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Spatial and age-related variation in nutrient concentrations of *Pinus sylvestris* needles

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TIIVISTELMÄ: MÄNNYN NEULASTEN RAVINNEPITOISUUKSIEN PAIKALLINEN JA IÄNMUKAINEN VAIHTELU

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Spatial and age-related variation in nutrient concentrations of Scots pine (*Pinus sylvestris* L.) needles was studied during 1984–1986 in three stands of differing stages of development. The dry weight of current needles was significantly ($p < 0.05$) higher in the tree top than in a composite sample representing the whole crown. However, there were no significant differences in the concentrations of nutrients in needles between upper and lower crown levels. The concentrations of mobile nutrients N, P, K and Mg decreased with increasing needle age whereas the concentrations of poorly mobile nutrients Ca, Mn and Fe increased during needle ageing. The coefficient of variation for nutrient concentrations varied irregularly when only a few trees were sampled but stabilized when tree number was ten or more.

Männyn neulasten ravinnepitoisuuksien paikallista ja iänmukaista vaihtelua tutkittiin vuosina 1984–1986 kolmessa eri ikävaiheen männikössä Ilomantsin Mekrijärvellä. Uusimpien neulasten kuivapaino oli merkitsevästi suurempi puun latvassa kuin koko latvusta edustavassa näytteessä. Ylä- ja alalatvuksesta kerättyjen neulasten ravinnepitoisuudet eivät kuitenkaan eronneet merkitsevästi toisistaan. Liikkuvien ravinteiden (N, P, K, Mg) pitoisuudet vähenivät neulasen iän mukaan kun taas heikosti liikkuvien ravinteiden (Ca, Mn, Fe) pitoisuudet lisääntyivät neulasten vanhetessa. Ravinnepitoisuuksien variaatiokerroin vaihteli epäsäännöllisesti kun koepuita oli vain muutama, mutta tasaantui kun puiden lukumäärä oli 10 tai suurempi.

Keywords: nutrients, conifer needles, sampling, nutrient concentration, spatial variation, *Pinus sylvestris*.
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1 Introduction

Nutrient concentrations in the needles of coniferous trees have been shown to vary with the availability of nutrients in soil (e.g. Bell and Ward 1984), needle and tree age (e.g. Florence and Chuoung 1974, Mälkönen 1974, Miller et al. 1981, Madgwick et al. 1983, Raitio 1987), the phase of the annual physiological cycle (Tamm 1955, van den Driessche 1974, Fife and Nambiar 1982, 1984, Nambiar and Fife 1987, Helmisaari 1990) and needle position within the crown (Will 1957, Wells and Metz 1963, Mead and Will 1976). Therefore, temporal and spatial variation of needle nutrient concentrations have to be carefully considered in planning the time and place of needle sampling.

This study is a continuation of earlier studies concerning the temporal variation of Scots pine nutrient concentrations (Helmisaari 1990). The objective of this study was to evaluate the variation in needle dry weight and nutrient concentrations between trees, with needle age and with the vertical position in the crown of Scots pine (*Pinus sylvestris* L.).

2 Material and methods

2.1 Experimental stands

The material was collected in three naturally regenerated Scots pine stands in Ilomantsi near Mekrijärvi Research Station (62° 47' N, 30° 58' E, 145 m a.s.l.) in eastern Finland. The long-term mean annual temperature (1931–1960) was 2.0 °C and amount of precipitation 600 mm. The stands represent different stages of stand development – sapling stand, pole stage stand and mature stand (Table 1). One experimental plot was established in each stand for nutrient cycling studies spring 1983.

The experimental plots were placed on as homogenous an area as possible with regard to site characteristics. The soil type of the site is a podsol, relatively poor in available nutrients (Helmisaari and Mälkönen 1989). The site type in each stand, according to the classification of Cajander (1949), is the *Vaccinium* type; the field layer vegetation being dominated by *Vaccinium vitis-idaea* L., *Vaccinium myrtillus* L. and *Calluna vulgaris* (L.) Hull. *Pleurozium schreberi* (Brid.) Mitt. is dominant in the bottom layer, but *Cladonia* species are also common, especially in the sapling stand.

2.2 Needle sampling

Sample trees were selected from each stand from the dominant canopy layer in spring 1983 for studying temporal (Helmisaari 1990), spatial and age-related variation in nutrient concentrations.

Table 1. Some characteristics of the research stands in 1983.

	Sapling stand	Pole stage stand		Mature stand	
Plot	1	2	3	4	5
Plot area, m^2	400	500	500	875	875
Age, years	15	35	35	100	100
Fertilization, N kg ha	0	0	150	0	150
Number of trees/ha^{-1}	7425	2660	2980	432	455
Mean diameter, cm	1.6	7.7	6.8	27.3	25.9
Mean height, m	2.0	6.8	5.6	20.1	19.4
Basal area, m^2 ha^{-1}	2.2	13.8	11.9	25.7	24.7
Stem volume, m^3 ha^{-1}	7.9	57.7	43.8	258.1	245.0
Volume increment, m^3 ha^{-1} yr^{-1}	1.8	5.2	4.5	3.5	4.1

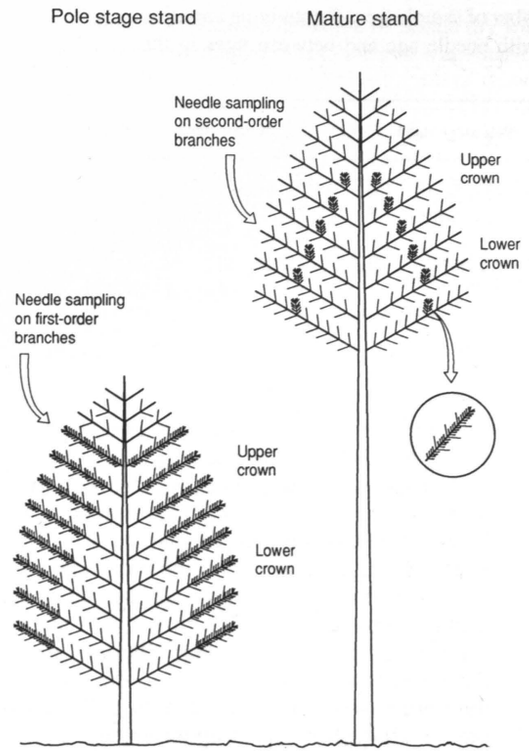

Fig. 1. Diagram showing needle sampling positions.

Dominant trees with a large needle mass were selected because same trees were sampled in many sampling occasions, and needle sampling is destructive. Also, upper crown needles of dominant trees have more similar light position in successive years than needles in trees representing dominated canopy layers.

For studying the *vertical variation* of needle nutrient concentrations, needles were collected in the two oldest stands from the upper and lower crown levels of six trees during summer 1984. For determining crown levels, living crown was divided into two parts based on the number of living whorls. The lower limit of living crown was determined as the lowest living branches above which there were less than two whorls of dead branches. The mature stand was sampled May 24th and July 10th and the pole stage stand May 12th, July 11th and September 18th, 1984. The effects of horizontal variation were minimised by collecting samples from different needle age classes in upper and lower crown of a tree as follows: in the pole stage stand in the upper half of the crown all healthy first-order branches below the fourth whorl from the top were selected (Fig. 1). In the lower half of the crown, all healthy first-order branches were selected. The light position of the branches in the upper and lower crown was clearly different. Upper crown branches were growing in light while lower crown branches were shaded. Twenty needles from each needle age class on each of these branches were collected at each sampling and the needles belonging to the same age class within the same crown level of the tree were combined for nutrient analyses. Thus, at each sampling time, there were two samples per needle age class for each of the sample trees. Sampling in the pole stage stand was carried out from a transportable 6 m high tower.

In the mature stand a 25 m high crane was used for sampling during the growing season. Six first-order branches were marked both in the upper crown and lower crown of each sample tree. At each sampling time one second-order branch from each of these first-order branches was cut (Fig. 1). First-order branches were not cut themselves because it would have been too damaging. Elongating needles were not sampled. Sampling of current year needles started in July when elongation had terminated.

In 1985 in the pole stage stand, the needles of three trees were sampled in May, July and September. One composite sample of current needles was taken from three branches in the fourth whorl from the top. One sample representing the current needles in the whole crown was sampled from every fourth branch spiralling downwards starting from the tree top.

The variation *between trees* in needle nutrient concentrations was studied in September–October 1983 in all stands (sampling dates listed in Table 2). Sampling was done from the upper half of the canopy using the same methods as for sampling upper and lower crown levels.

The variation with *needle age* in needle nutrient concentrations was analyzed by sampling the same needle age-class in all stands during its ageing in successive years (Table 2). Sampling was done from the same sample trees each sampling time in the mature stand, but in the younger stands sample trees were changed in the autumn 1983 (see Helmisaari 1990). Each needle age-class was sampled as long as it existed in the trees. Sampling was done from the upper crown in the pole stage stand using the same methods as for sampling upper and lower crown levels (sampling was started each year from the fourth branch whorl downwards, Fig. 1). Thus

Table 2. Needle sampling dates and number of sample trees for studying variation in needle nutrient concentrations with needle age and between trees in the experimental stands.

Year	Sapling stand		Pole stage stand		Mature stand	
1983	27. Sept.– 3. Oct.	27	26.–27. Sept.	24	29. Sept.	12
1984	5. Sept.	6	18.–20. Sept.	5	29. March	12
1985	-		-		11. March	12
1986	8.–10. Sept.	8	8.–29. Sept.	8	18. March	12
1987	21. Sept.	8	22. Sept.	8	19. March	11

the light position of the sample branches was as same as possible each year.

During the nonactive period (October–March), sampling in the mature stand was done by shooting down the branches. Three second-order branches were shot down from the upper crown of each sample tree. The same number of needles from each needle age class on each of the second-order branches was collected and the needles from the same age-class and tree were combined for analyses.

2.3 Laboratory analysis and data processing

The needle samples were dried at 70 °C for 48 hours, weighed, and the dried samples stored in paper bags. Concentrations of P, K, Ca, Mg, Mn, Cu, Zn, Fe, B and Al were determined by dry ashing and using methods described by Halonen et al. (1983). The nutrient analyses were made each year some months after sampling. Nitrogen concentration was determined using the Kjeldahl method and phosphorus was determined colorimetrically with the molybdate-hydrazine method. Potassium, calcium and magnesium were determined with a flame atomic absorption spectrophotometer (Perkin Elmer 3030). Micronutrients (Mn, Cu, Zn, Fe) and aluminium were determined with a flameless atomic absorption spectrophotometer (Perkin Elmer AS 40). Boron was determined colorimetrically. Aluminium is included in this study, although it is not considered to be a nutrient element.

The means were compared by using ANOVA (unbalanced data) and t-tests from the SAS statistical package (SAS/STAT... 1989).

3 Results and discussion

3.1 Vertical variation

The dry weight per needle was smaller in the lower crown but because of the large variation in dry weight the differences between upper and lower crown levels were not significant. There were also no significant differences in the concentrations of nutrients between crown levels (Tables 3–4) except for potassium in needle age class C+2 in the mature stand. The variation of nutrient concentrations between crown levels was similar for all sampling times (May, July, September).

Nutrient concentrations of current needles sampled from the tree top were also compared with a composite sample representing the whole crown. The needle dry weight of the composite sample was significantly smaller than that in the tree top (Table 5). Nutrient concentrations did not differ significantly except aluminium which was present in higher concentrations in the tree top.

Many other reports also show that the variation in the needle nutrient concentrations within the crown is very small (Peterson 1961, Morrison 1972, Mälkönen 1974). Tamm (1955, 1968)

Table 3. Mean and standard deviation of needle dry weight and nutrient concentrations in needles of various ages in the two canopy levels of the pole stage stand, sampled in 11.7.1984 (C+1 = needles formed in 1983 etc.).

Needle age class	Crown level		Number of sampled trees	Needle dry weight, mg	N	P	K	Ca	Mg	Mn	Cu	Zn	Fe	B
					g/kg					mg/kg				
C+1	Upper	x	12	17.2	9.1	0.9	3.6	1.9	0.8	537	2.0	27.9	69.1	6.2
		sd		3.9	0.7	0.3	0.5	0.5	0.1	151	1.1	5.3	32.6	1.3
	Lower	x	6	11.3	10.9	0.8	3.4	1.8	0.7	531	2.5	22.8	40.6	7.2
		sd		3.5	2.4	0.2	0.5	0.7	0.1	133	1.7	3.1	13.2	1.9
C+2	Upper	x	12	17.3	8.9	0.9	3.1	2.6	0.6	625	1.5	32.1	88.8	4.9
		sd		3.9	0.6	0.3	0.6	0.8	0.0	193	0.5	3.7	36.6	0.5
	Lower	x	6	10.9	9.5	0.8	3.1	2.3	0.6	619	2.4	25.8	57.5	5.6
		sd		2.6	0.6	0.2	0.4	0.8	0.1	175	1.4	3.1	17.0	0.9
C+3	Upper	x	12	18.1	8.5	0.8	2.8	3.1	0.5	779	2.0	34.9	105.3	5.1
		sd		5.3	1.3	0.2	0.5	0.9	0.1	265	0.9	3.3	71.1	0.4
	Lower	x	6	11.6	9.5	0.8	2.9	3.2	0.5	822	2.3	27.0	68.9	5.7
		sd		1.8	0.7	0.2	0.5	1.0	0.0	272	1.4	3.1	17.8	0.7

Table 4. Mean and standard deviation of needle dry weight and nutrient concentrations in needles of various ages in the two canopy levels of the mature stand, sampled in 10.7.1984 (C+1 = needles formed in 1983 etc.). Values marked with the same letter differ significantly ($p < 0.05$) between canopy levels.

Needle age class	Number of trees	Crown level		Needle dry weight, mg	N	P	K	Ca	Mg	Mn	Cu	Zn	Fe	B	Al
					g/kg					mg/kg					
C+1	6	Upper	x	13.7	9.8	0.8	2.8	2.5	1.1	310	3.0	24.0	51.0	11.5	154
			sd	4.7	2.0	0.1	0.4	0.5	0.3	56	0.9	3.2	11.8	1.8	18
	3	Lower	x	11.6	11.2	0.9	3.1	2.7	1.0	261	3.4	21.1	64.9	13.8	131
			sd	3.5	1.1	0.1	0.2	0.6	0.2	82	1.2	1.1	16.1	3.4	-
C+2	6	Upper	x	14.2	9.0	0.8	2.7 a	2.6	0.8	271	2.8	21.6	72.6	8.9	187
			sd	5.2	0.9	0.1	0.3	0.8	0.2	64	0.8	5.5	16.1	2.0	29
	3	Lower	x	13.9	10.4	0.9	3.2 a	3.1	1.0	262	3.4	19.0	58.6	11.0	132
			sd	2.8	1.8	0.2	0.3	1.0	0.1	111	0.3	1.3	13.2	3.1	-
C+3	6	Upper	x	15.8	9.1	0.8	2.5	3.1	0.8	313	3.3	22.7	78.3	7.3	188
			sd	8.6	1.0	0.1	0.3	0.8	0.1	95	2.1	9.2	13.8	0.7	53
	3	Lower	x	13.0	10.0	0.9	3.1	3.4	0.7	273	2.9	19.6	77.5	10.8	138
			sd	2.1	1.5	0.1	0.3	0.8	0.1	91	0.6	5.3	6.5	1.8	-

Table 5. Mean and standard deviation of needle dry weight and nutrient concentrations in current needles in the fourth whorl below the top and in the whole crown of three trees in the pole stage stand, sampled in May, July and September 1985. Mean values marked with the same letter differ significantly ($p < 0.05$) between sampling places.

Crown level		Needle dry weight, mg	N	P	K	Ca	Mg	Mn	Cu	Zn	Fe	B	Al
			g/kg					mg/kg					
Tree top	x	20.9 a	10.9	1.3	4.6	2.3	1.1	625	3.5	60.1	76.7	3.5	566 a
	sd	6.4	0.2	0.2	0.1	0.6	0.1	144	0.7	12.1	17.3	1.3	79
Whole crown	x	9.4 a	12.0	1.2	4.3	2.4	0.9	671	3.0	45.7	61.4	4.1	365 a
	sd	3.0	1.3	0.2	0.2	0.7	0.3	109	0.2	12.6	27.3	0.5	54

Table 6. Mean and standard deviation of needle dry weight and nutrient concentrations in needles formed in 1983 in the experimental stands. Mean values marked with the same letter differ significantly ($p < 0.05$) between sampling years.

Sampling date		Needle dry weight, mg	N	P	K	Ca	Mg	Mn	Zn	Fe	B	Al
			g/kg					mg/kg				
Sapling stand												
830927–	x	7.5	12.8 a	1.3 a	4.7 a	2.4 a	0.9 a	744	41.6	37.6 a	14.1	263
831003	sd	1.7	1.20	0.10	0.40	0.40	0.10	147	6.9	4.3	2.7	71
840905	x	8.8	9.6 a	0.9 a	3.0 a	3.3 a	0.6 a	854	41.5	60.4 a	8.7	343
	sd	2.9	1.20	0.10	0.40	1.20	0.10	357	11.5	7.2	-	41
Pole stage stand												
830926 –	x	12.8	13.1 ab	1.4 ab	5.3 a	1.9 a	1.1 ab	513 a	45.3 a	43.3 a	11.8 ab	ND
830927	sd	2.5	1.3	0.1	0.7	0.3	0.1	126	5.5	8.1	4.6	-
840918–	x	11.9	10.1 a	1.2 a	4.3 a	2.7 b	0.9 a	635 b	41.8 b	117.5 ab	6.6 a	394
840920	sd	2.4	0.6	0.2	0.4	1.7	0.1	111	11.0	54.9	1.4	23
860908–	x	14.8	9.1 b	1.1 b	3.2 a	4.0 ab	0.7 b	985 ab	55.6 ab	38.3 b	7.2 b	417
860929	sd	2.8	0.8	0.1	0.4	0.9	0.2	224	14.3	6.3	1.8	156
Mature stand												
840329	x	11.5	10.2 a	1.2 a	3.9 ab	2.0 ab	1.2 ab	244 ab	29.9 a	37.4 ab	13.6	168 abc
	sd	3.0	1.0	0.1	0.5	0.5	0.2	80	4.7	11.9	1.0	33
850311	x	11.3	8.9 ab	1.0 abc	3.1 ac	2.7 ac	1.2 c	334 cd	29.8 b	48.9 a	14.8 a	253 a
	sd	2.6	1.0	0.1	0.5	0.6	0.1	111	9.4	10.9	5.7	44
860318	x	9.9	11.9 ab	1.2 b	3.8 cd	3.4 a	1.0 a	486 ac	40.3 ab	73.5 a	11.1 ab	267 b
	sd	2.9	1.0	0.1	0.5	0.6	0.2	134	6.9	7.5	2.5	64
870319	x	11.3	10.5 b	1.1 c	2.8 bd	3.4 bc	0.9 bc	581 bd	35.7	55.3 b	15.1 b	255 c
	sd	5.1	1.0	0.1	0.5	0.6	0.3	212	15.5	10.7	0.9	61

suggested that elemental concentration in the needles does not consistently differ with branch aspect and age. However, van den Driessche (1974) stated that since growth is very dependent on light through photosynthesis, shaded foliage could be expected to show higher nutrient concentrations than otherwise comparable unshaded foliage. Many reports show also that the concentrations of N, P and K decrease down the crown (White 1954, Lowry and Award 1965, Lehtonen 1977, Madgwick et al. 1983, Miller 1983, White and Jokela 1980).

Thus, the variation in nutrient concentrations and especially needle dry weight within the canopy could be affected by light environment. In this study, both research stands had a closed canopy layer (canopy cover approximately 60 %) and thus there was less available light in the lower canopy. This explains why needle dry weight was smaller in the lower canopy, though not always significantly.

3.2 Variation with needle age

There were no significant differences in the needle dry weight (Table 6) when the same needle age class was sampled during successive years. The concentrations of Ca, Mn and Fe increased significantly during ageing but the concentration of iron decreased again in the oldest needles. These nutrients are poorly mobile and accumulate in needles with needle age (Helmisaari 1990). The concentrations of N, P, K and Mg were significantly highest in the youngest needles in the two youngest stands but in the mature stand there were no clear trends, except for magnesium, which decreased with needle age. N, P, K and Mg are clearly mobile (Helmisaari 1992a,b). Because needles were collected from cut branches in the mature stand, sampling positions were not as precisely defined as in the two youngest stands, where needles were collected from the same branches during successive years. Many earlier reports also show that the concentrations of poorly mobile nutrients Ca, Mn and Fe increase in needles with needle age while the concentrations of mobile nutrients decrease in needles during ageing (Keay et al. 1968, Florence and Chuoung 1974, Mälkönen 1974, Mead and Will 1976, Bell and Ward 1984, Raitio 1987).

Only the youngest needle age class is generally sampled for needle analysis (Leyton and Armson 1955, Wells and Metz 1963, Lowry 1970). This means measuring mobile nutrients at their maximum and poorly mobile elements at their minimum concentrations. The recently developed young needles are physiologically most active and the content of mobile nutrients in them represent both nutrient uptake and retranslocation from older tissues. The mobile nutrients are retranslocated from older needles to younger ones and therefore also the differencies between the nutrient concentrations of younger and older foliage have been suggested to be used to indicate the depth of nutrient deficiency (Tamm 1955, Florence and Chuoung 1974).

3.3 Variation between trees

Coefficient of variation (CV) for macronutrient concentrations varied most when only a few trees were sampled but leveled off when the tree number was ten or greater (Fig. 2). The coefficient of variation was highest in the oldest stand. In the pole stage and mature stands P, K and N had lowest CV (< 10 %) while in the sapling stand CV was smallest for N, P, K and also Mg. CV was always less than 16 % also for the other macronutrients except for calsium in the mature stand (Fig. 2). CV for micronutrient concentrations varied more than for macronutrients. However, when the tree number was ten or more, the variation in CV was small in the two youngest stands also for micronutrients. CV for Fe and Zn was always lower than 16 %, for B and Mn it was between 15–20 % in the pole stage and mature stands and between 25–35 % in the sapling stand.

These results suggest that at least ten trees should be sampled in each stand to minimize the between-tree variation in nutrient concentrations. Wells (1969) also suggested that ten trees per plot would satisfactorily indicate the nutrient status of pole stage *P. taeda*. Lowry and Avard (1969) working with mature *Picea marina* and *Pinus banksiana*, suggest that foliage should be selected from 20 trees per plot. Also Knight (1978) suggested at least 20 trees per sample to be sampled for detecting differences of 20 % or more.

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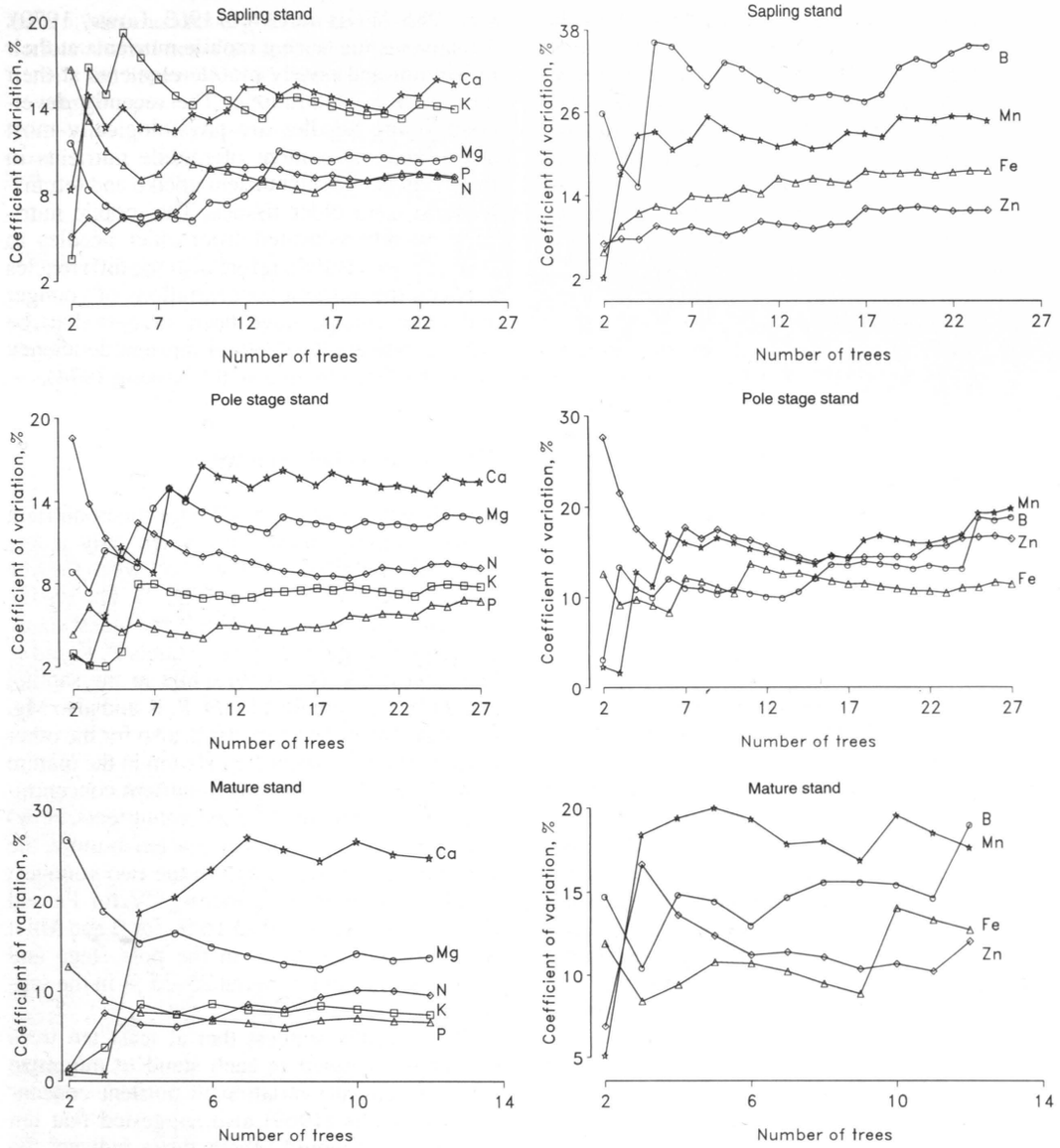

Fig. 2. Coefficient of variation for needle nutrient concentrations (current needles, sampled in September 1983) with varying number of sample trees in the research stands.

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