Variation in Needle Nutrient Concentrations in the Crown of Scots Pine on Peatland

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Variation in needle nutrient concentrations with age and vertical location in the crown was studied in three Scots pine stands growing on peat soils in eastern Finland. The concentrations of N, P, Fe and Zn decreased down the crown and those of Ca and Mn increased. Potassium and magnesium concentration patterns differed between sites.

Potassium and Mg concentrations were highest in the current needles at all heights in the crown, which was presumably due to retranslocation from the older needles. Calcium, iron and manganese concentrations were highest in the oldest needles. The concentrations of N, P and Zn did not vary with needle age.

The results emphasized the importance of careful selection of sampling point for needle nutrient analysis in the crown of Scots pine.

Keywords crown, conifer needles, leaf age, plant analysis, nutrient content, *Pinus sylvestris*.

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1 Introduction

Needle nutrient concentrations are used to diagnose the nutrient status of trees (Leyton and Armson 1955, Paarlahti et al. 1971, Mead 1984). Needle analysis is widely used for diagnosing Scots pine nutrient deficiencies and fertilization requirement on drained peatlands in Finland. Needle sampling is done on the dominant trees during the dormant period. Only the current needles of the topmost whorl on the southern side of the tree are sampled.

Needle nutrient concentrations vary seasonally as a result of the annual physiological cycle of trees (Tamm 1955, Nambiar and Fife 1987, Helmisaari 1990). Mobile nutrients are transported to the growing tissues in spring and translocated from senescing needles to the storage units of trees in autumn. The concentrations of mobile nutrients are low in summer and high in winter. Poorly mobile nutrients are not retranslocated and hence accumulate in the needles. The dormant period is the most convenient time for sampling because the nutrient concentrations remain rather stable for several months.

Needle dry mass and nutrient concentrations vary according to needle age (Mälkönen 1974, Paavilainen 1980, Raitio 1987, Helmisaari 1990, 1992a, Finér 1992). The dry mass of the youngest needles is lower than that of the older needles (Mälkönen 1974, Helmisaari 1990, 1992b). The concentration of mobile nutrients decreases with increasing age, and that of immobile nutrients increases (e.g. Helmisaari 1990). The current needles are preferred for diagnostical use since their nutrient concentrations are better correlated with the growth of trees than those of the other age classes (Leyton and Armson 1955). Nutrient concentrations in current needles have also less between-tree variation than in older needles (Mead and Will 1976, Morrison 1972).

Restricting sampling to one side of the crown of dominant trees is done to minimise variance. Dominant trees often have lower nutrient concentrations than suppressed trees (Wright and Will 1958, van den Driessche 1974). However, the aspect of the sample point in the crown probably has no importance (White 1954, Tamm 1955).

The results concerning the importance of sampling height in the crown are somewhat contradictory. There probably are some vertical nutrient concentration patterns related to species, stand and site (White 1954, Wells and Metz 1963, Madgwick 1964, van den Driessche 1974). However, some of the nutrient patterns that have been found in a vertical direction are biased by the sampling technique. The differences in nutrient concentrations between the top and base of the crown may be related to the light conditions and fertility of the site (Wells and Metz 1963, Madgwick 1964, van den Driessche 1974, Mead 1984). According to some model calculations, maximal use of N in photosynthesis occurs in stands where N concentrations decrease down the canopy, and the benefit obtained from such a vertical N distribution is the greatest in stands with dense canopies (Hirose and Werger 1987).

The aim of this study was to investigate vertical and age-related differences in needle nutrient concentrations in the crown of Scots pine (*Pinus sylvestris* L.) growing on peat soils in eastern Finland. This study is a part of two projects: a Nordic countries' project, the main objectives of which are to study the distribution and cycling of nutrients on drained ombrotrophic pine bogs in different climatic conditions, and the Finnish nationwide LAVAME project, the aim of which is to study the effects of fertilization on forest ecosystems.

2 Material and Methods

2.1 Sites

The material of the study was collected at three sites of different fertility in northern Karelia, Finland. One of them is located in Rääkkylä (64 km SE of Joensuu, 62°14'N; 20°50'E, 81 m a.s.l.) and the other two in Ahvensalo, Ilomantsi (90 km NE of Joensuu, 62°51'N; 30°53'E, 155 m a.s.l.). The climatic data for the site in Rääkkylä have been reported by Brække and Finér (1990).

The site in Rääkkylä was classified as a dwarf-shrub type (Vtkg) according to the classification of Laine (1989), and it has been drained in 1967. One of the sites in Ilomantsi was classified as a *Vaccinium vitis-idaea* type II (Ptkg) and the other as a *Vaccinium myrtillus* type II (Mtkg). The peat layer was more than one meter thick on all sites. The amounts of nutrients in the surface peat are presented in Table 1. The sites in Ilomantsi had been drained for the first time in the 1930s. Supplementary ditches were dug in the 1960s and in 1979.

Table 1. Amounts of nutrients (kg/ha) in the 0-20 cm peat layer in 1980 on the Ptkg and Mtkg sites and in 1984 on the Vtkg site (Finér 1989, Brække and Finér 1991).

Nutrient	Vtkg	Ptkg	Mtkg
N	1912	2570	5880
P	105	125	380
K	64	90	220
Ca	392	830	1650
Mg	69	140	200
Fe	213	340	1295
Mn	11	9	19
Zn	4.2	17	16
B	0.36	–	–

Table 2. Tree stand characteristics in 1984 on the Vtkg site and in 1985 on the other sites (Finér 1989, 1991a).

	Vtkg	Ptkg	Mtkg
Stem number,			
pines/ha	2364	1049	727
birches/ha		138	359
Mean diameter,			
pine, cm	9	15	18
birch, cm		11	15
Mean height,			
pine, m	9	11	16
birch, m		10	15
Mean length of the living crown,			
pine, m	5.7	6.2	5.8
Volume,			
pine, m^3/ha	81	73	109
birch, m^3/ha		5	40
Volume growth,			
pine, m^{3}ha/a	5.9	2.9	2.0
birch, m^3/ha/a			2.0

Table 3. Mean characteristics of the sample branches at different relative heights (%) in the living crown in 1984 on the Vtkg site and in 1985 on the other sites (Finér 1989, 1991b).

	Height	Vtkg	Ptkg	Mtkg
Diameter, mm	85	10	11	11
	75	13	15	14
	65	16	20	16
	55	18	22	22
	40	18	20	20
	15	19	21	17
Length, cm	85	54	61	62
	75	87	98	83
	65	110	136	107
	55	123	164	146
	40	129	157	142
	15	149	180	147
Age, years	85	3	3	4
	75	5	4	6
	65	8	7	9
	55	10	9	11
	40	13	10	14
	15	19	17	17

All the Scots pine stands were naturally regenerated, and their age about 85 years on the Vtkg, 40–50 years on the Ptkg and 40–60 years on the Mtkg site (Table 2). There were also some birches (*Betula pubescens*) growing on the Ptkg site in Ilomantsi.

2.2 Sampling

The needles were sampled in September–October in 1984 in Rääkkylä and one year later in Ilomantsi. Nineteen trees were sampled in Rääkkylä, and five sample trees on the Ptkg site and six sample trees on the Mtkg site in Ahvensalo. The sample trees represented different diameter classes and were chosen from the control plots by random stratified sampling based on breast height diameter (Finér 1989, 1991a). All the sample trees were felled. All the needles on six branches at the relative heights of 15, 40, 55, 65, 75 and 85 % from the lower limit of the living crown were collected from each sample tree. The needles were divided into three age classes as follows: current year needles (C), one-year-old needles (C + 1) and two-year-old and older needles (C ≥ 2). The sample branch characteristics are presented in Table 3.

2.3 Nutrient Analyses and Calculations

Nitrogen was analysed by the Kjeldahl method. The needle samples were ashed at 550°C, the ash extracted with HCl, and phosphorus determined photometrically by the molybdate-hydrazine method, and K, Ca, Mg, Fe, Mn and Zn by atomic absorption spectrophotometry. Boron was determined colorimetrically by the azothomethine method. The methods are described in detail by Halonen at al. (1983).

Differences in nutrient concentrations were tested by the paired t-test. All calculations were done by the SPSS/PC+ statistical package (SPSS/PC+... 1988).

Table 4. Variation in needle macro nutrient concentrations within the crown of Scots pine on different sites. Statistically significant ($p < 0.05$) differences in the mean nutrient concentrations between the different relative heights in the crown are indicated with the same small letters and the differences between the different needle age classes by the same capital letters. (C = current needles, C + 1 = one year old needles, C ≥ 2 = two year old and older needles).

Relative height		N %			P %			K %			Ca %			Mg %		
		C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2
	Vtkg															
85	$\bar{x}$	1.30a	1.20a	1.17	0.131ab	0.128abc	0.136a	0.411	0.325	0.307	0.184abcde	0.268abcd	0.395a	0.114a	0.113ab	0.082
	sd	0.14 AB	0.14 A	0.18 B	0.014	0.015	0.019	0.114 AB	0.072 A	0.124 B	0.034 AB	0.069 AC	0.067 BC	0.015 A	0.021	0.021 A
	cv%	11	12	15	10	12	15	28	22	40	18	26	17	13	19	26
	n	19	19	7	14	14	5	15	14	5	15	14	5	14	14	5
75	$\bar{x}$	1.30b	1.22bc	1.23	0.128c	0.122d	0.137	0.415	0.337	0.309	0.232a	0.357a	0.466b	0.119bcde	0.109cde	0.085
	sd	0.09 AB	0.10 A	0.11 B	0.013 A	0.012 A	0.058	0.091 AB	0.068 A	0.092 B	0.055 AB	0.087 AC	0.107 BC	0.012 AB	0.017 AC	0.017 BC
	cv%	7	8	9	10	9	42	22	20	30	24	24	23	10	16	20
	n	18	19	17	17	18	14	17	18	15	17	18	15	17	18	15
65	$\bar{x}$	1.29c	1.22d	1.25a	0.127d	0.122	0.125b	0.409	0.331	0.328	0.233b	0.357b	0.475cd	0.115efg	0.102e	0.081
	sd	0.11 AB	0.11 A	0.12 B	0.012	0.011	0.025	0.076 AB	0.061 A	0.057 B	0.053AB	0.074 AC	0.120 BC	0.015 AB	0.019 AC	0.021 BC
	cv%	8	9	9	9	9	20	19	18	17	23	21	25	13	18	26
	n	19	19	17	19	18	16	19	18	16	19	18	16	19	18	16
55	$\bar{x}$	1.27d	1.21e	1.24	0.123b	0.121b	0.119a	0.412	0.325	0.333a	0.238c	0.377c	0.500ade	0.108adhi	0.100bd	0.081
	sd	0.11 A	0.08 A	0.12	0.011	0.012	0.016	0.062 AB	0.066 A	0.052 B	0.056 AB	0.079 AC	0.101 BC	0.011 AB	0.014 AC	0.016 BC
	cv%	9	7	9	9	10	14	15	20	16	23	21	20	10	14	26
	n	19	19	17	19	17	16	19	17	16	19	17	16	18	17	16
40	$\bar{x}$	1.21abcd	1.19cf	1.26b	0.121acd	0.119cd	0.119	0.421	0.326	0.340	0.237d	0.400b	0.499	0.104cgi	0.098ac	0.081
	sd	0.09	0.09 A	0.12 A	0.010	0.009	0.011	0.069 AB	0.062 A	0.055 B	0.067 AB	0.084 AC	0.133 BC	0.014 AB	0.017 AC	0.018 BC
	cv%	8	8	9	8	8	9	16	19	16	28	21	27	13	17	22
	n	19	19	17	17	16	16	17	16	16	17	16	16	17	16	16
15	$\bar{x}$	1.10abcd	1.09abdef	1.18ab	0.123	0.113ad	0.112b	0.444	0.334	0.353a	0.261e	0.420d	0.554bce	0.102bfh	0.097c	0.082
	sd	0.08 A	0.18 B	0.13 AB	0.012 A	0.012 A	0.017	0.049 AB	0.049 A	0.050 B	0.059 AB	0.081 AC	0.138 BC	0.013 AB	0.012 AC	0.018 BC
	cv%	8	16	11	9	11	15	11	15	14	23	19	25	13	13	22
	n	19	18	16	11	12	15	11	12	15	11	12	15	11	12	15

Relative height		N %			P %			K %			Ca %			Mg %		
		C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2
	Ptkg															
85	$\bar{x}$	1.63abc	1.57a	1.59	0.197abc	0.154	0.168	0.509a	0.384a	0.361	0.188abc	0.240abc	0.252a	0.113	0.107ab	0.078ab
	sd	0.14 A	0.17 A	0.12	0.018	0.039	0.001	0.099 A	0.077 A	0.031	0.021 A	0.058 A	0.021	0.011	0.020	0.014
	cv%	8	11	8	9	25	8	19	20	9	11	24	8	10	18	18
	n	6	6	2	5	5	2	5	5	2	5	5	2	5	5	2
75	$\bar{x}$	1.60def	1.54b	1.53a	0.178abc	0.163abc	0.169ab	0.473bc	0.388bcd	0.375	0.207a	0.297acd	0.337bcd	0.113	0.118a	0.087bcd
	sd	0.07	0.12	0.10	0.012 A	0.012 A	0.014	0.087 AB	0.087 A	0.074 B	0.031 AB	0.063 AC	0.091 BC	0.011 A	0.019 B	0.014 AB
	cv%	5	8	6	7	7	9	18	22	20	15	21	27	10	16	16
	n	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
65	$\bar{x}$	1.53ae	1.54c	1.50b	0.164b	0.148	0.154ac	0.438	0.380e	0.378ab	0.210	0.304e	0.466cd	0.112	0.120b	0.098a
	sd	0.07	0.12	0.12	0.007 A	0.029	0.009 A	0.044 A	0.105	0.049 A	0.035 AB	0.069 AC	0.120 BC	0.011 A	0.022 B	0.017 AB
	cv%	5	8	8	4	20	6	10	28	13	16	23	26	10	18	17
	n	6	6	6	6	6	6	6	6	6	5	6	6	6	6	6
55	$\bar{x}$	1.45cf	1.51a	1.50	0.158c	0.148a	0.157d	0.415ac	0.356d	0.357c	0.221b	0.360c	0.497be	0.106	0.122	0.097d
	sd	0.13 A	0.09 A	0.12	0.009 A	0.004 AB	0.010 B	0.094 AB	0.076 A	0.069 B	0.031 AB	0.056 AC	0.109 BC	0.009 A	0.016 AB	0.013 B
	cv%	9	6	8	6	3	6	23	21	19	14	16	22	8	13	13
	n	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
40	$\bar{x}$	1.42be	1.44abc	1.45a	0.153a	0.144b	0.149cd	0.424b	0.339c	0.334bc	0.216	0.381bd	0.541de	0.096	0.117	0.099c
	sd	0.09	0.11	0.10	0.012 A	0.010 AB	0.007 B	0.110 AB	0.081 A	0.067 B	0.065 AB	0.085 AC	0.114 BC	0.005 A	0.017 AB	0.015 B
	cv%	6	8	7	8	7	5	26	24	20	30	22	21	5	14	15
	n	6	6	6	5	6	6	5	6	6	5	6	6	5	6	6
15	$\bar{x}$	1.32ad	1.30abc	1.29ab	0.155	0.140c	0.136b	0.454	0.319abe	0.337a	0.221c	0.383ae	0.579abc	0.094	0.116	0.106c
	sd	0.14	0.11	0.18	0.016 A	0.010 A	0.020	0.157	0.095	0.068	0.053 AB	0.089 AC	0.118 BC	0.008	0.019	0.016
	cv%	11	9	14	11	7	15	34	30	20	24	23	20	9	16	15
	n	6	6	6	4	6	6	4	6	6	4	6	6	4	6	6

Table 4 continued.

Relative height		N %			P %			K %			Ca %			Mg %		
		C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2
	Mtkg															
85	$\bar{x}$	1.58ab	1.54a	1.56	0.122	0.099	0.108	0.459	0.321	0.282a	0.183	0.231a	0.274ab	0.097a	0.091a	0.060a
	sd	0.27	0.17	0.18	0.012 A	0.020 AB	0.021 B	0.086 A	0.084 A	0.103	0.054 AB	0.082 A	0.098 B	0.013 A	0.017 B	0.015 AB
	cv%	17	11	11	10	20	19	19	26	37	30	35	36	13	18	25
	n	5	5	4	5	5	4	5	5	4	5	5	4	5	5	4
75	$\bar{x}$	1.60c	1.52bc	1.54	0.123	0.100	0.111ab	0.466	0.326	0.275b	0.190a	0.248	0.309c	0.094	0.094b	0.062
	sd	0.11	0.17	0.10	0.008	0.018 A	0.017 A	0.036 AB	0.091 AC	0.081 BC	0.071 AB	0.087 AC	0.118 BC	0.018 A	0.018 B	0.017 AB
	cv%	7	11	7	7	18	15	8	28	29	38	35	38	19	19	27
	n	5	5	5	4	5	5	4	5	5	4	5	5	4	5	5
65	$\bar{x}$	1.49d	1.43c	1.47a	0.122	0.098	0.105a	0.462a	0.312	0.295c	0.186ab	0.249a	0.361a	0.091	0.089	0.065a
	sd	0.17	0.14	0.06	0.010 AB	0.021 A	0.019 B	0.107 AB	0.092 A	0.069 B	0.077 AB	0.080 AC	0.151 BC	0.010 A	0.016 B	0.016 AB
	cv%	11	10	4	8	21	18	23	29	23	41	32	42	11	18	24
	n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
55	$\bar{x}$	1.46c	1.46d	1.44b	0.122	0.102a	0.107	0.459	0.311	0.314d	0.161b	0.214	0.362c	0.085a	0.078ab	0.064
	sd	0.16	0.09	0.04	0.009 AB	0.016 A	0.017 B	0.106 AB	0.096 A	0.084 B	0.063 AB	0.079 AC	0.125 BC	0.007 A	0.012 B	0.014 AB
	cv%	11	6	3	8	16	16	23	31	27	39	37	34	9	15	22
	n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
40	$\bar{x}$	1.31bc	1.37e	1.40c	0.120	0.099	0.105b	0.446a	0.335	0.327b	0.182	0.269	0.425b	0.083b	0.090c	0.067
	sd	0.14	0.13	0.08	0.008 AB	0.012 AC	0.015 BC	0.106 AB	0.106 A	0.083 B	0.067 AB	0.101 AC	0.186 BC	0.009 A	0.013 B	0.013 AB
	cv%	10	9	6	7	12	14	24	32	25	37	37	44	11	15	20
	n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
15	$\bar{x}$	1.14acd	1.20abde	1.30abc	0.111	0.094a	0.104	0.390	0.314	0.350abcd	0.209	0.276	0.489bc	0.081b	0.075c	0.071
	sd	0.19 A	0.12B	0.12 AB	0.015 AB	0.017 AC	0.015 BC	0.052 A	0.114 A	0.078	0.108 AB	0.136 AC	0.190 BC	0.011	0.011	0.014
	cv%	16	10	9	13	18	15	13	36	22	52	49	39	13	15	19
	n	5	5	5	3	5	5	3	5	5	3	5	5	3	5	5

3 Results

The concentrations of N, P, Fe and Zn were higher in the top than in the lower branches (Fig. 1, Tables 4, 5 and 6). Apart from Zn, this pattern was observed in all needle age classes. Potassium concentrations decreased down the crown on the Ptkg site but not on the Vtkg site. On Mtkg the K concentrations increased down the crown in the oldest needle age class. Magnesium concentrations decreased down the crown in the two youngest age classes on Mtkg and Vtkg. On Ptkg the Mg concentrations were higher at the base than at the top of the crown in the oldest needle class. The concentrations of Ca and Mn increased down the crown. There were some indications that the lowest B concentrations may occur in the middle of the crown.

The concentrations of K and Mg decreased and those of Ca, Fe and Mn increased with needle age irrespective of the location of the branch in the crown (Tables 4 and 5). The highest P concentrations were found in the current needles and the lowest in the one-year-old needles on Mtkg and Ptkg. The nitrogen and Zn concentrations and that of P on Vtkg showed no clear relationship with needle age.

The variation coefficients were lowest for N, P, Mg and Fe, and there were no clear differences due to the vertical location in the crown (Tables 4 and 5). The variation coefficients for the N, Ca and Mn concentrations were almost the same in all needle age classes. The variation coefficients for the other elements increased with needle age.

4 Discussion

2.1 Spatial Variation

The concentrations of N, P, Fe and Zn decreased down the tree crown. The crown layer in all stands was closed, and the tops of the trees in the upper tree classes, especially, were exposed to higher irradiances than the bases. The movement of nutrients in the upper level of crown could be increased by stimulated photosynthetic activity and transpiration. The N concentrations espe-

Table 5. Variation in needle micro nutrient concentrations within the crown of Scots pine on different sites. Statistically significant ($p < 0.05$) differences in the mean nutrient concentrations between the different relative heights in the crown are indicated with the same small letters and the differences between the different needle age classes by the same capital letters. (C = current needles, C + 1 = one year old needles, C ≥ 2 = two year old and older needles).

Relative height		Fe ppm			Mn ppm			Zn ppm			B ppm		
		C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2
	Vtkg												
85	x̄	32a	55ab	77	353abcd	547abcde	856	42a	44	48		14ab	13
	sd	7 AB	14 A	24 B	87 AB	156 A	269 B	11	20	21		6	0
	cv%	21	25	31	25	29	31	25	45	44		41	
	n	15	14	5	16	14	5	15	14	5		14	1
75	x̄	32bcd	56cd	64	431a	671a	661a	45bc	51	48	8	12bc	12a
	sd	5 AB	20 A	18 B	99 AB	184 A	271 B	6 A	11 A	26	0	5	4
	cv%	15	36	28	23	27	41	14	21	54		40	31
	n	17	18	15	17	18	15	17	18	14	1	18	9
65	x̄	32ef	48ef	72	423b	661b	773	42cd	50	42		11bc	12b
	sd	4 AB	9 AC	18 BC	83 AB	139 AC	195 BC	7 A	14 AB	11 B		4	3
	cv%	13	19	24	20	21	25	17	28	27		35	26
	n	18	18	16	19	18	16	19	18	16		18	12
55	x̄	29de	49 gh	69	418c	670c	720c	40ce	47	41	8	10ad	12c
	sd	3 AB	15 AC	15 BC	90 AB	140 AC	126 BC	8 A	13 A	11	0	3	4
	cv%	12	30	21	21	21	18	20	27	27		33	31
	n	19	17	16	19	17	16	19	17	16	1	17	13
40	x̄	28acf	45bdfh	70	430d	753d	838a	36ac	47	41		11e	13d
	sd	3 AB	10 AC	14 BC	101 AB	236 A	263 B	8 A	17 AB	17 B		4	4
	cv%	11	23	20	23	31	31	23	36	41		38	35
	n	17	16	16	17	16	16	16	16	16		16	14
15	x̄	27eb	40aceg	86	439	815e	940c	38bde	53	41	10	15cde	18abcd
	sd	4 AB	7 AC	54 BC	105 AB	256 A	403 B	6 A	11 AB	11 B	0	4	5
	cv%	16	18	63	24	31	43	16	21	27		26	27
	n	11	12	15	11	12	15	10	12	15	1	12	10

Relative height		Fe ppm			Mn ppm			Zn ppm			B ppm		
		C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2
	Ptkg												
85	x̄	49a	58abc	96a	184ab	240abcd	310a	40ab	35	28a	7	13	14
	sd	8 A	9 A	5	48 A	78 A	110	8	10	2	0	7	0
	cv%	16	15	5	26	33	35	21	28	7	1	56	
	n	5	5	2	5	5	2	5	5	2	2	5	1
75	x̄	46 ab	59de	84b	216a	318a	320bcd	39cd	37	47	7a	12a	11a
	sd	6 AB	14 AC	15 BC	55 AB	85 A	59 B	7	14	26	0	6	3
	cv%	12	23	18	25	27	19	19	38	55	5	48	29
	n	6	6	6	6	6	6	6	6	5	3	6	4
65	x̄	47 c	51c	81c	236	318	407bd	38ef	39	36	10	12b	11b
	sd	3 A	9 B	10 AB	62 A	136	94 A	7	9	8	4	6	4
	cv%	6	18	12	26	43	23	19	23	22	41	52	37
	n	6	6	6	6	6	6	6	6	6	5	6	6
55	x̄	44d	48gf	76d	233b	376b	441d	35ac	43	32a	8ab	12c	12c
	sd	7 A	4 B	11 AB	73 AB	106 AC	109 BC	5	15	6	2	6	5
	cv%	15	8	14	31	28	25	13	36	23	31	47	41
	n	6	6	6	6	6	6	6	6	6	4	6	6
40	x̄	38bd	43beg	74e	225	379c	466c	32bdf	38	32	8	13d	12d
	sd	6 A	7 B	9 AB	59 AB	117 AC	107 BC	6	9	5	3	6	6
	cv%	15	17	13	26	31	23	19	24	20	34	44	49
	n	5	6	6	5	6	6	5	6	6	4	6	6
15	x̄	35c	40adf	64abcde	245	402d	453ab	30ace	39	32	11b	16abcd	15abcd
	sd	2 A	6 B	6 AB	50 AB	103 A	75 B	4	10	16	3	6	5
	cv%	6	15	10	20	26	17	13	27	16	23	39	33
	n	4	6	6	4	6	6	4	6	6	3	6	6

Table 5 continued.

Relative height		Fe ppm			Mn ppm			Zn ppm			B ppm		
		C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2
	Mtkg												
85	x̄	42a	49	60	378	491ab	494ab	32a	25a	20	12	11	9
	sd	2	7	14	128	174	143	7	11	15	0	4	3
	cv%	6	14	23	34	35	29	23	43	73		36	29
	n	5	5	4	5	5	4	5	5	4	1	5	3
75	x̄	40	43	66	342	511	549ac	30b	24b	23	10	11	11a
	sd	6 A	5 B	5 AB	144 AB	163 A	178 B	6	9	18	2	3	2
	cv%	15	11	7	12	32	32	19	39	80	15	24	20
	n	4	5	5	4	5	5	4	5	5	2	5	4
65	x̄	38b	44	64	326a	505	577de	30	21ab	18	7	10	9a
	sd	4 A	3	10 A	118 AB	102 A	224 B	10 AB	9 AC	8 BC	2	2	2
	cv%	11	7	15	36	20	39	32	42	46	35	20	26
	n	5	3	5	5	5	5	5	5	5	3	5	5
55	x̄	41ac	44	66	302a	519	608	25b	19c	17	8	9	9
	sd	8 A	4 B	8 AB	119 AB	177 AC	227 BC	3 AB	4 A	6 B	2	2	3
	cv%	19	9	13	39	34	37	14	23	38	29	25	30
	n	5	5	5	5	5	5	5	5	5	5	5	5
40	x̄	35ab	47	57	326	569a	711be	22a	19d	16	8	10a	10c
	sd	5 A	17	6 A	131 AB	225 A	320 B	3 A	5	6 A	2	4	4
	cv%	16	36	10	40	40	45	13	28	36	31	39	44
	n	5	5	5	5	5	5	5	5	5	5	5	5
15	x̄	34c	46	54	381	573b	706cd	16	15cd	15	11	12a	13c
	sd	8	17	14	176 AB	216 AC	299 BC	2	4	6	0	5	6
	cv%	25	37	25	46	38	42	12	24	42		37	45
	n	3	5	5	3	5	5	3	5	5	1	5	5

Table 6. The correlation coefficients between the needle nutrient concentrations and relative height in the crown on the different sites, (C = current needles, C + 1 = one year old needles, C ≥ 2 = two year old and older needles).

	Vtkg			Ptkg			Mtkg		
	C	C+1	C≥2	C	C+1	C≥2	C	C+1	C≥2
N	0.54**	0.29*	0.05	0.72**	0.61**	0.60**	0.70**	0.66**	0.68**
P	0.24*	0.32**	0.18	0.66**	0.31	0.67**	0.32	0.10	0.10
K	–0.11	–0.00	–0.22	0.19	0.30	0.24	0.22	0.01	–0.32
Ca	0.30*	0.44**	0.30*	–0.23	0.55**	–0.63**	–0.06	–0.16	0.46*
Mg	0.37**	0.29*	0.03	0.62**	0.07	0.43*	0.45*	0.35	0.25
Fe	0.38**	0.36*	0.19	0.66**	0.63**	0.65**	0.43	0.09	0.32
Mn	–0.20	–0.36**	0.27*	–0.25	0.42*	0.46*	0.02	–0.18	–0.32
Zn	0.30*	–0.09	0.17	0.50*	–0.07	0.26	0.66**	0.43*	0.21
B		–0.06	–0.42**	–0.27	–0.20	–0.30	0.11	–0.17	–0.30

* = $p < 0.05$
** = $p < 0.01$

cially are known to be closely correlated with photosynthetic capacity (Field and Mooney 1986, Leuning et al. 1991). Hirose and Werger (1987) have even hypothesized that N concentrations should fall exponentially in closed canopies along with the decrease in irradiance if N utilization by trees is optimal. In this study the decrease in N, P, Fe and Zn concentrations down the crown was linear rather than exponential (see Tables 4,5 and 6), which could be connected to the known simultaneous decrease in needle dry weight (White 1954, van den Driessche 1974). The possible decrease in dry weight could also explain the observed increase in Ca and Mn con-

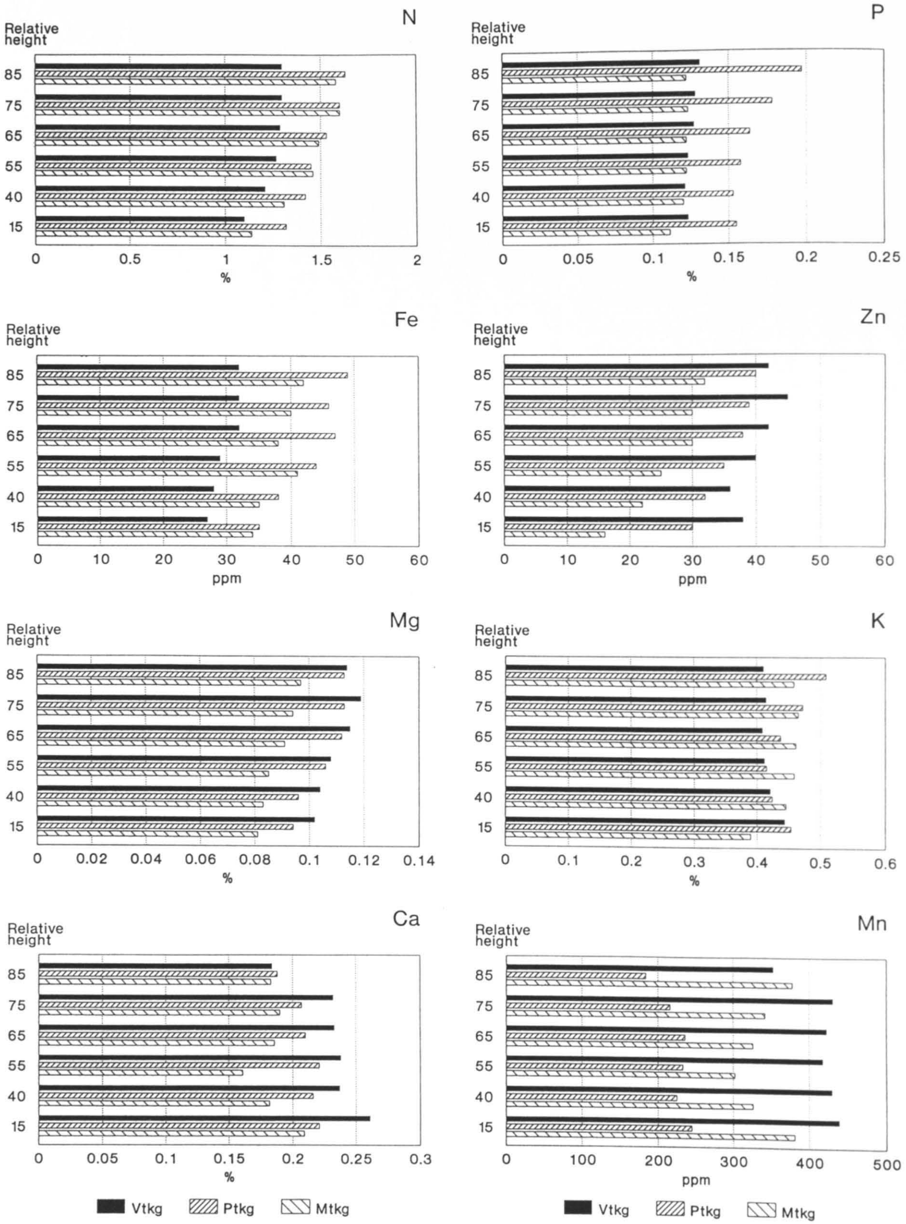

Fig. 1. Variation in current needle nutrient concentrations within the crown of Scots pine on different sites.

centrations down the crown. Calcium and Manganese are also poorly mobile and are mainly transported passively within plants (Mengel and Kirkby 1982). The vertical nutrient patterns occurred in all age classes as in the study by Madgwick (1964); not only in the youngest needles as in *Pinus banksiana* stands studied by Morrison (1972) or *Pinus resinosa* stands studied by Comerford (1981).

Earlier studies have not revealed any consistent vertical nutrient distribution patterns in the crowns of conifers (van den Driessche 1974). However, a decrease in P, K and Fe concentrations and simultaneous increase in Ca and Mn concentrations have been reported for *Pinus banksiana* (Morrison 1972). A decrease in N, P and K concentrations down the crown has been observed in *Pinus sylvestris* (Leyton and Armson 1955, Wright and Will 1958, Lehtonen 1977) and *Pinus resinosa* (White and Jokela 1980) on mineral soils. However, Mälkönen (1974) and Helmisaari (1992b) found no vertical pattern in the foliar nutrient concentrations of Scots pines growing in closed stands on mineral soil in Finland. The differences in nutrient patterns can be explained by species and site specific factors. There were also differences in sampling between Helmisaari's (1992b) and this study. The analysis of the results differed between this and Mälkönen's (1974) study.

The study deals with three sites of different fertility. It has been suggested that vertical nutrient concentration differences are positively correlated with the fertility of the site and tree growth (Wells and Metz 1963, Madgwick 1964, van den Driessche 1974). The material of this study was too small to verify this hypothesis. However, the decrease in N and P concentrations down the tree seemed to be the more marked, the greater the corresponding needle nutrient concentration on the site.

The changes in needle K, Ca, Mg, Fe, Mn and Zn concentrations with age were in accordance with earlier findings (Mälkönen 1974, Paavilainen 1980, Helmisaari 1990, 1992a, Finér 1992). Thus K and Mg can be regarded as mobile nutrients, Ca, Mn and Fe poorly mobile and the mobility of Zn intermediate. The differences in needle nutrient concentrations with age were the same at all levels in the crown (Madgwick 1964, Comerford 1981). Nitrogen and P are both regarded as mobile and their concentrations usually decrease with needle age (Mälkönen 1974, Helmisaari 1990, 1992a). However, our results did not show any clear changes in N and P concentrations with age. The changes in N concentrations with age are small in Scots pine stands growing on peat soils (see Paavilainen 1980, Reinikainen and Silfverberg 1983, Finér 1989, 1991b), and the same has been observed in *a Pinus banksiana* stand growing on poor mineral soil (Morrison 1972). In this study the changes in needle nutrient concentrations were not followed in the same needles as they aged, and hence the results could be affected by the weather conditions in the year when the needles were formed (Leaf et al. 1970, Helmisaari 1990).

4.2 Needle Analysis

The following criteria are often set when taking needle sample from a tree: the lowest possible between tree and within tree variation, the greatest correlation with growth or nutrient deficiency and ease of sampling (Morrison 1972, Comerford 1981). A single needle sampling point in the crown cannot satisfy these requirements for all nutrients, or usually not even for a single nutrient.

This study showed clear horizontal and vertical gradients for most of the studied nutrients, thus emphasizing the importance of sample location for needle analysis. Although, the sampling in this study did not include samples taken according to the present needle sampling procedure for diagnostic purposes on peatlands, it would appear that the mobile nutrients are usually taken at their local maximum and the immobile ones at their local minimum. This would suggest that different sampling point should be employed for different nutrients and different purposes. However, this is not supported by the fact that the nutrient concentrations of the current needles, especially those from the top of the crown are better correlated with growth than those taken from other parts of the crown, (Leyton and Armson 1955). The oldest needles are known to die and fall first if the trees are suffering from severe nutrient imbalances or other stress (Tikkanen and Raitio 1990, Finér 1991b), which does not always favour sampling old needles for nutrient analysis.

The differences in needle nutrient concentrations between the base and top of the crown are probably as much dependent on light as on the nutrient status of the tree (Mead 1984). Thus the differences in crown closure between stands has an effect on the vertical variation in needle nutrient concentrations, and it is probable that the nutrient concentrations of shade needles are the most affected. This would favour sampling in the top instead of the base (Wells and Metz 1963). The fact that the vertical nutrient concentration pattern is affected by the fertility of the site would give sampling preference to the top of the crown.

The results for *Pinus banksiana* have shown the lowest between tree variation in the base of the crown for most nutrients (Morrison 1972). In this study the youngest needles had lower between tree variation than the older ones for most of the nutrients, which could give them a preference for needle analysis (Tables 4 and 5, Morrison 1972, Mead and Will 1976). The samples included the whole stem diameter distribution and all needles of the sample branches. Thus the variation coefficients of K, Ca, Mn and Zn were somewhat higher than those presented for the dominant trees and needles of first-order or second-order branches in the whorl of Scots pine stands (Helmisaari 1992b).

The results of this study emphasize the importance of precise needle sampling, which is not always easy to put into practice in older stands. The vertical location and the age of the needles have an effect on the needle analysis results.

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