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Relationships between needle nutrient composition in Scots pine and Norway spruce stands and the respective concentrations in the organic layer and in percolation water

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We explored how N, S, P, Ca, K, Mg, Zn and Mn concentrations in percolation water (PW) and organic layer (OL) are reflected in the respective element concentrations in Scots pine and Norway spruce current needles. For both tree species, N and Ca had the highest covariation ($R_{\mathrm{adj}}^2 \geq 0.73$) between nutrient concentrations in the OL and in the needles. Mean N, S, P, K, Zn and Mn concentrations in PW significantly explained the variation in the respective needle concentrations on the spruce plots, and of K, Zn, and Mn in PW on the pine plots. The annual variation in needle element concentrations did not account for the respective variation in PW. Our results suggest that plant metabolism regulates the nutrient concentrations in the current needles more strongly in pine than in spruce, whereas the supply of soil nutrients is more clearly reflected in the nutrient concentrations of spruce.

Introduction

Mineral nutrients play an essential role in plant metabolism. Knowledge about nutrient requirements of plants and factors affecting their availability in the soil is therefore crucial for understanding the functioning of forest ecosystems and for ensuring the sustainable management of forests. Impaired forest (tree) condition has often been reported to be related to nutrient deficiencies and imbalances (Raitio 1990, Huettl 1993).

In general, uptake of nutrients, i.e. transfer of solutes from the soil solution into the root cells, is mediated by mass flow driven by the transpiration stream and by diffusion along concentration gradients between the nutrient sources (e.g. soil-mycorrhiza-root interfaces) and sinks (e.g. active meristems; Marschner 1995). The strength of the sinks, i.e. growth activity of the meristems, is physiologically controlled by the plant hormonal system which, in turn, is regulated by the availability of resources (sink-source hypothesis; Clifford 1992, Haukioja and Honkanen 1997). The source-sink dynamics greatly control plant growth and, consequently, the demand for mineral nutrients (Kaitaniemi and Honkanen 1996, Honkanen *et al*. 1999). The symbiotic association between trees and ectomycorrhizal fungi plays a crucial role in nutrient and water uptake by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Lucash *et al*. 2007). In exchange for the acquisition of photosynthates from the plant, the mycelia of the ectomycorrhizal fungi contribute to plant metabolism by increasing the surface area for resource acquisition (Rousseau *et al.* 1994), by enhancing the solubility and availability of soil nutrients (Bending and Read 1995, Perez-Moreno and Read 2000, Landeweert *et al.* 2001, Fomina *et al.* 2006, Corratge *et al.* 2007), and by increasing the tolerance of trees to elevated heavy metal concentrations (Jentschke and Godbold 2000). The classical studies of Ingestad (1971, 1979, 1981) demonstrated that the optimum growth of higher plants was achieved when the ratios between the macronutrients were within a certain range. These relationships, together with the fact that nitrogen availability is frequently the primary growth-limiting factor in boreal forest ecosystems (Tamm 1991), imply that, in theory, if the sink strength decisively regulates the uptake of nutrients in relation to demand rather than to supply, then the nitrogen status of the tree would strongly determine the concentration of other nutrients in the foliage.

In boreal forest ecosystems, the organic layer serves as an important stock of mineral nutrients and, for example, the total nitrogen concentration in the organic layer is the best chemical soil variable explaining site quality in both Scots pine and Norway spruce stands on mineral soil sites in Finland (Tamminen 1993). Chemical analysis of the soil thus provides information about the capacity of a soil to supply nutrients to the plants. However, chemical soil analysis fails to take into account many biological (e.g. microbial activity, root distribution, mycorrhizal associations, availability of carbohydrates to roots, competition) and physico-chemical (e.g. temperature, water availability, aeration, interactions between chemical compounds) factors affecting the uptake and availability of nutrients to plants. Furthermore, determination of the reserves of e.g. exchangeable nutrients in the soil does not necessarily provide information about the actual uptake of nutrients by the tree stand, because it represents the "net" reserves in the soil, i.e. the difference between the amount of mineral nutrients released through mineralization and weathering and the amount taken up by the trees and other vegetation. Chemical analysis of the tree foliage is therefore preferred for assessing the current nutrient status of a plant (Kimmins 1987, Walworth and Sumner 1988). Several studies have investigated the relationship between foliar and soil chemistry in forest ecosystems (Huntington *et al.* 1990, Landmann *et al.* 1995, Bauer *et al.* 1997, Jandl and Herzberger 2001), but studies carried out in the boreal region are rare. Even less is known about the relationship between soil solution chemistry and the nutrient status of trees (Aitkenhead-Peterson *et al.* 2006). In theory, the concentrations of individual nutrients in the soil solution should be more closely related to the nutrient status of the trees than the concentrations in the organic layer, because nutrient uptake takes place via the liquid phase in the soil.

When investigating the relationships between foliar, soil and soil solution chemistry, there are a number of spatial and temporal problems associated with sampling. Obtaining spatially representative samples is relatively straightforward with respect to the needles and soil, and these questions have been extensively studied and suitable sampling and analytical procedures developed (Anon. 2000, 2006). Soil solution sampling is more problematic because it is difficult to obtain spatially representative samples without causing major disturbances to the soil, and there is also a relatively wide choice of techniques available for sampling different fractions of the soil solution, e.g. the water present in micro- and macropores, and seepage/percolation water (Anon. 2002). Temporal variation in foliar, soil and soil solution samples can have a considerable effect on the outcome of studies on the nutrient status of forest ecosystems, because the chemical composition of these attributes varies considerably at different times of the year. The element concentrations in needles fluctuate according to variations in the dry matter content of the needles, which varies seasonally and increases along with needle age (Linder 1995). Therefore, needles are normally sampled during the dormancy period, but this inevitably means that the results are not necessarily comparable to those obtained for soil and soil solution sampled during the growing period. Although a number of studies have been carried out on the temporal variation in chemical soil properties (e.g. pH, total and exchangeable nutrient concentrations), it is extremely difficult to quantify the temporal variation owing to the confounding interaction between the temporal and spatial variation in the soil. It is clear, however, that there is considerable variation during the growing season (Lehtonen *et al*. 1976, Lockman and Molloy 1984). Taking into account the temporal variation in the chemical composition of the soil solution is less of a problem because most of the lysimeter techniques used for sampling soil solution are based on continuous sampling at the same points in a stand, and mean values representing the whole growing season can be calculated.

In this study, we explored how the concentrations of macronutrients (Ca, Mg, K, N, P and S) and micronutrients (Zn and Mn) in percolation water (collected immediately below the organic layer) and in the organic layer are reflected in the concentrations of the respective elements in Scots pine and Norway spruce needles. As a reference for these relationships, we also evaluated the dependence of needle S, P, Ca, K, Mg, Zn and Mn concentrations on the needle N concentration. This information will contribute to our understanding of the dependence of the nutrient status of trees on the supply of soil nutrients.

Material and methods

Study sites

Thirteen Scots pine (*Pinus sylvestris*) and fourteen Norway spruce (*Picea abies*) plots belong to the European intensive forest monitoring network (Level II), established under the EU/Forest Focus and UN-ECE/ICP Forests monitoring programmes (Derome *et al*. 2007, Merilä 2007; *see* also Preface to this issue). The plots were located on mineral soil sites throughout Finland (for the site, stand and soil characteristics *see* Table 1) covering Cajanderian forest site types ranging from herb-rich to xeric heath forests (Cajander 1926, Salemaa *et al*. 2008). The organic layer on all the sites was classified as mor. All the plots, except for the four Integrated Monitoring plots established in nature conservation areas (ICP-IM plots nos. 19, 20, 21, 22), are located in semi-natural, managed forests.

Sampling and analysis of needles

In determining the nutrient status of the stands, we utilized a dataset comprising plotwise mean concentrations of nitrogen (N), sulphur (S), phosphorus (P), calcium (Ca), potassium (K), magnesium (Mg), zinc (Zn), and manganese (Mn) in the current needles of the 13 Scots pine and 14 Norway spruce plots collected in 1999, 2001, 2003 and 2005. Current needles developed in favourable light conditions were chosen as being representatives of the most recent and significant sink for mineral nutrients. The concentrations of current needles were also considered to be least affected e.g. by translocation processes or by deposition on the needle surfaces (Helmisaari 1992a, Honkanen *et al*. 1999). Two sets of 10 predominant or dominant sample trees were selected for needle chemistry analyses on each of the plots belonging to the intensive monitoring plot network. Sample branches were taken from 10 of these trees every second year. The two tree sets were sampled in rotation, i.e. each set was sampled every 4 years. Needle samples were collected from the bottom part of the uppermost third of the living crown (between the 7th and the 15th whorls) with a pruning device during October and November (Anon. 2000).

The branches were stored in a freezer (–18 °C) during the period between sampling and pre-treatment. In the pre-treatment procedure, the branches were cut into separate shoot sections bearing different needle-year classes. Shoots with the same needle-year class of each tree were pooled and subsequently treated as a separate sample. The shoots were dried at 60 °C for 10 days and the needles then removed from the shoots. The dry needles were milled using an ultracentrifugal mill (mesh size 1 mm).

Unwashed current needles on each tree (n = 10) and on each plot were analysed separately for total N, S, P, Ca, K, Mg, Zn, and Mn. The N concentration was determined without any further pre-treatment on a CHN analyser (Leco).

The S, P, Ca, K, Mg, Zn, and Mn concentrations were determined, following closed HNO_3/H_2O_2 digestion in a microwave oven, by inductively coupled plasma emission spectrometry (ICP/AES). The results were calculated as mean concentrations per plot per 105 °C dry weight (Anon. 2000).

Sampling and analysis of percolation water

Percolation water (PW) was collected at 4-week intervals during the snowfree period in 1999–2005 using zero tension lysimeters (diam. 20 cm) located immediately below the organic horizon (5–10 cm below the ground surface, for details of lysimeter construction and installation, *see* Derome *et al*. 1991) in 7–8 of the pine and 6–8 of the spruce plots (Table 1). There were 5 replicate lysimeters at the same depth on each plot. The soil type on the plots is podzolic; most of the pine plots are located on sorted glaciofluvial material, and the spruce plots on till soils. The samples were filtered through membrane filters (0.45 μm) under positive pressure by means of a peristaltic pump. Dissolved organic carbon (DOC) was determined using a TOC analyzer, and Ca, K, Mg, SO_4 and NO_3 with ion chromatography (IC). Total N and NH_4 were determined by means of flow injection analysis, and NO_3, SO_4 and PO_4 using ion chromatography. Ca, Mg, K, Zn and Mn were determined with ICP/AES following preservation of the samples with

Table 1. Site, stand (in 2004) and soil characteristics of the study plots. The plots with percolation water sampling are indicated with an asterisk (*).

No.	Plot	Lat. N	Long. E	Forest site type[1)]	Age	Stem volume (m^3 ha^{-1})	Mean height (m)	Soil type[2)]
Pine plots								
1*	Sevettijärvi	69°35´	28°54´	UVET	205	76.4	11.5	Ferric Podzol
2	Pallasjärvi	67°57´	24°03´	EMT	95	80.4	10.7	Ferric Podzol
4	Sodankylä	67°20´	26°39´	EMT	85	137.1	13.9	Ferric Podzol
6*	Kivalo	66°22´	26°44´	EMT	60	167.3	13.3	Carbic Podzol
8	Oulanka	66°20´	29°21´	HMT	85	174.1	16.8	Cambic Arenosol
9*	Ylikiiminki	64°58´	26°24´	ECT	95	100.1	14.3	Ferric Podzol
10*	Juupajoki	61°52´	24°13´	VT	85	210.6	22.4	Ferric Podzol
13*	Tammela	60°37´	23°51´	VT	65	254.5	21.1	Haplic Podzol
14	Lapinjärvi	60°38´	26°06´	VT	55	255.6	17.9	Ferric Podzol
16*	Punkaharju	61°46´	29°20´	VT	85	358.6	22.8	Ferric Podzol
18*	Miehikkälä	60°42´	27°51´	CT	125	177.8	20.2	Ferric Podzol
20*	Lieksa	63°10´	30°42´	EVT	135	298.1	22.8	Haplic Podzol
22	Kevo	69°44´	26°57´	UEMT	185	68.6	11.5	Haplic Podzol
Spruce plots								
3*	Pallasjärvi	68°00´	24°14´	HMT	145	72.8	11.0	Ferric Podzol
5*	Kivalo	66°20´	26°39´	HMT	75	133.3	11.6	Ferric Podzol
7	Oulanka	66°18´	29°28´	HMT	195	192.7	15.4	Haplic Arenosol
11*	Juupajoki	61°51´	24°19´	OMT	85	375.5	21.9	Dystric Cambisol
12*	Tammela	60°39´	23°49´	MT	65	309.4	21.6	Haplic Podzol
15	Lapinjärvi	60°40´	26°08´	OMT	70	327.7	22.8	Ferric Podzol
17*	Punkaharju	61°49´	29°19´	OMT	75	386.7	27.1	Cambic Arenosol
19*	Evo	61°14´	25°04´	OMT	175	658.1	26.3	Cambic Podzol
21*	Oulanka	66°18´	29°30´	HMT	175	182.0	14.3	Haplic Podzol
23*	Uusikaarlepyy	63°34´	22°29´	OMT	60	387.2	20.7	Cambic Podzol
24	Närpiö	62°28´	21°32´	MT	60	244.4	19.5	Gleyic Podzol
25	Vilppula	62°03´	24°23´	OMT	80	392.3	27.2	Carbic Podzol
28	Solböle	60°02´	23°03´	OMT	80	326.8	24.3	Cambic Podzol
31	Kivalo	66°20´	26°39´	HMT	80	140.7	12.7	Cambic Podzol

[1)] Cajander (1926). [2)] Nomenclature *see* World Reference Base for Soil Resources (1998).

HNO_3. Dissolved organic nitrogen (DON) was calculated as $N_{tot} – (NH_4\text{-}N + NO_3\text{-}N)$.

The annual mean element/ion concentrations of all the PW samples from each plot, weighted by the volume, were utilized in statistical analyses.

Sampling and analysis of the organic layer

The organic layer (OL) was sampled for chemical analyses at the beginning of the monitoring programme during 1995–1997 on all the plots (*n* = 27). The OL (L, F, H layers combined) samples were taken systematically from 20 points on the plot, bulked, air dried and milled to pass through a 1 mm sieve. Sub-samples were taken for the determination of dry weight (drying at 105 °C to constant weight) and organic matter content (dry ashing for 3 hours at 550 °C in a muffle furnace). Total element concentrations of Ca, Mg, K, Zn, Mn, P and S were determined, following closed HNO_3/H_2O_2 digestion in a microwave oven, using ICP/AES. Total N was determined with a CHN analyzer (Leco). Exchangeable Ca, Mg, K, Zn, Mn and extractable P were determined, following extraction with 0.1 M $BaCl_2$ (ISO 11260 1994, Anon. 2006), using ICP/AES.

The results were calculated as mean concentrations for each plot per dry weight (DW) and per organic matter (OM).

Statistical analysis

Linear mixed model analysis (SPSS 15.0 for Windows) was used to investigate the degree to which the mean concentration of an element (N, S, Ca, K, Mg, Zn, Mn) or ion/chemical component (NH_4-N, NO_3-N, total N, DON, SO_4-S, PO_4-P) in PW accounted for the variation in the concentration of this element (N, S, P, Ca, K, Mg, Zn, Mn) in the needles. The sampling years (1999, 2001, 2003 and 2005) were treated as repeated measures in the model. The two tree species were analysed separately. Prior to the analysis, the variables were ln-transformed in order to normalize their distributions. The significance of the interaction term year × PW concentration was tested in all models.

Linear regression analysis (SPSS 15.0 for Windows) was applied to study the relationship between the element concentration in the needles and the concentration of this element in the OL (total and exchangeable/extractable element concentrations calculated per dry weight (DW) and per organic matter (OM)). Similarly, linear regression analysis was used to test the dependence of needle P, K, Ca, Mg, S, Zn and Mn concentrations on the needle N concentration.

The results from spruce plot no. 23, located on an acid sulphate soil in the vicinity of a fur farm, was included in the datasets only in the case of nitrogen (NH_4, NO_3, DON and total N in PW and total N in the OL).

Results

The mean concentrations of elements/ions/other chemical components in the current needles, in PW and in the OL on the pine and spruce plots are presented in Tables 2, 3 and 4, respectively.

Needle chemistry *vs*. percolation water chemistry

In spruce, the mean element concentration in PW significantly ($0.003 < p < 0.054$) explained the variation in the concentration of the respective element in the current needles in the case of all elements except Ca and Mg (Table 5). In pine, the mean concentrations of K, Zn, and Mn in PW significantly explained the variation in the concentration of these elements in the current needles ($0.013 < p < 0.086$; Table 5). However, the year-to-year variation in the element needle concentrations did not account for the respective variation in the PW: most of the needle elements showed significant ($0.000 < p < 0.092$) differences between the years when the element concentration in PW was included in the model (Table 5). The only exceptions in this respect were Ca and K in spruce, and Mn in pine. The needle concentrations of these elements showed no significant differences between years, irrespective of whether the respective element in PW was included in the model as an independent variable or not. The interaction term year × PW concentration was insignificant ($p > 0.1$) in all models.

The concentration of inorganic forms of N (i.e. NO_3-N and NH_4-N) did not explain the variation in the N concentration in the needles (data not shown). In contrast, the N concentration in spruce needles showed a significant covariation with total N and DON, which accounted for 50%–97% of the total N in PW (Table 5).

Needle chemistry *vs.* organic layer chemistry

The needle concentration of N, S, Ca and Zn showed a significant positive relationship with the respective total element concentrations in the OL (per DW and per OM) on both the pine and spruce plots (Table 6), and for Ca and Zn also with the exchangeable/extractable concentrations. In addition, the regression between needle and OL concentrations was significant for extractable P per OM on the spruce plots, for K on the spruce plots (with the exception of the exchangeable concentrations per DW), and for Mg (apart from the total concentration per OM) and for Mn on the pine plots. The highest coefficient of determination (R_{adj}^2) for the regression between the element concentration in the OL and the respective element in the needles was for N ($0.746 \le R_{adj}^2 \le 0.837$) and for Ca ($0.727 \le R_{adj}^2 \le 0.809$) on the spruce plots. Expressing the element concentration in the OL per OM instead of per DW resulted in a clearly higher R_{adj}^2 value for the regression model in the case of N, Ca, and also slightly higher for Zn and Mn on the pine plots, as well as for the needle N concentration on the spruce plots.

Needle N *vs.* other needle nutrient concentrations

The needle N concentration significantly explained the variation in the S, P, Ca, K and Zn concentrations in pine needles, the coefficient of determination decreasing in this order (Table 7). In spruce, the S concentration strongly covaried with N, while Ca and Mg showed a weak but still significant ($0.05 < p < 0.1$) relationship with the N concentrations.

Table 2. Annual and total means and standard deviations for the nitrogen (N), sulphur (S), phosphorus (P), calcium (Ca), potassium (K), magnesium (Mg), zinc (Zn) and manganese (Mn) concentrations in the current needles on the Scots pine (*n* = 13) and Norway spruce (*n* = 14 for N, and 13 for other elements) plots.

	1999		2001		2003		2005		Total	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pine needles										
N (mg g^{-1})	11.9	1.73	12.6	1.25	12.7	0.81	13.2	1.70	12.6	1.46
S (mg g^{-1})	0.774	0.072	0.850	0.072	0.793	0.062	0.813	0.074	0.807	0.074
P (mg g^{-1})	1.36	0.14	1.53	0.13	1.43	0.12	1.44	0.12	1.44	0.14
Ca (mg g^{-1})	1.70	0.30	2.01	0.49	1.93	0.28	2.00	0.42	1.91	0.39
K (mg g^{-1})	5.17	0.29	5.21	0.40	5.23	0.29	5.52	0.35	5.28	0.35
Mg (mg g^{-1})	0.90	0.10	1.06	0.08	1.04	0.17	1.11	0.10	1.02	0.14
Zn (mg kg^{-1})	36.0	3.4	40.8	5.2	37.5	4.0	40.0	5.4	38.6	4.8
Mn (mg g^{-1})	0.39	0.137	0.43	0.13	0.39	0.10	0.45	0.14	0.42	0.12
Spruce needles										
N (mg g^{-1})	11.6	1.69	12.6	1.76	11.7	1.86	12.7	1.44	12.1	1.72
S (mg g^{-1})	0.790	0.063	0.855	0.065	0.770	0.071	0.808	0.048	0.817	0.079
P (mg g^{-1})	1.49	0.21	1.65	0.17	1.56	0.24	1.65	0.16	1.60	0.21
Ca (mg g^{-1})	3.95	0.59	3.63	0.69	3.75	0.81	3.78	0.58	3.72	0.68
K (mg g^{-1})	6.77	0.74	6.77	0.63	6.19	0.83	6.96	0.81	6.74	0.82
Mg (mg g^{-1})	1.06	0.10	1.11	0.14	1.11	0.10	1.21	0.12	1.14	0.14
Zn (mg kg^{-1})	36.3	8.3	35.5	6.0	32.9	7.5	35.6	7.1	34.6	7.1
Mn (mg g^{-1})	0.77	0.16	0.66	0.19	0.67	0.20	0.75	0.17	0.69	0.19

Table 3. Annual mean concentrations (mg l^{-1}) and standard deviations for elements, ions or chemical components in percolation water on the Scots pine (n = 7–8) and Norway spruce (n = 6–8) plots. DON = dissolved organic nitrogen.

	1999		2001		2003		2005	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pine								
N	1.36	0.33	1.16	0.45	1.22	0.55	1.33	0.46
DON	1.08	0.36	0.99	0.38	0.99	0.53	1.08	0.34
NH_4-N	0.24	0.11	0.13	0.09	0.21	0.09	0.23	0.25
NO_3-N	0.04	0.05	0.05	0.03	0.03	0.02	0.02	0.02
S	2.27	0.84	2.28	1.19	1.78	0.45	1.38	0.36
SO_4-S	0.85	0.45	1.26	1.17	0.85	0.39	0.73	0.37
PO_4-P	0.04	0.03	0.04	0.01	0.05	0.03	0.02	0.02
Ca	1.56	0.97	1.41	1.13	1.35	0.82	1.07	0.58
K	2.16	1.54	1.17	1.19	0.94	0.62	0.57	0.37
Mg	0.33	0.17	0.21	0.08	0.26	0.18	0.23	0.09
Zn	0.04	0.01	0.04	0.02	0.04	0.02	0.04	0.02
Mn	0.29	0.20	0.21	0.17	0.25	0.19	0.13	0.10
Spruce								
N	2.18	1.82	2.00	0.92	2.10	1.52	1.83	0.70
DON	1.47	0.82	1.45	0.54	1.54	1.00	1.42	0.55
NH_4-N	0.56	0.78	0.46	0.39	0.36	0.19	0.30	0.23
NO_3-N	0.15	0.29	0.08	0.11	0.20	0.42	0.12	0.13
S	2.81	1.86	2.10	1.60	2.24	1.39	1.75	1.36
SO_4-S	1.24	1.08	1.33	1.29	1.18	0.77	1.22	1.28
PO_4-P	0.06	0.05	0.18	0.23	0.11	0.11	0.03	0.02
Ca	1.54	0.74	1.82	0.79	1.85	1.41	1.44	0.83
K	2.42	0.99	2.42	1.96	1.95	1.02	1.48	0.74
Mg	0.56	0.23	0.48	0.25	0.46	0.20	0.46	0.26
Zn	0.03	0.01	0.03	0.00	0.04	0.01	0.03	0.01
Mn	0.29	0.13	0.28	0.14	0.23	0.16	0.18	0.08

Table 4. Total (tot) and exchangeable/extractable (exch/extr) element concentrations in the organic layer of the Scots pine (n = 13) and Norway spruce (n = 14 for N, and 13 for other elements) plots sampled once during 1995–1997. Concentrations are given per dry weight (DW^{-1}) and per organic matter (OM^{-1}).

	Pine DW^{-1}		Pine OM^{-1}		Spruce DW^{-1}		Spruce OM^{-1}	
Element	Mean	SD	Mean	SD	Mean	SD	Mean	SD
N_{tot} (g kg^{-1})	9.8	2.0	13.0	2.3	12.2	3.1	16.3	4.2
S_{tot} (g kg^{-1})	1.18	0.25	1.55	0.27	1.35	0.34	1.82	0.50
P_{tot} (g kg^{-1})	0.79	0.14	1.42	0.34	0.95	0.13	1.77	0.51
P_{extr} (g kg^{-1})	0.15	0.05	0.19	0.05	0.15	0.07	0.19	0.07
Ca_{tot} (g kg^{-1})	2.48	0.49	3.30	0.64	4.04	1.95	5.62	3.09
Ca_{exch} (g kg^{-1})	2.14	0.58	2.82	0.66	3.40	1.52	4.69	2.36
K_{tot} (g kg^{-1})	1.04	0.30	1.39	0.35	1.27	0.23	1.73	0.42
K_{exch} (g kg^{-1})	0.77	0.29	1.01	0.30	0.88	0.22	1.16	0.17
Mg_{tot} (g kg^{-1})	0.55	0.15	0.74	0.22	0.80	0.31	1.12	0.56
Mg_{exch} (g kg^{-1})	0.29	0.12	0.37	0.13	0.40	0.16	0.53	0.16
Zn_{tot} (mg kg^{-1})	47.8	15.2	63.6	19.3	57.8	39.2	79.1	57.8
Zn_{exch} (mg kg^{-1})	35.6	10.4	47.2	12.4	38.5	20.0	51.3	27.2
Mn_{tot} (g kg^{-1})	0.25	0.20	0.33	0.24	0.77	0.67	1.08	0.98
Mn_{exch} (g kg^{-1})	0.22	0.19	0.29	0.22	0.53	0.30	0.73	0.45

Discussion

Needle chemistry *vs.* percolation water chemistry

We chose the annual mean concentration of an element or ion/chemical component in percolation water (PW) collected immediately below the organic layer (OL) as an indicator of nutrient availability, and used it as an independent variable to explain the observed variation in the element concentration in the current needles of spruce and pine. This relatively rough indicator of nutrient availability was found to significantly covary with the respective needle elements in the case of total N, DON, total S, SO_4-S, PO_4-P, K, Mg and Zn on the spruce plots, while on the pine plots only the effects of K, Zn and Mn were significant. Thus, the PW concentrations showed a significant relationship with the respective needle concentrations more consistently on the spruce than on the pine plots. In pine needles the ratios between N and the other nutrients appeared to be more constant than in spruce needles and, as a result, N significantly explained the variation in S, P, Ca, K and Zn in pine needles, but only in S, Ca, and Mg in spruce. Interestingly, needle Ca and Mg were the only nutrients in spruce showing no covariation with the concentrations of the respective elements in PW. This suggests that the concentration of these elements in spruce needles is mediated more strongly by the tree's metabolism, i.e. by demand rather than by supply. In pine, the covariation between the concentrations in PW and in needles for K and Mn may be due to the fact that these two elements are strongly leached from the canopy to the forest floor (Hyvärinen 1990), and that the cycling of K especially is extremely rapid and efficient between the soil and trees. Overall, the results suggest that plant metabolism, i.e. internal translocation (Helmisaari 1992b, Proe *et al.* 2000) and/or uptake of nutrients driven by nutrient demand, i.e. the sink strength of the active meristems (Haukioja and Honkanen 1997, Honkanen *et al.* 1999), regulates the nutrient concentrations in the current needles more strongly in pine than in spruce, whereas the supply of soil nutrients is more clearly reflected in the nutrient concentrations of spruce. On the other hand, the lack of relationships between the concentration of most nutrients in PW and in needles in the pine stands may also result from the efficient consumption of available nutrients. Both efficient internal translocation and active and efficient uptake of nutrients could represent adaptation mechanisms to conditions of low nutrient and water availability. In fact, Scots pine is known to be well adapted to poor nutrient availability and, under conditions of low fertility, the productivity of Scots pine exceeds that of Norway spruce (Ilvessalo 1927). However, the output flux of N in PW was higher on the pine plots than on the spruce

Table 5. *F* statistics for the effects of sampling year and mean element (or ion/chemical component) concentration in percolation water (PW) on the concentrations of the respective element in current-year needles on the Scots pine (n = 7–8) and Norway spruce (n = 6–8) plots. Years 1999, 2001, 2003, 2005 are included in the statistical analyses.

	Pine		Spruce	
	F	*p*	*F*	*p*
Needle N				
Year	2.67	0.084	12.45	0.000
tot. N in PW	1.03	0.325	4.43	0.048
Needle N				
Year	2.60	0.092	15.26	0.001
DON in PW	1.15	0.295	4.14	0.054
Needle S				
Year	2.83	0.071	10.28	0.002
tot. S in PW	0.12	0.737	8.67	0.012
Needle S				
Year	2.83	0.073	8.72	0.007
SO_4-S in PW	0.01	0.943	7.39	0.029
Needle P				
Year	6.09	0.007	13.70	0.010
PO_4-P in PW	0.91	0.361	5.46	0.039
Needle Ca				
Year	2.29	0.080	1.60	0.233
Ca in PW	1.11	0.302	0.25	0.627
Needle K				
Year	9.45	0.001	2.20	0.140
K in PW	4.64	0.043	10.36	0.006
Needle Mg				
Year	8.32	0.002	7.43	0.005
Mg in PW	0.13	0.723	0.46	0.506
Needle Zn				
Year	2.91	0.074	3.27	0.066
Zn in PW	3.36	0.086	6.77	0.025
Needle Mn				
Year	0.86	0.484	5.63	0.012
Mn in PW	7.96	0.013	11.30	0.003

plots (Mustajärvi *et al.* 2008), which does not support the conclusion of more efficient uptake of N on the pine plots.

The typically tight nitrogen cycle (Tamm 1991), i.e. efficient consumption of available nitrogen in boreal coniferous ecosystems, may explain the lack of a significant relationship between inorganic forms of N and the N concentration in both pine and spruce needles. However, the N concentration in spruce needles showed a significant covariation with total N and DON, which accounted for 50%–97% of the total N in PW. Although the true plant availability of DON in PW is difficult to evaluate, the result suggests that the DON concentration in PW may serve as an indicator of N availability in spruce stands at least.

The difference in the patterns between pine and spruce could also indicate that the sampling depth of 5–10 cm, i.e. immediately below the

Table 6. Linear regression models for the Scots pine (n = 13) and Norway spruce (n = 14 for N, and 13 for other nutrients) plots. The dependent variable is plot mean element concentration in current-year needles sampled in 1999, 2001, 2003 and 2005. The independent variable is either total (tot) or exchangeable/extractable (exch/extr) element concentration in the organic layer, calculated per dry weight (DW) or per organic matter (OM).

	Pine				Spruce			
	Constant	Coeff.	$R_{adj.}^2$	p	Constant	Coeff.	$R_{adj.}^2$	p
Needle N								
N_{tot} (g kg^{-1} DW)	9.45	0.32	0.23	0.056	6.64	0.45	0.75	0.000
N_{tot} (g kg^{-1}OM)	6.86	0.44	0.71	0.000	6.57	0.34	0.84	0.000
C:N	18.83	–0.15	0.59	0.001	17.54	–0.16	0.87	0.000
Needle S								
S_{tot} (g kg^{-1} DW)	0.66	0.12	0.21	0.065	0.66	0.11	0.50	0.004
S_{tot} (g kg^{-1}OM)	0.66	0.07	0.25	0.047	0.73	0.03	0.27	0.041
Needle P								
P_{tot} (g kg^{-1} DW)	1.29	0.20	–0.02	0.411	1.50	0.09	–0.09	0.844
P_{tot} (g kg^{-1}OM)	1.24	0.14	0.11	0.141	1.61	–0.02	–0.09	0.878
P_{extr} (g kg^{-1} DW)	1.45	–0.07	–0.09	0.921	1.38	1.35	0.15	0.108
P_{extr} (g kg^{-1}OM)	1.44	0.03	–0.09	0.962	1.28	1.54	0.28	0.036
Needle Ca								
Ca_{tot} (g kg^{-1} DW)	1.00	0.37	0.26	0.043	2.70	0.27	0.80	0.000
Ca_{tot} (g kg^{-1}OM)	0.65	0.38	0.56	0.002	2.88	0.16	0.73	0.000
Ca_{exch} (g kg^{-1} DW)	1.29	0.29	0.22	0.061	2.61	0.35	0.81	0.000
Ca_{exch} (g kg^{-1}OM)	0.83	0.38	0.61	0.001	2.76	0.22	0.78	0.000
Needle K								
K_{tot} (g kg^{-1} DW)	5.21	0.07	–0.08	0.796	4.22	1.90	0.39	0.013
K_{tot} (g kg^{-1}OM)	5.13	0.11	–0.07	0.644	4.98	0.96	0.32	0.025
K_{exch} (g kg^{-1} DW)	5.29	–0.01	–0.09	0.977	6.02	0.71	–0.03	0.439
K_{exch} (g kg^{-1}OM)	5.27	0.01	–0.09	0.967	3.98	2.29	0.30	0.030
Needle Mg								
Mg_{tot} (g kg^{-1} DW)	0.81	0.38	0.28	0.037	1.14	–0.03	–0.08	0.750
Mg_{tot} (g kg^{-1}OM)	0.93	0.13	0.00	0.336	1.13	–0.01	–0.08	0.800
Mg_{exch} (g kg^{-1} DW)	0.87	0.52	0.37	0.017	1.17	–0.13	0.03	0.437
Mg_{exch} (g kg^{-1}OM)	0.85	0.48	0.33	0.023	1.19	–0.13	–0.03	0.434
Needle Zn								
Zn_{tot} (mg kg^{-1} DW)	30.10	0.18	0.46	0.006	28.43	0.12	0.40	0.012
Zn_{tot} (mg kg^{-1}OM)	28.63	0.16	0.61	0.001	29.34	0.07	0.34	0.022
Zn_{exch} (mg kg^{-1}DW)	30.90	0.22	0.30	0.032	25.86	0.24	0.47	0.006
Zn_{exch} (mg kg^{-1}OM)	27.94	0.23	0.51	0.004	26.06	0.18	0.46	0.006
Needle Mn								
Mn_{tot} (g kg^{-1} DW)	0.32	0.39	0.41	0.011	0.66	0.06	–0.03	0.449
Mn_{tot} (g kg^{-1}OM)	0.29	0.38	0.55	0.002	0.67	0.03	–0.05	0.508
Mn_{exch} (g kg^{-1} DW)	0.32	0.41	0.41	0.011	0.59	0.21	0.07	0.200
Mn_{exch} (g kg^{-1}OM)	0.30	0.41	0.55	0.002	0.62	0.12	0.02	0.278

OL for PW, succeeded in targeting the site (i.e. soil layer) of major water and nutrient uptake better in the case of spruce than of pine. A higher proportion of Norway spruce fine roots occurs in the uppermost soil layers compared to the situation in Scots pine stands (Helmisaari *et al.* 2000, 2007), which typically grow on coarse-textured soil with a low water holding capacity. In these conditions, water rapidly percolates down through the soil profile and the allocation of fine roots to deeper soil layers appears to be a relevant functional strategy for pine. Moreover, periods with low precipitation during the growing season more frequently resulted in relatively dry upper soil layers on the pine plots, as demonstrated by the lower number of PW samples obtained on the pine plots than on the spruce plots (data not shown), indicating that water availability more frequently limits nutrient uptake from the surface soil by pine. This finding probably reduced the capacity of seasonal mean concentrations in PW to depict the average nutrient availability on the pine plots.

The variation in PW chemistry did not explain the year-to-year variation in needle chemistry. This suggests that fluctuations in environmental conditions (temperature, moisture) and in annual biomass production may influence the year-to-year variation in needle chemistry more than the nutrient concentration in PW.

Table 7. Adjusted coefficients of determination ($R_{adj.}^2$) for the dependence of nutrient (sulphur, phosphorus, calcium, potassium, magnesium, and manganese) concentrations on the nitrogen concentrations in the needles of Scots pine ($n = 13$) and Norway spruce ($n = 13$). The variables are plot mean element concentrations in current-year needles sampled in 1999, 2001, 2003 and 2005.

	Pine		Spruce	
	$R_{adj.}^2$	p	$R_{adj.}^2$	p
Needle S	0.75	0.000	0.76	0.000
Needle P	0.58	0.001	0.01	0.305
Needle Ca	0.47	0.006	0.18	0.081
Needle K	0.34	0.022	–0.06	0.601
Needle Mg	–0.09	0.920	0.23	0.056
Needle Zn	0.33	0.024	0.10	0.152
Needle Mn	–0.04	0.481	–0.08	0.732

Needle chemistry *vs.* organic layer chemistry

Needle biomass constitutes a major proportion of stand litterfall in coniferous forests (Starr *et al.* 2005, Saarsalmi *et al.* 2007, Ukonmaanaho *et al.* 2008). Therefore, the nutrient composition of the needles and of the OL are to some extent interdependent: the OL is an important source of nutrients for trees while, on the other hand, the chemical composition of needles, although altered with age and during senescence before shedding as litterfall (Helmisaari 1990, 1992b), plays an important role in determining the quality of the OL. This interdependence may partly explain our finding that the patterns in the relationships between the nutrient concentration in the OL and in the needles appeared to be more similar between pine and spruce than in the case of the relationships between the needles and PW. The regression models explaining needle nutrient concentrations on the basis of the respective nutrient in the OL showed the highest coefficient of determination (R_{adj}^2) for N and Ca in both tree species. The concentration of these two nutrients in the soil have been found to covary with the site index (Tamminen 1993). Nitrogen is frequently the primary growth-limiting macronutrient and is effectively assimilated by the vegetation, while Ca is an essential base cation in the soil and an immobile nutrient that is strongly bound to the cell structures, resulting in an increase in the Ca concentration of conifer needles with age (Helmisaari 1992b). Consequently, the covariation between the concentrations of N and Ca in the needles and in the OL is understandable. Our finding of a significant relationship between Ca concentrations in the needles and in the OL resembles the results that Jandl and Herzberger (2001) obtained for Norway spruce stands growing on non-calcareous parent rock material in Austria, but they are in contrast to their results which showed no relationship between N concentration in the needles and in the OL. On the other hand, Raitio *et al.* (2000) reported N to be the only nutrient with a significant correlation between the organic layer and the needles. The fact that more significant relationships were found in the nutrient concentrations of the OL and the needles in our material than in that of Raitio *et al*. (2000), may be because our study plots were originally chosen to be relatively homogeneous in respect e.g. to stand age, while the dataset used in the study of Raitio *et al*. (2000) was more heterogeneous.

In addition to N and Ca, the models for S and Zn were significant for both pine and spruce. In the case of S however, it is important to note that in both pine and spruce ca. 75% of the variation in the needle S concentration was explained by the needle N concentration, and that this relationship could in actual fact be described relatively satisfactorily ($R_{\text{adj}}^2 = 0.701$) with a regression model in which both pine and spruce were included. The differences between the tree species appeared in the relationships for K, Mg and Mn: the regression model was significant for K only in spruce, and for Mg and Mn only in pine. Moreover, extractable P per OM showed a significant relationship with needle P in spruce. It is difficult to find well-reasoned explanations for these differences between the tree species, but they may be related to differences in the characteristics of the mineral soil on the pine and on the spruce plots, or in the nutrient uptake mechanisms of the two tree species.

Expressing the nutrient concentration per OM generally improved the R_{adj}^2 of the regression models for pine (N, S, Ca, Zn, Mn), Mg being the only exception. However, there was no corresponding trend for spruce; there was a slight improvement in R_{adj}^2 only for N. This was undoubtedly due to the unavoidable inclusion of mineral soil particles in the OL samples: this has a greater effect on the pine sites because, as the OL is thinner, the inclusion of mineral soil particles has a proportionally greater effect on the results expressed per DW.

In this study, both the total (HNO_3/H_2O_2 digestion) and exchangeable ($BaCl_2$ extraction) concentrations of P, Ca, K, Mg, Zn and Mn in the OL were compared with the corresponding nutrient concentrations in the needles. However, the differences between the linear regression models obtained with total concentrations and with exchangeable concentrations were, in most cases, only minor. This is probably partly due to the fact that the average proportions of exchangeable Ca and Mn out of total Ca and Mn in the OL in the whole material were ca. 85 and 83%, respectively, i.e. most of the Ca and Mn were in fact in an exchangeable form. The proportions were approximately the same in both the pine and spruce materials. The corresponding values for Zn, K, Mg and P were 73%, 72%, 54% and 17%, respectively.

Conclusions

The nutrient concentrations in percolation water and in the current needles showed significant relationships more consistently on the spruce than on the pine plots, whereas the ratios between N and the other nutrients appeared to be more constant in the pine needles than in spruce needles. The results suggest that plant metabolism, i.e. internal translocation and/or uptake of nutrients driven by nutrient demand, i.e. the sink strength of the growing meristems, regulates the nutrient concentrations in the current needles more strongly in pine than in spruce, whereas the supply of soil nutrients is more clearly reflected in the nutrient concentrations of spruce. This difference between pine and spruce could reflect the adaptation of Scots pine to conditions of low nutrient and water availability. The variation in percolation water chemistry did not explain the year-to-year variation in needle chemistry, suggesting that fluctuations in environmental conditions (temperature, moisture) and in annual biomass production may influence the year-to-year variation in needle chemistry more than the supply of nutrients. The patterns in the relationships between the nutrient concentration in the organic layer and in the needles appeared to be more similar between pine and spruce than in the case of the relationships between the needles and percolation water, indicating a strong interdependence between the nutrient status of the organic layer and needles, which are the two important nutrient pools in boreal forest ecosystems. For both tree species, the highest covariation between nutrient concentrations in the organic layer and in the needles was found for N and Ca, both of which are essential macronutrients and strong determinants of site fertility. This study represents a considerable step forward in understanding the relationships between the nutrient status of forest trees and the nutrient concentrations in the aqueous phase of the soil.

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