarjala and Kaunisto (1993).

Statistical analyses were performed using correlation graphs and matrixes and BMDP 2R stepwise and BMDP AR nonlinear regression analyses (BMDP..1992). The whole material (129 samples = current needles in years 93+94 together) was used for analyses comparing the needle nutrient and polyamine concentrations.

3 Results

3.1 Needle Nutrient Concentrations

The variation in the needle nutrient concentrations was considerably high in the material (Table 1). The concentrations ranged from severe deficiency to good nutrition in the case of all analyzed nutrients. Except potassium, the average concentrations were at satisfactory or near satisfactory levels (Paarlahti et al. 1971). The additional sampling in winter 1995 increased the average needle potassium concentration, and 32 samples instead of the former 6 had a needle K concentration of over 4.0 mg/g in the combined 1993+1994 current-year-needle data. Even so, the average potassium concentration was under the deficiency limit for pine (3.5 mg/g dry weight, Sarjala and Kaunisto 1993).

Table 1. Variation of needle nutrient concentrations in 93 and 93+94 current-year needles.

Nutrient	93			93+94		
	$\bar{x}$	Sd	Range	$\bar{x}$	Sd	Range
N	1.31	0.12	1.03–1.60	1.34	0.13	1.03–1.62
P	1.31	0.28	0.88–2.15	1.37	0.33	0.88–2.74
K	2.68	1.05	1.15–5.61	3.20	1.49	1.15–7.36
Mg	1.08	0.28	0.57–1.95	1.10	0.27	0.57–1.95
B	13.4	4.2	5.3–25.4	14.3	4.7	5.3–26.9
Cu	2.4	0.37	1.5–3.7	2.5	0.4	1.5–3.7
Zn	15.1	7.0	5.2–40.8	15.8	6.6	5.2–40.8

3.2 Free Polyamines

3.2.1 *Concentrations*

Putrescine, spermidine and spermine concentrations showed wide variation between the trees. The putrescine concentrations of the current needles varied from 112.2 to 2835.3 nmol/g fresh weight, the spermidine concentrations from 17.1 to 307.3 nmol/g fresh weight and the spermine concentrations from 16.4 to 260.9 nmol/g fresh weight. The mean putrescine concentrations were lower in the 1994 than in the 1993 needles.

3.2.2 *Regression between Potassium and Polyamines*

Stepwise linear regression analysis between free putrescine and potassium concentrations revealed that a statistically significant increase ($p < 0.05$) in putrescine was first found when the potassium concentration was below 5.4 mg/g dry weight when all the data was included ($K > 5.4$ mg/g in 16 samples, Table 2). The coefficients of determination of non-linear regressions were higher than those of the linear ones when the potassium levels were below 4.2–4.6 mg/g dry weight (30 samples included, Table 2). This represents a severe deficiency limit for potassium in Norway spruce, assuming that the response of putrescine to potassium has a similar mechanism as in our earlier study with Scots pine (Sarjala and Kaunisto 1993).

Table 2. Coefficients of determination (R^2) of nonlinear and linear regressions between putrescine and K at different K concentrations in all needles, in needles with P above 1.4 mg/g dry weight and with P values above 1.1 mg/g dry weight. Values for K and P above those indicated are included in regression equations. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

K mg/gDW	all P values			P > 1.4 mg/gDW			P > 1.1 mg/gDW		
	nonlinear	linear	n	nonlinear	linear	n	nonlinear	linear	n
≥ 5.8	0.282	0.279	9	0.880	0.808*	5	0.282	0.274	9
≥ 5.6	0.322	0.318	12	0.681	0.653*	7	0.407	0.385*	11
≥ 5.4	0.418	0.378*	16	0.314	0.343	9	0.469	0.424**	15
≥ 5.2	0.103	0.116	20	0.000	0.001	12	0.109	0.123	19
≥ 5.0	0.146	0.154	22	0.040	0.046	13	0.151	0.161	21
≥ 4.8	0.184	0.193*	25	0.113	0.114	16	0.186	0.197*	24
≥ 4.6	0.225	0.223**	30	0.228	0.202*	20	0.270	0.258**	28
≥ 4.4	"	"	30	"	"	20	"	"	28
≥ 4.2	0.281	0.267**	33	0.366	0.283*	21	0.336	0.306**	30
≥ 4.0	0.393	0.331***	35	0.483	0.366**	23	0.454	0.352***	32
≥ 3.8	"	"	35	"	"	23	"	"	32
≥ 3.6	0.678	0.337***	36	0.777	0.390**	24	0.722	0.374***	33
All	0.440	0.421***	129	0.560	0.595***	51	0.577	0.516***	99

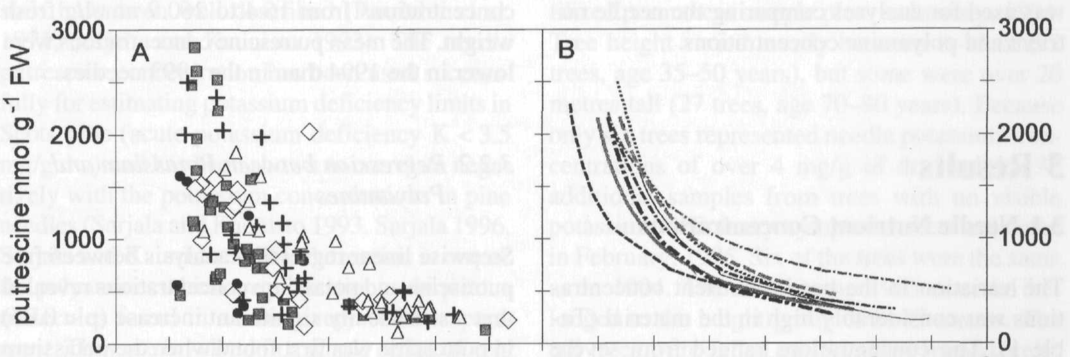

Fig. 1. (a) Free putrescine concentrations at different K levels divided into groups according to their P level (P < 1.0, 1.0–1.2, 1.2–1.4, 1.4–1.6 and > 1.6 mg/g dry weight) and (b) the corresponding regression curves ($y = ax^b$) at different P levels.

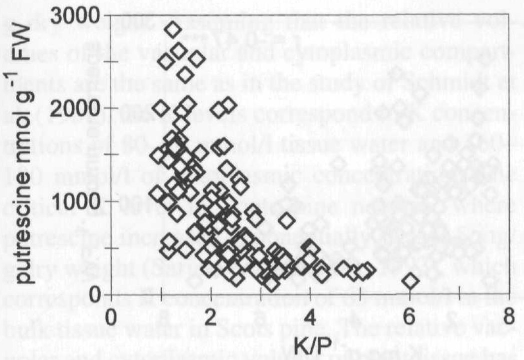

Fig. 2. Putrescine concentrations of the needles at different K/P levels.

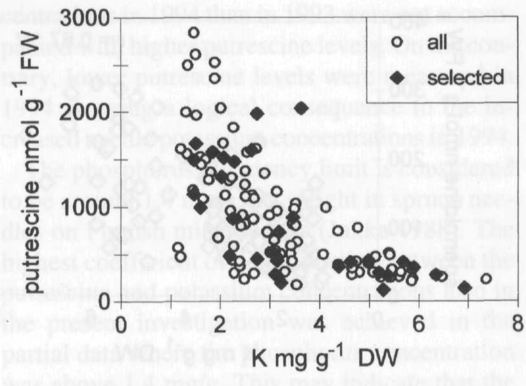

Fig. 3. Putrescine concentrations at different K levels in all needles and in selected group of needles with sufficient levels of other nutrients (except P > 1.0 mg/g DW).

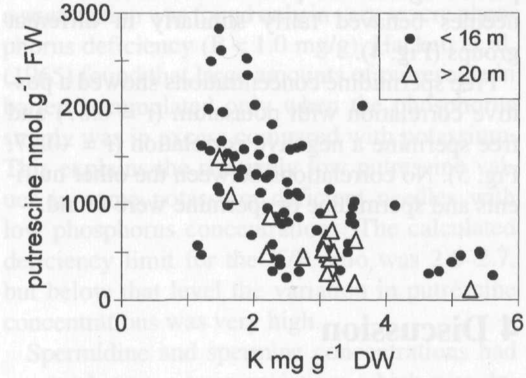

Fig. 4. Putrescine concentrations of the needles at different K levels in trees in different size (< 16 m and > 20 m) groups.

Regressions between potassium and putrescine were also calculated by dividing the data into groups according to the needle phosphorus concentrations in order to see if the low phosphorus level in some samples had any effect on the putrescine accumulation. The coefficients of determination for the non-linear regression at the needle phosphorus levels higher than 1.1 mg/g did not differ from those having a P concentration higher than 1.4 mg/g dry weight (Table 2). However, a slight decrease in the putrescine accumulation was found at phosphorus levels under 1.0 mg/g, which was seen as relatively low putrescine concentrations in some needle samples with both low potassium and low phosphorus concentrations (Fig. 1).

The putrescine concentrations were plotted also against the K/P ratio (Fig. 2) and the linear and non-linear regressions calculated in the similar way as for the putrescine-potassium relationship starting from the highest K/P ratios. The coefficients of determination for the non-linear regression between these variables were higher than the linear ones below the K/P ratio 2.6–2.7 (n = 37–40).

A great number of samples were below the nutrient deficiency limits of the studied nutrients. Therefore part of the data was selected for further calculations in order to find out if the overall nutritional status of trees had any effect on the relationship between the putrescine and potassium concentrations. Except phosphorus and potassium, the data was selected according to the deficiency limits for spruce suggested by Veijalainen (personal communication). The selected needle nutrient levels were as follows: N > 11.5 mg/g, P > 1.0 mg/g and Mg > 1.0 mg/g, B > 7 mg/kg, Zn > 16 mg/kg and Cu > 2.0 mg/kg and the number of samples 31. Fig. 3 shows that there was no difference between the selected group and the rest of the data.

Sample trees in the 1994 data represented two distinct size groups: 8–15 m (72 trees) and over

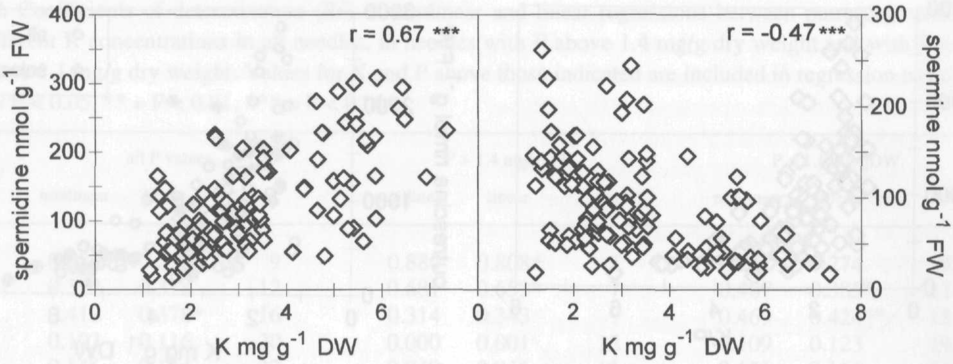

Fig. 5. Free spermidine and spermine concentrations of the needles at different K levels (*** = $P < 0.001$).

20 m (18 trees) in height. However, putrescine plotted against the potassium concentration in needles behaved fairly similarly in different groups (Fig. 4).

Free spermidine concentrations showed a positive correlation with potassium (r = 0.67) and free spermine a negative correlation (r = –0.47, Fig. 5). No correlations between the other nutrients and spermidine or spermine were found.

4 Discussion

About 5 million hectares of peatlands have been drained for forestry in Finland. Low pH and low amounts of potassium and available phosphorus compared with the amount of nitrogen are typical features of drained peatlands (Kaunisto and Paavilainen 1988). Potassium is not fixed in the organic material, but only bound at cation exchange sites in peat and thus readily available to trees. Even so, potassium deficiency is quite common, because the amounts fixed by trees are considerably high compared with the amounts in the root layer. The determination of the critical needle potassium limits is important for practical forestry for estimating the need of fertilization and of other forest improvement measures.

The needle potassium concentration, where the regression between putrescine and potassium in this investigation changed from a linear to a nonlinear form, was 4.2–4.6 mg/g dry weight. Lauchert and Wild (1995) reported a linear correlation between putrescine and potassium in spruce needles, but according to their original data, there occurred an exponential increase in putrescine, which seemed to begin at a slightly higher K level than in this study. However, their data had been sampled during the growing season, but the present data during dormancy. According to our earlier results with Scots pine (Sarjala and Kaunisto 1993, 1996) the K deficiency limit, indicated by an exponential increase in putrescine, is at a higher concentration level during the growing season (K 4.3 mg/g) than in winter (K 3.5 mg/g).

Leigh and Wyn Jones (1984) suggest that the point where cytoplasmic K begins to decline is within the range of the critical concentration of K in many plants. An unimpaired physiological and biochemical performance requires cytoplasmic concentrations of 100 to 200 mM, and vacuolar concentrations must not be lower than 10–15 mM (Leigh and Wyn Jones 1984, Lüttge and Clarkson 1988). Schmidt et al. (1989) reported that on the basis of the water and potassium content and the relative vacuolar volume of the mesophyll cells of spruce needles K levels between 3.5 to 5 mg/g dry weight correspond to 45–100 mmol/l tissue water. K concentrations below 50 mmol/l tissue water correspond to 100 mmol/l cytoplasmic concentration, which would be too low for metabolic requirements. The exponential accumulation of putrescine began in this study at the K concentrations of 4.2–4.6 mg/

g dry weight. Assuming that the relative volumes of the vacuolar and cytoplasmic compartments are the same as in the study of Schmidt et al. (1989), the K levels correspond to K concentrations of 80–90 mmol/l tissue water and 160–180 mmol/l of cytoplasmic concentration. The critical K level in Scots pine needles, where putrescine increased exponentially, was 3.5 mg/g dry weight (Sarjala and Kaunisto 1993), which corresponds K concentration of 65 mmol/l in the bulk tissue water in Scots pine. The relative vacuolar and cytoplasmic volume of plant tissue has a strong effect on the minimum K^+ levels in dry matter or bulk tissue water required for the maintenance of metabolism (Leigh and Wyn Jones 1984, Schmidt et al. 1989). Therefore the differences in the potassium demand between plant species may be affected by different relative volumes of vacuoles and cytoplasm. The vacuoles are considered as a compartment for polyamine storage as well, which suggests that the accumulation of polycationic putrescine under K deficiency may replace potassium ions to maintain the ionic balance.

The polycationic nature of polyamines at physiological pH is one of the main properties believed to mediate their biological activity in plants. Although they play a role in a variety of physiological processes such as cell division, embryogenesis (Egea-Cortines and Mizrahi 1991), and response to various stresses (Flores 1991), the molecular mechanism of their action remains still obscure. In cereals, the activity of one of the major polyamine biosynthetic enzymes, arginine carboxylase, is rapidly and dramatically increased by almost every studied external stress (Galston and Kaur-Sawhney 1990). The physiological significance of this increase is not yet clear, although an adaptive, protective role has been suggested (Galston and Kaur-Sawhney 1990). The homeostatic effect of polyamines, i.e. the maintenance of cellular pH in plants is one of the proposed mechanisms of the action of polyamines and a highly relevant factor in viewing mineral nutrition, especially potassium deficiency (Altman and Levin 1993).

Nitrogen nutrition, especially the ammonium/nitrate relationship has been reported to affect polyamine levels in plants (Altman and Levin 1993). However, in this case higher needle N concentrations in 1994 than in 1993 were not accompanied with higher putrescine levels. On the contrary, lower putrescine levels were measured in 1994 showing a logical consequence to the increased needle potassium concentrations in 1994.

The phosphorus deficiency limit is considered to be around 1.4 mg/g dry weight in spruce needles on Finnish mineral soils (Jukka 1988). The highest coefficient of determination between the putrescine and potassium concentrations also in the present investigation was achieved in the partial data where the phosphorus concentration was above 1.4 mg/g. This may indicate that the indicator value of putrescine is at its best when phosphorus nutrition is at a satisfactory level. However, the difference in the degree of determination was quite small between the phosphorus concentrations of 1.4 and 1.1 mg/g and a distinct effect of phosphorus on the putrescine accumulation was found only in very severe phosphorus deficiency ($P < 1.0$ mg/g). Hackett et al. (1965) found that large amounts of putrescine in barley accumulated only when the phosphorus supply was in excess compared with potassium. This explains the relatively low putrescine values in some potassium deficient needles with low phosphorus concentrations. The calculated deficiency limit for the K/P ratio was 2.6–2.7, but below that level the variation in putrescine concentrations was very high.

Spermidine and spermine concentrations had a great between-trees variation, which was dependent on the potassium level of needles. A slight decrease in spermidine and spermine at low K levels in Scots pine needles was found in field samples by Sarjala and Kaunisto (1993, 1996), but the decline was not statistically significant. Under controlled growth conditions Scots pine seedlings showed also lower levels of spermidine and spermine under K deficiency (Sarjala 1996). However, increased levels of spermine were found in K deficient spruce needles in this study indicating that the response of spermine on K concentrations in Norway spruce seems to be the opposite to Scots pine.

According to our investigation it seems that the needle putrescine concentration can be used quite reliably for describing the potassium nutrition of Norway spruce, and that neither the tree size nor the nitrogen, magnesium, boron, copper or zinc concentrations of needles seem to interfere with the results. A very severe phosphorus deficiency (P < 1.0 mg/g dry weight) may, however, decrease putrescine accumulation under potassium deficiency.

References

Aaltonen, V.T. 1950. Die Blattenanalyse als Bonitierungsgrundlage des Waldbodens. Communicationes Instituti Forestalis Fenniae 37. 41 p.

Altman, A. & Levin, N. 1993. Interactions of polyamines and nitrogen nutrition in plants. Physiologia Plantarum 89: 653–658.

BMDP statistical software manual. 1992. Volume 2. University of California Press. Berkeley. Los Angeles. Oxford. 1500 p.

Egea-Cortines, M. & Mizrahi, Y. 1991. Polyamines in cell division, fruit set and development, and seed germination. In: Slocum, R.D. & Flores, H.E. (eds.). Biochemistry and physiology of polyamines in plants. CRC Press, Boca Raton, Florida. p. 143–158. ISBN 0-8493-6865-0.

Flores, H.E. 1991. Changes in polyamine metabolism in response to abiotic stress. In: Slocum, R.D. & Flores, H.E. (eds.). Biochemistry and physiology of polyamines in plants. CRC Press, Boca Raton, Florida. p. 213–228. ISBN 0-8493-6865-0.

— & Galston, A.W. 1982. Analysis of polyamines in higher plants by high performance liquid chromatography. Plant Physiology 69: 701–706.

Galston, A.W. & Kaur-Sawhney, R. 1990. Polyamines in plant physiology. Plant Physiology 94: 406–410.

Hackett, C., Sinclair, C. & Richards, F.J. 1965. Balance between potassium and phosphorus in the nutrition of barley. I. The influence on amine content. Annales Botanici 29: 331–345.

Halonen, O., Tulkki, H. & Derome, J. 1983. Nutrient analysis methods. Metsäntutkimuslaitoksen tiedonantoja 121: 1–28.

Holmen, H. 1964. Forest ecological studies on drained peatland in the province of Uppland, Sweden. Studia Forestalia Suecica 16. 236 p.

Jukka, L. 1988. (ed.). Metsän terveysopas. Metsätuhot ja niiden torjunta. Samerka Oy, Helsinki.168 p.

Kaunisto, S. 1989. Jatkolannoituksen vaikutus puuston kasvuun vanhalla ojitusalueella. Summary: Effect of refertilization on tree growth in an old drainage area. Folia Forestalia 724. 15 p.

— & Paavilainen, E. 1988. Nutrient stores in old drainage areas and growth of stands. Seloste: Turpeen ravinnevarat vanhoilla ojitusalueilla ja puuston kasvu. Communicationes Instituti Forestalis Fenniae 145. 39 p.

Lauchert, U. & Wild, A. 1995. Studies on the correlation of putrescine and potassium contents in the needles of spruce trees. Journal of Plant Physiology 147: 267–269.

Leigh, R.A. & Wyn Jones, R.G. 1984. A hypothesis relating critical potassium concentrations for growth to the distribution and functions of this ion in the plant cell. New Phytology 97: 1–13.

Leyton, L. 1948. Mineral nutrient relationships of forest trees. Forestry Abstracts 9: 399–408.

Lundegårdh, H. 1941. Die Tripelanalyse. Landbrukshögskolans Annaler 9: 127–221.

Lüttge, U. & Clarkson, D.T. 1988. Mineral nutrition: potassium. Progress in Botany 50: 51–73.

Paarlahti, K., Reinikainen, A. & Veijalainen, H. 1971. Nutritional diagnosis of Scots pine stands by needles and peat analysis. Seloste: Maa- ja neulasanalyysi turvemaiden männiköiden ravitsemustilan määrityksessä. Communicationes Instituti Forestalis Fenniae 74. 58 p.

Paavilainen, E. 1975. Koetuloksia lannoituksen vaikutuksesta korpikuusikoissa. Summary: On the response to the fertilization application of Norway spruce growing on peat. Folia Forestalia 239. 10 p.

Sarjala, T. 1996. Growth, potassium and polyamine concentrations of Scots pine seedlings in relation to potassium availability under controlled growth conditions. Journal of Plant Physiology 147: 593–598.

— & Kaunisto, S. 1993. Needle polyamine concentrations and potassium nutrition in Scots pine. Tree Physiology 13: 87–96.

— & Kaunisto, S. 1996. Effect of different potassium sources on the seasonal variation of potassium and free polyamines in Scots pine needles. Silva Fennica 30: 387–398.

Schmidt, R., Lüttge, U. & Kramer, D. 1989. Supply and compartmentalization of potassium in mesophyll cells of the needles of spruce, Picea abies (L.) Karst. Trees 3: 154–160.

Total of 24 references