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Effect of Different Potassium Sources on the Seasonal Variation of Potassium and Free Polyamines in Scots Pine Needles

Tytti Sarjala and Seppo Kaunisto

Sarjala, T. & Kaunisto, S. 1996. Effect of different potassium sources on the seasonal variation of potassium and free polyamines in Scots pine needles. Silva Fennica 30(4): 387–398.

Seasonal fluctuations in free polyamines, spermidine, spermine, putrescine and potassium concentrations were studied for two years (1992–1993) in three needle years of Scots pine (*Pinus sylvestris* L.) grown on a drained mire in western Finland. Seven different fertilizer treatments involving five different sources of potassium were used.

Putrescine concentrations were high in winter and in May but low in summer. High peaks in putrescine in March and May could be found in non-refertilized or rock phosphate treatments. Spermidine and spermine concentrations were high in March and May. In December spermine concentrations were low. Biotite increased the needle potassium concentrations less than the other potassium fertilizers but the putrescine concentrations or the putrescine/spermidine ratio to about the same level. This suggests that biotite, although very slowly soluble, can reasonably satisfy potassium nutrition of young pine trees.

The potassium concentrations of needles in all the fertilization treatments were higher in winter than in summer. The response of putrescine to the potassium concentration was strongly negative in all the needle years and sampling times. In March, May and December the response of putrescine to potassium was fairly similar in both years but not in June and August. The results suggest that the potassium concentrations during the growing season cannot be used for estimating the potassium nutrition of trees, because the variation between the years may be substantial, whereas the needle putrescine concentration or putrescine/spermidine ratio indicates the suboptimum potassium status of Scots pine fairly well. Needle putrescine concentrations over 500 nmol g^{-1}FW quite regularly coincided with a nonsatisfactory potassium nutrition and concentrations over 1000 nmol g^{-1}FW were a reliable indication of potassium deficiency. Putrescine/spermidine ratios below 5 indicated a satisfactory potassium nutrition in all needle years throughout the year.

Keywords *Pinus sylvestris*, potassium deficiency, putrescine, seasonal fluctuation, spermidine, spermine

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1 Introduction

The most common polyamines in plants are putrescine, spermidine and spermine. Seasonal changes in polyamine levels in Scots pine needles have been observed by Sarjala and Savonen (1994). The fluctuation of polyamines in conifers may be related to the beginning and ending of dormancy, sprouting or cambial activity (Königshofer 1989, 1991). The diamine putrescine is known to accumulate under potassium deficiency in many plant species (Richards and Coleman 1952, Basso and Smith 1974, Smith 1985) including Scots pine (Sarjala and Kaunisto 1993). Chilling stress may also cause changes in polyamine concentrations during a cold period (Königshofer 1989), and cold hardening in many plant species correlates with increases in polyamines (Kushad and Yelenosky 1987). As polyamines are involved in cell division (Maki et al. 1991), growth and developmental processes (Smith 1985; Evans and Malmberg 1989), and the regulation of nucleic acid metabolism (Kaur-Sawhney and Galston 1991) reflecting hormone-like properties, the changes in polyamine levels may affect the growth of trees. It has also been shown that the polyamines regulate the long-distance transport of potassium in plants (Feray et al. 1992).

Needle samples collected during dormancy have been used for estimating the potassium status of trees (Paarlahti et al. 1971). According to the results of Sarjala and Kaunisto (1993) putrescine accumulation indicates different critical limits for potassium during the growing season and dormancy. Because the polyamine (Sarjala and Savonen 1994) and potassium concentrations (Helmisaari 1990) in Scots pine vary during the year, seasonal variation in the response of polyamines to the potassium status may also occur.

Phosphorus and potassium fertilization increases tree growth quite frequently in peatland forests (Kaunisto 1992, Kaunisto et al. 1993). Water insoluble rock phosphate or apatite is used as phosphorus sources, but water soluble potassium chloride as a potassium source in these fertilizers. Because of its solubility potassium is highly susceptible to leaching (Ahti 1983, Malcolm and Cuttle 1983, Kaunisto 1992). This means that trees suffer from potassium deficiency while they may still have enough phosphorus. Some fairly promising results have been achieved with biotite which is completely insoluble in water (Kaunisto et al. 1993). However, biotite increases the needle potassium concentrations during the years right after the fertilization less than potassium chloride.

In this study, the seasonal variation of the polyamine levels together with potassium concentrations are monitored in Scots pine needles in order to find out how the response of polyamines to potassium differ during the year. The purpose is to find out how the dormant samples reflect the potassium status of trees during the growing season, and if it is possible to have a reliable estimate of the potassium status from samples collected during the growing season by using needle potassium and polyamine analysis. Also nitrogen and phosphorus were analysed in order to find out if their concentrations were at a satisfactory level.

Also the effect of the potassium sources of different solubility on needle potassium and polyamine concentrations are compared in order to find out if the usually weaker response of needle potassium concentrations to biotite than potassium chloride fertilization is also reflected in the polyamine concentrations and if biotite can provide pine trees with satisfactory potassium nutrition.

2 Material and Methods

The material was collected from a fertilization experiment on an ombrotrophic, low-sedge bog located at Kuru (61°55'N, 23°44'E) in western Finland. Seven fertilization treatments with two replicates were used: a non-refertilized and rock phosphate-fertilized control, four potassium sources of differing solubility (KCl, K_2CO_3, $(KPO_3)_x$, biotite), and a mixture of KCl and biotite. All the potassium fertilized plots were fertilized also with rock phosphate. A previous study had been performed in the same area in 1992 and a more detailed description of the experimental area was reported by Sarjala and Kaunisto (1993).

Combined needle samples from six Scots pines (*Pinus sylvestris* L.) per plot separately from the current, current+1 and current +2 needles of the third whorl were collected at each sampling time (March, May, June, August and December in 1992 and 1993). In June only two needle years, the current+1 and current+2 needles, were available. The oldest needle years fell off during the study, the needle year 1989 fell off in summer 1992 and the needle year 1990 in summer 1993. Newly developed needles were collected for the analyses for the first time in August. Climatological data in the area were ascertained from the Meteorological Yearbook of Finland 1992 and 1993.

The samples were sealed in plastic bags, placed on ice and taken to the laboratory. The needles for polyamine analyses were stored in a deep-freezer (–80°C). Needles for nutrient analyses were stored at –20°C and subsequently dried (60°C for 24 h) and ground. The mean water content (%) of each needle year was determined at every sampling time by drying the needles at 105°C for 24 hours.

For free polyamine analyses the needles were ground in liquid nitrogen and extracted in 5 % (v/v) $HClO_4$ with a small amount of insoluble polyvinylpyrrolidone. After centrifugation at 37 000 g for 15 min the supernatant fraction was analysed for soluble polyamines. After dansylation the separation of the polyamines was performed by HPLC (Merck Hitachi Model) with LiChroCART 125-4 LiChrospher 100 RP-18 5 µm column (Merck) with a methanol-water gradient by fluorescence spectrophotometry (Merck Hitachi F-1050). The extraction and dansylation procedures as well as the separation were modifications from those of Flores and Galston (1982), Smith and Davies (1985) and Langebartels et al. (1991) and are described in more detail by Sarjala and Kaunisto (1993).

Needle nutrients (N, P, K) were analysed with the methods routinely used at the Finnish Forest Institute and described in detail by Halonen et al. (1983). The total N was measured by the Kjeldahl method. The analyses of K were performed by a flame atomic spectrophotometer (Varian AA-30). The analyses of P were made spectrophotometrically from dry-ashed material with the vanado-molybdate method.

In an earlier study by Sarjala and Kaunisto (1993) linear and nonlinear regression models were compared when analysing putrescine and potassium data. On the basis of that study the nonlinear regression analysis (AR, BMDP Statistical Software) was used here to analyse the relationship between putrescine and potassium concentrations. The fitness of the nonlinear model to the data is indicated by pseudo R-square (R^2), which is defined $R^2 = 1.0$ minus the ratio of weighted residual sum of squares to (n–1) times weighted variance. The analysis of variance and t-test as provided by BMDP Statistical Software were used when comparing the effects of different fertilization treatments on the potassium and putrescine concentrations and on the putrescine/spermidine ratio. The data were analysed separately for each sampling time.

3 Results

3.1 Needle Nutrient Concentrations and Water Content

The potassium concentrations on dry weight basis varied during the year in all the needle years from March 1992 to December 1993. The longest time series was analyzed from the needles developed in 1991 when they were current needles to the end of the study period when they were current+2 needles. A decreasing trend in potassium concentrations was found in all the fertilization treatments when the needles were getting older (Fig. 1). Potassium concentrations in the needle years 1990 and 1991 were higher in March 1992 than in March 1993. A similar decrease could be seen in the needle years 1991 and 1992 when the needles in December 1992 were compared with those in December 1993 (Fig. 1).

Needles from the non-refertilized and rock phosphate refertilized treatments had the lowest potassium concentrations during the study period in all the needle years (Fig. 1). The potassium concentrations of the current needles were usually below the severe deficiency limit 3.5 mg g^{-1}DW (Paarlahti et al. 1971, Sarjala and Kaunisto 1993) during the dormant periods and always below 4.0 mg g^{-1}DW. Potassium fertilization in-

Table 1. Water content (%) of the needles in 1992 and 1993, n = 14.

Needle year	1992 March	1992 May	1992 June	1992 August	1992 December	1993 March	1993 May	1993 June	1993 August	1993 December
1989	54.1	46.2								
1990	56.9	48.5	43.2	48.6	55.8	35.2	48.2			
1991	59.3	51.1	44.9	53.1	57.5	55.2	46.9	44.1	51.8	56.8
1992				60.9	58.8	48.9	47.6	45.2	51.8	57.5
1993									63.9	58.9

creased the concentrations to a satisfactory or good level and in most cases statistically significantly compared with the rock phosphate fertilized control (Table 2). Biotite fertilization increased the needle potassium concentrations only to 0.5–0.6 mg g^{-1}DW. The needle potassium concentrations in the other treatments (K_2CO_3, KCl, $(KPO_3)_x$ and the mixture of biotite and KCl) were at about the same level with each other and constantly at higher levels than in non-refertilized, and rock and rock phosphate or biotite fertilized treatments in all the needle years (Fig. 1).

In 1992 the needle years 1990 and 1991 showed an increase in the potassium concentration from August to December, but the needle year 1992 showed either a slight decrease or increase depending on the treatment. In 1993 the situation was different and the potassium concentrations of all the needle years decreased from August to December in all the treatments (Fig. 1).

The variation in the needle nitrogen and phosphorus concentrations followed roughly the same seasonal pattern as that of potassium, but the decrease during the growing season was much more pronounced. Nitrogen concentrations of current needles varied from near the deficiency limit to a satisfactory nitrogen nutrition (13.1–14.5 mg g^{-1}DW, cf. Paarlahti et al. 1971, Kaunisto 1982) during the dormant period, and phosphorus concentrations from satisfactory to excellent phosphorus levels (1.50–1.90 mg g^{-1}DW, cf. Paarlahti et al. 1971) in 1992 and 1993.

The water contents of the needles did not differ much between the years (Table 1), except in March, when the trees are exposed to varying drought stress. Water content of the needles (Table 1) was used to calculate the potassium concentrations of the needles as mol m^{-3} tissue water. This revealed that the highest potassium concentrations as mol m^{-3} in the needles were measured in May (from 70 to 120 mol m^{-3}) and June (from 80 to 150 mol m^{-3}) and the lowest in December (from 60 to 100 mol m^{-3}), which differ from the fluctuation of potassium concentrations analysed on the dry weight basis.

Table 2. Significances of the differences according to t-tests on needle potassium concentrations during dormancy in 1992 and 1993 between potassium fertilized treatments and controls (non-fertilized and rock phosphate fertilized treatments) and between biotite fertilized and other K fertilized treatments. CONTR = non-fertilized, RP = rock phosphate, BIOT = biotite, MIX = mixture of biotite and KCl, K2CO3 = K_2CO_3, KPO3 = $(KPO_3)_x$. (*) = P < 0.10, * = P < 0.05, ** = P < 0.01

Potassium source	CONTR Needle year 91	CONTR 92	CONTR 93	RP Needle year 91	RP 92	RP 93	BIOT Needle year 91	BIOT 92	BIOT 93
BIOT	–	(*)	–	(*)	(*)	–			
MIX	(*)	(*)	–	*	–	*	(*)	–	–
K2CO3	(*)	*	–	**	*	*	**	(*)	–
KPO3	*	*	–	*	*	*	*	(*)	–
KCI	(*)	*	–	*	*	(*)	*	*	–

3.2 Free Polyamines

Putrescine levels in all the needle years of non-refertilized and rock phosphate fertilized treatments were higher than in the needles from the other treatments (Fig. 2). The peak values were in March and May in both years and in June 1993. According to t-test the putrescine concen-

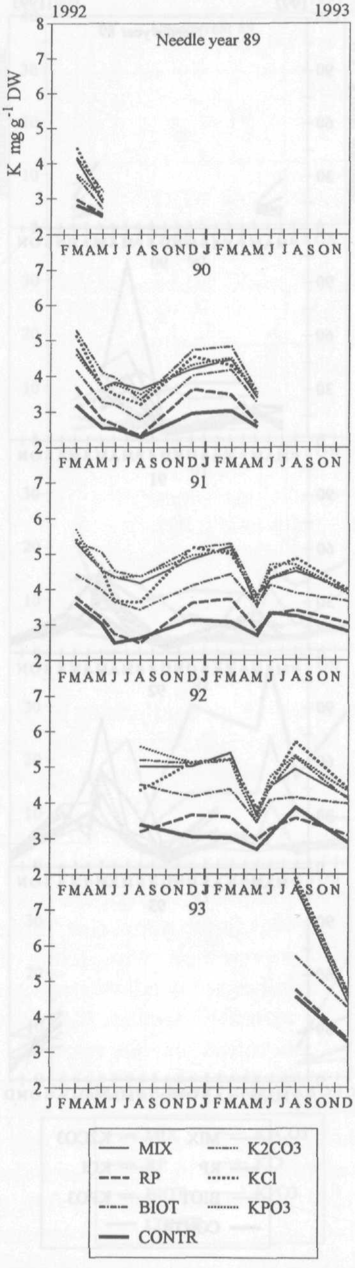

Fig. 1. Seasonal variation in potassium concentrations (mg g^{-1} DW) in different needle years in 1992 and 1993 on seven different fertilizer treatments. Each line consists of the mean values from two replicate plots of the treatments. MIX = mixture of biotite and KCl; RP = rock phosphate; BIOT = biotite; CONTR = non-refertilized; K2CO3 = K_2CO_3; KCl = KCl; KPO3 = $(KPO_3)_x$.

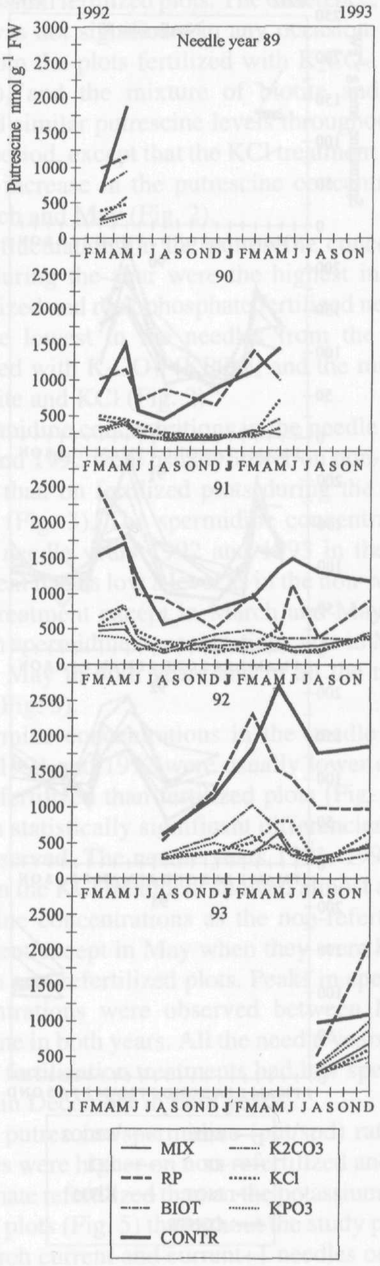

Fig. 2. Seasonal variation in putrescine concentrations (nmol g^{-1} FW) in different needle years in 1992 and 1993 on different fertilizer treatments. See Fig. 1 for explanation of the abbreviations.

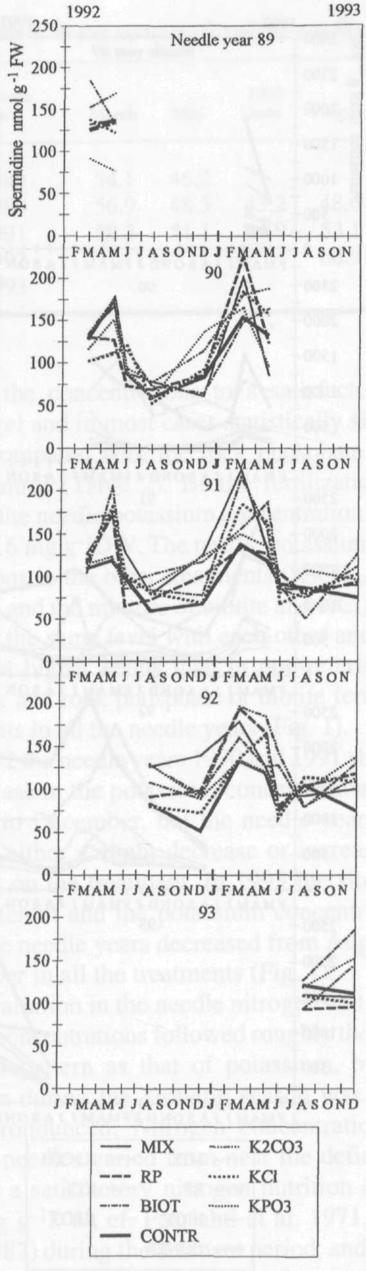

Fig. 3. Seasonal variation in spermidine concentrations (nmol g^{-1} FW) in different needle years in 1992 and 1993 on different fertilizer treatments. See Fig. 1 for explanation of the abbreviations.

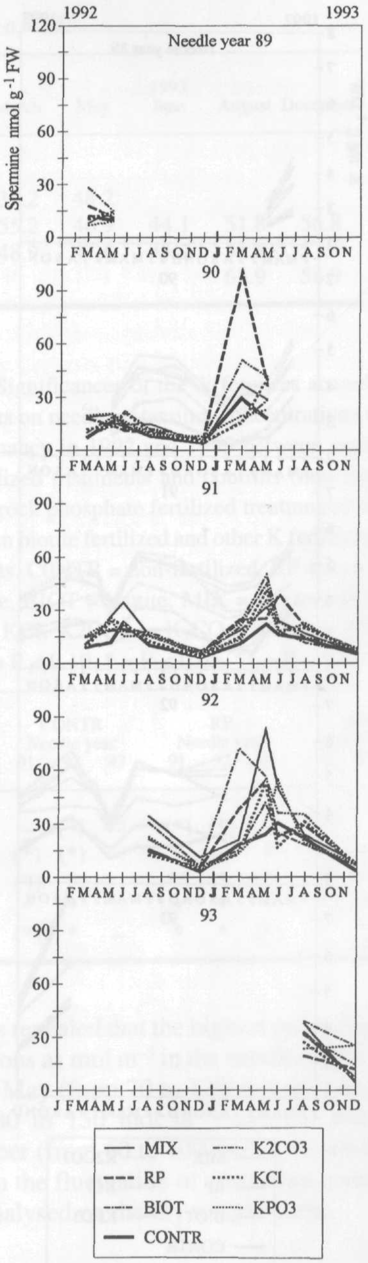

Fig. 4. Seasonal variation in spermine concentrations (nmol g^{-1} FW) in different needle years in 1992 and 1993 on different fertilizer treatments. See Fig. 1 for explanation of the abbreviations.

trations of the current needles were significantly lower in all the potassium fertilization treatments than in the rock phosphate fertilized ones in March in both years ($p < 0.05$) and in December 1993 ($p < 0.05$). The trend was similar during the spring and summer months, but differences

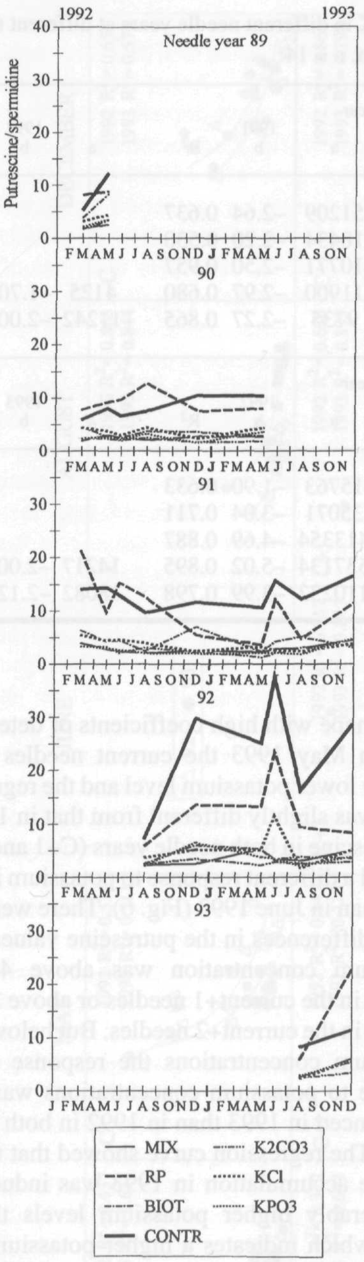

Fig. 5. Seasonal variation in putrescine/spermidine ratio in different needle years in 1992 and 1993 on different fertilizer treatments. See Fig. 1 for explanation of the abbreviations.

were not statistically significant in most cases. The needles fertilized with biotite had slightly higher putrescine values than those from the other potassium fertilized plots. The difference, however, was not significant in any occasion. Needles from the plots fertilized with K_2CO_3, KCl, $(KPO_3)_x$ and the mixture of biotite and KCl showed similar putrescine levels throughout the study period, except that the KCl treatment had a higher increase in the putrescine concentration in March and May (Fig. 2).

The fluctuations in the putrescine concentrations during the year were the highest in non-refertilized and rock phosphate fertilized needles and the lowest in the needles from the plots fertilized with K_2CO_3, $(KPO_3)_x$ and the mixture of biotite and KCl (Fig. 2).

Spermidine concentrations in the needle years 1991 and 1992 were usually lower on non-refertilized than on fertilized plots during the study period (Fig. 3). The spermidine concentrations of the needle years 1992 and 1993 in the KCl treatment had as low a level as in the non-refertilized treatment except in March and May. The peak in spermidine concentrations was in March and/or May in both years and in all the needle years (Fig. 3).

Spermine concentrations in the needle years 1990, 1991 and 1992 were usually lower on the non-refertilized than fertilized plots (Fig. 4) although statistically significant differencies were not observed. The needle years 1991, 1992 and 1993 in the KCl treatment showed almost as low spermine concentrations as the non-refertilized treatment except in May when they were higher than in non-refertilized plots. Peaks in spermine concentrations were observed between March and June in both years. All the needle years from all the fertilization treatments had low spermine levels in December in both years.

The putrescine/spermidine (put/spd) ratios of needles were higher on non-refertilized and rock phosphate refertilized than on the potassium refertilized plots (Fig. 5) throughout the study period. In March current and current+1 needles on rock phosphate plots had significantly higher put/spd ratio (t-test, $p < 0.05$) than on potassium fertilized plots. The ratio in the needles from potassium refertilized plots was quite stable throughout the study period and usually below 5 in all the needle years. Put/spd in the needles from the non-refertilized and rock phosphate refertilized plots were almost constantly over 5 and very

Table 3. Nonlinear regression ($y = a \cdot x^b$) between putrescine and K in different needle years at different times of collection in 1992 and 1993. R^2 = coefficient of determination, n = 14.

1992	Needle year											
	1989			1990			1991			1992		
	a	b	R^2	a	b	R^2	a	b	R^2	a	b	R^2
March	9950	−2.42	0.450	6111	−1.72	0.322	51209	−2.64	0.637			
May	1334595	−7.55	0.714	77381	−4.22	0.845	18434	−2.20	0.530			
June				4278	−2.14	0.550	10771	−2.50	0.957			
August				5819	−2.80	0.539	11900	−2.97	0.680	4125	−1.70	0.863
December				34013	−3.42	0.761	9735	−2.27	0.865	11242	−2.00	0.655

1993	Needle year											
	1990			1991			1992			1993		
	a	b	R^2	a	b	R^2	a	b	R^2	a	b	R^2
March	95630	−3.87	0.556	106721	−2.12	0.694	15763	−1.90	0.633			
May	45699	−3.93	0.785	28451	−3.57	0.718	35071	−3.04	0.711			
June				$8051 \cdot 10^6$	−13.25	0.870	413354	−4.69	0.887			
August				$122 \cdot 10^6$	−10.26	0.859	537134	−5.02	0.895	14217	−2.00	0.844
December				38822	−3.44	0.902	110232	−3.99	0.798	18082	−2.12	0.570

often between 10 and 20. Peaks in put/spd were observed in the 1992 needle year on non-refertilized, rock phosphate and KCl treatments in June 1993 and on the non-refertilized treatment also in December 1992 and 1993.

3.3 Regression Analyses Between Potassium and Putrescine Concentrations

The curvilinear regression analysis revealed that in every needle year and at every sampling time the correlations between the potassium and putrescine concentrations were negative. The nonlinear regression parameters and R^2 for each needle year and sampling time are shown in Table 3. In March the potassium and putrescine concentrations were at the same level in 1992 and 1993 and the regression equations were very similar (Fig. 6). In March 1992 a higher coefficient of determination (R^2) and less variation was observed in the current needles than in the current+1 and the current+2 needles.

In May the current+1 and the current+2 needles showed the same potassium and putrescine values and the regression curves were of the same shape with high coefficients of determination. In May 1993 the current needles had a slightly lower potassium level and the regression curve was slightly different from that in 1992.

Putrescine in both needle years (C+1 and C+2) showed a different response to potassium in June 1992 than in June 1993 (Fig. 6). There were only minor differences in the putrescine values if the potassium concentration was above 4.5 mg g^{-1}DW in the current+1 needles or above 3.5 mg g^{-1}DW in the current+2 needles. But below these potassium concentrations the response of putrescine to potassium concentrations was more pronounced in 1993 than in 1992 in both needle years. The regression curve showed that the putrescine accumulation in 1993 was induced by considerably higher potassium levels than in 1992, which indicates a higher potassium deficiency limit in June 1993 than in 1992 for both needle years. Other stress factors did not disturb the response of putrescine to potassium in June, which was reflected by the low variation and high coefficients of determination of the regression curves. The strongest response of putrescine to potassium during the study period could be found in the current+1 needles in June (R^2=0.957 in 1992 and R^2=0.887 in 1993) (Fig. 6).

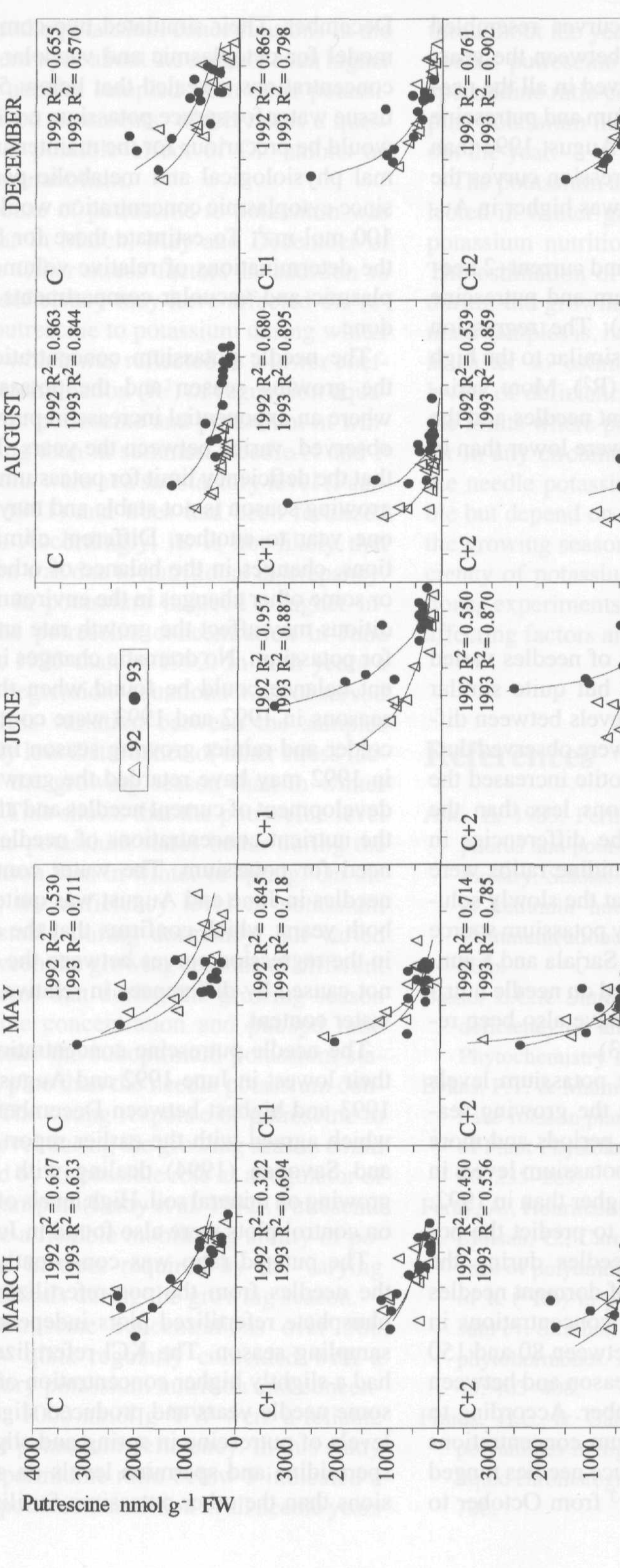

Fig. 6. Nonlinear regression curves between putrescine and potassium concentrations in different needle years and sampling times. Each point represents a combined sample of six trees from an experimental plot.

In August the regression curves resembled those in June. The difference between the years 1992 and 1993 could be observed in all the needle years (Fig. 6). Both potassium and putrescine concentrations were higher in August 1993 than in 1992. According to the regression curves the deficiency limit of potassium was higher in August 1993 than in 1992.

In December the current+1 and current+2 needles had very similar potassium and putrescine values in both years (Fig. 6). The regression curves proved also to be very similar to the high coefficients of determination (R^2). More variation was observed in the current needles and the coefficients of determination were lower than in the older needles.

4 Discussion

The potassium concentrations of needles varied between the sampling times, but quite similar differences at the potassium levels between different fertilization treatments were observed during the years. Even though biotite increased the needle potassium concentrations less than the other potassium fertilizers, the differencies in putrescine or putrescine/spermidine ratios were rather small. This indicates that the slowly soluble biotite may be a satisfactory potassium source for young pine trees (See also Sarjala and Kaunisto 1993). Similar results based on needle nutrient analyses and tree growth have also been reported by Kaunisto et al. (1993).

The variation at the needle potassium levels was more pronounced during the growing seasons than during the dormant periods and more so in 1993 than in 1992. The potassium levels in June and August 1993 were higher than in 1992. This means that it is difficult to predict the potassium concentrations of needles during the growing season on the basis of dormant needles or vice versa. The potassium concentrations in the bulk tissue water varied between 80 and 150 mol m^{-3} during the growing season and between 60 and 100 mol m^{-3} in December. According to Schmidt et al. (1989) potassium concentrations in the bulk tissue water of spruce needles ranged from about 65 to 105 mol m^{-3} from October to December. Their simulated two-compartmental model for cytoplasmic and vacuolar potassium concentrations revealed that below 50 mol m^{-3} tissue water for spruce potassium concentrations would be precarious for the maintenance of normal physiological and metabolic performance, since cytoplasmic concentration would be below 100 mol m^{-3}. To estimate these for Scots pine, the determinations of relative volumes of cytoplasmic and vacuolar compartments should be done.

The needle potassium concentrations during the growing season and the potassium level, where an exponential increase in putrescine was observed, varied between the years. This means that the deficiency limit for potassium during the growing season is not stable and may vary from one year to another. Different climatic conditions, changes in the balance of other nutrients or some other changes in the environmental conditions may affect the growth rate and the need for potassium. No dramatic changes in the nutrient balance could be found when the growing seasons in 1992 and 1993 were compared. The colder and rainier growing season in 1993 than in 1992 may have retarded the growth rate and development of current needles and affected also the nutrient concentrations of needles and their need for potassium. The water content of the needles in June and August was quite similar in both years, which confirms that the differences in the regression curves between the years were not caused by differences in relative amount of water content.

The needle putrescine concentrations were at their lowest in June 1992 and August 1992 and 1993 and highest between December and May, which agreed with the earlier report by Sarjala and Savonen (1994) dealing with Scots pine growing on mineral soil. High levels of putrescine on control plots were also found in June 1993.

The put/spd ratio was consistently higher in the needles from the non-refertilized and rock phosphate refertilized plots independent of the sampling season. The KCl refertilized samples had a slightly higher concentration of put/spd in some needle years and produced slightly higher levels of putrescine in spring and slightly lower spermidine and spermine levels on some occasions than the other potassium fertilizers. However, the needle potassium concentrations in the KCl treatment were about the same or even higher than in the needles sampled from other potassium refertilized treatments, which raises a question about a possible effect of Cl^- anions on polyamine metabolism.

The response of putrescine to potassium was quite similar in March, May and December of both years. Other stress factors in addition to potassium deficiency may have affected the response of putrescine to potassium during winter and spring, which was reflected as a lower coefficient of determination (R^2) of regression equations between putrescine and potassium in winter and spring than in summer. Needle N and P concentrations were at a satisfactory level (Paarlahti et al. 1971) and trees had been fertilized with boron. Accordingly, its is not likely that this variation was due to nutritional discrepancy. A decrease in potassium induced a higher increase in the putrescine concentration in June and August 1993 than in 1992. In both years a high R^2 of regression equations was observed indicating less variation between the samples and probably less disturbance of other stress factors during the growing season than in winter and spring. This shows that the putrescine level indicated the potassium status better during the growing season than in winter or spring. On the other hand, the deficiency level of potassium was more stable during dormancy, but varied greatly between the growing seasons of different years. It seems that during the growing season the putrescine concentration and put/spd ratio indicates better the suboptimum potassium status of Scots pine than the needle potassium concentration. The strong response of putrescine to potassium level during the growing season could be explained by its possible role as a regulator of potassium transport (Feray et al. 1992). Putrescine could enable a flexible mobilizing ability of potassium sink in trees required by the varying growth conditions during the growing season.

Needle putrescine concentrations over 500 nmol g^{-1}FW quite regularly coincided with a nonsatisfactory potassium nutrition and concentrations over 1000 nmol g^{-1}FW were a reliable indication of potassium deficiency. In this study putrescine/spermidine ratio below 5 indicated a satisfactory potassium nutrition in all needle years throughout the year. The results suggest that the needle putrescine concentration or putrescine/spermidine ratio could be used as an indicator of pine potassium nutrition fairly reliably throughout the year.

The potassium analysis of needle samples collected in winter gives a reliable estimate of the potassium nutrition of trees during dormancy. The estimation of the sufficiency of potassium during the growing season on the basis of dormant samples is, however, susceptible to error. It is easier to estimate the minimum potassium levels of deficiency but more difficult to define the limits where potassium is not a limiting factor in any circumstances. The critical limits for the needle potassium concentration are not stable but depend on several growth factors during the growing season. In order to model the sufficiency of potassium in different growth conditions, experiments with more control over the affecting factors are required.

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