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Litterfall production and nutrient return to the forest floor in Scots pine and Norway spruce stands in Finland

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The main objective of this study was to determine the importance of nutrient return in litterfall (LF) to forest nutrient cycling. Therefore, we investigated the quality and quantity of LF in relation to the above-ground tree biomass (AGT) and determined the turnover rates. The study was carried out on seven Norway spruce (*Picea abies*) and six Scots pine (*Pinus sylvestris*) plots. LF was sampled during 1996–2003, and AGT in 2005–2006. The studied nutrients were N, Ca, K, Mg, P, S, Mn, Zn, Fe. Overall, the results indicated that there are quality, quantity and spatial differences in LF and AGT compartments. In general, both concentrations and mass of LF and AGT were higher on the spruce plots; 2% of the AGT biomass returned to the forest floor as LF on the plots. Magnesium turnover rate was higher on the spruce plots. The turnover rates of other nutrients were slightly higher on the pine plots, indicating faster nutrient cycling via LF. More litter needles (kg ha^{-1}) ended up on the forest floor in relation to living needles on the spruce plots.

Introduction

A significant proportion of terrestrial net primary production is recycled from the trees as litterfall to the forest floor and, subsequently, into the detritus food web. Therefore, in forest ecosystems litterfall is the major pathway through, which the pool of nutrients in the soil, depleted by nutrient uptake and leaching, is replenished (Morrison 1991). Moreover, litterfall represents one of the primary links between producers and decomposers (Fyles *et al*. 1986). Thus the amount and quality of litterfall provide considerable information about the dynamics of nutrient cycling within forest ecosystems.

Foliar litter is the major component of above-ground litterfall in boreal forest ecosystems, although other components like bark can be important in some other regions e.g. in Eucalyptus forests (Kimmins 1987). The quantity of above-ground litterfall is closely linked to the proportion of the senescent foliage biomass, which varies from year to year and between species: the longer the retention of foliage in the canopy, the smaller is the litterfall mass. Furthermore, there is variation in the timing of foliage litterfall between tree species, e.g. deciduous trees shed most of their foliar biomass in the autumn. Some coniferous species, such as Scots pine (*Pinus sylvestris*), shed their oldest needles during August–October, whereas Norway spruce (*Picea abies*) sheds its needles evenly through-out the year (Viro 1956, Mälkönen 1974, Finér 1996). The element concentrations in needle litter are affected by several factors, of which tree species and soil properties have generally been considered to be the most important (Lutz and Chandler 1946, Stachurski and Zimka 1975, Miller *et al*. 1979). However, most of the recent studies conclude that the growth intensity of the trees determines the nutrient retranslocation efficiency rather than the nutrient status of the soil (Birk and Vitousek 1986, Nambiar and Fife 1987, Helmisaari 1992). Furthermore, climatic factors may strongly affect the nutrient concentrations of litter because storms and dry periods may give rise to early litterfall. Litter that is inadvertently shed earlier contains larger amounts of mobile nutrients (e.g. N, P, K), which are normally translocated to the remaining tree compartments from tissues that are becoming senescent (Gosz *et al*. 1972, Johansson 1995). On the other hand, the concentrations (mg kg^{-1}) of immobile nutrients (e.g. Ca and Mn), which steadily accumulate in the tissues of some tree species, can be lower than those in senescent needles simply because the decrease in carbohydrate concentrations during senescence decreases the weight of the needles (Kramer & Kozlovski 1979, Johansson 1995, Helmisaari 1992).

Nutrient concentrations also vary in the above-ground tree compartments (foliage, bark, branches, stemwood) according to the intensity of nutrient uptake, the phase in the annual cycle (e.g. Tamm 1955, Fife and Nambiar 1982, 1984, Helmisaari 1990) and the size and age of the tree (e.g. Mälkönen 1974, Helmisaari 1990). According to some studies, forest fertilization generally increases the concentrations of the applied nutrients in stemwood and other tree compartments (e.g. Paavilainen 1980, Ingerslev and Hallbäcken 1999, Finér and Kaunisto 2000). Nutrient retranslocation, i.e. redistribution or resorption from aging needles and other tissues, may supply a considerable part of a tree's nutrient requirements for new biomass production (Sollins *et al*. 1980, Meier *et al*. 1985, Lim and Cousens 1986, Helmisaari 1990).

The main objective of this study was to determine the importance of nutrient return in litterfall to forest nutrient cycling. Therefore, we investigated the quality and quantity of litterfall in relation to the standing above-ground tree biomass and determined the turnover rates. The hypothesis was that there are tree-species related and spatial differences in nutrient concentrations and amounts in the litterfall and above-ground tree compartments, and that these differences are reflected in the nutrient inputs to the forest floor. Six Scots pine and seven Norway spruce plots were included in the study. The nutrients studied were nitrogen (N), calcium (Ca), potassium (K), magnesium (Mg), phosphorus (P), sulphur (S), manganese (Mn), zinc (Zn) and iron (Fe).

Material and methods

Study area

The study was carried out on seven Norway spruce and six Scots pine plots (Fig. 1 and Table 1) that form a part of the UN-ECE/ICP Forests, UN-ECE/Integrated Monitoring and EU/Forest Focus forest condition monitoring programmes. Eleven of the plots are located in commercially managed forests, and two (Nos. 19, 20) are located in protected conservation areas where forestry management has not been carried out during at least the past 50 years. Some of the Norway spruce and Scots pine plots are located relatively close to each other. The Scots pine plots were located on soils composed of sorted sand, and the Norway spruce stands on till soils. Each plot consists of three subplots (30 × 30 m) and a surrounding mantle. The width of the mantle and buffer zones varies from 10–30 m. The design of the monitoring plot is described in detail in Derome *et al*. (2007).

Litterfall

Litterfall was collected using 12 traps located systematically on a 10 × 10 m grid on one subplot (30 × 30 m) in each spruce and pine stand during 1996–2003; sampling on some of the plots started later than 1996. The top of the funnel-shaped traps, with a collecting area of 0.5 m^2, stood at a height of 1.5 m above the forest floor. The litterfall was collected in a replaceable cotton bag attached to the bottom of the litterfall trap. Litterfall was sampled bi-weekly during the snow-free period (May to November, depending on the latitude of the plot), and once at the end of winter. After collection, all the litter samples were combined (per plot), air-dried and sorted into at least four fractions: (1) green and (2) senescent Scots pine needles, (3) green and senescent Norway spruce needles, and (4) the remaining material (miscellaneous = branches, leaves, cones, bark, flowers, etc.). Sorting into different fractions varied from year to year and between the plots, i.e. in some years even green broadleaves were taken as a separate fraction on some of the plots. The mass of each fraction was determined by weighing and a sub-sample of each fraction was analysed for mineral nutrients. Before the nutrient analyses, sub-samples of two to four sampling events were combined to form one sample 'period'. During one year, there was a total of six to nine sampling periods (depending on the year and plot), on the basis of which we calculated the annual mean concentrations. Nutrient concentrations in litterfall are presented for all fractions, but nutrient fluxes (amounts of nutrients returned to the forest floor via litterfall) in litterfall were calculated for two fractions: needles and miscellaneous. The needle fraction consists of both senescent and green needles (needles of spruce were initially not separated into senescent and green) and the miscellaneous fraction covers all other types of stand litterfall.

Needle sampling

Tree-specific sample branches with current (C) and previous-year (C + 1) needles were collected from the uppermost third of predominant or dominant trees (n = 10) on each study plot once during October–November 2005. The branches were taken to the laboratory, and 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 from 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.

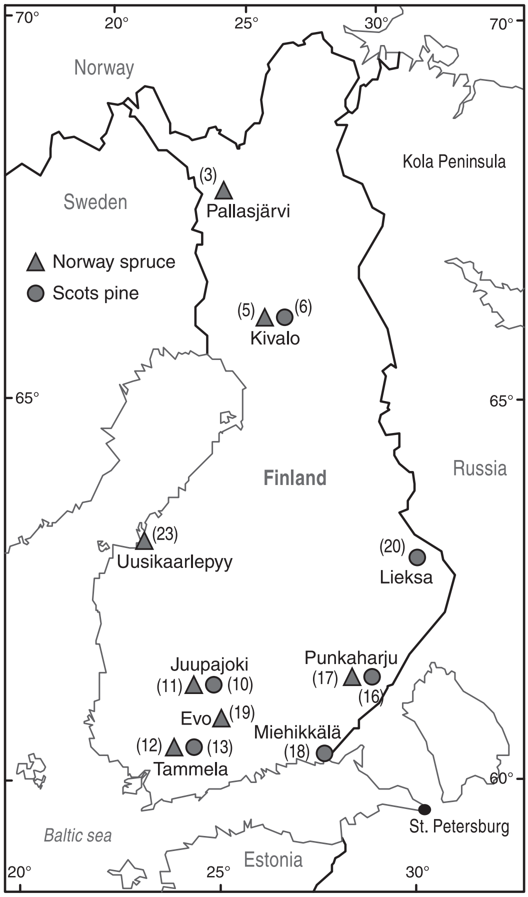

Fig. 1. Location of the study plots.

Above-ground tree biomass sampling

Five trees were felled on each plot during spring 2006. As all the trees on the plots had been numbered in the beginning of the monitoring programme, it was possible to pick a random sample of five trees for felling and five trees as a reserve (in case a selected tree was severely damaged). However, in the unmanaged forests in Evo (No. 19) and Lieksa (No. 20), only 1 and 3 trees were felled, respectively. The felled trees represented the dominant canopy layer of the stand by height. A 5-cm thick disc was cut from each trunk at a height of 1.3 m above ground level (breast height). The tree discs were separated into at least two fractions: bark and stemwood of all discs, and sap- and heartwood whenever possible. The living canopy of each tree was divided into four sectors by height. Three sec-

Table 1. General characteristics of the study plots. The plots are arranged in order of decreasing latitude.

Plot (no.)	Forest site type[1)]	Stem density[2)] (ha^{-1})	Stem volume with bark[2)] ($m^3 ha^{-1}$)	Mean diameter, weighted with basal area[2)] (cm)	Mean height[2)] (m)	Dominant species (%)	Age of dominant trees[2)] (years)	Precipitation[3)] (mm)	Soil type[4)]
Norway spruce									
Pallasjärvi (3)	*Hylocomium–Myrtillus*	1104	72.8	17.6	11.0	100	145	545	Ferric podzol
Kivalo (5)	*Hylocomium–Myrtillus*	1663	133.3	11.6	11.6	98	75	585	Ferric podzol
Uusikaarlepyy (23)	*Oxalis–Myrtillus*	963	387.2	24.0	20.7	100	60	462	Cambic podzol
Juupajoki (11)	*Oxalis–Myrtillus*	852	375.5	25.2	21.9	91	85	629	Dystric cambizol
Punkaharju (17)	*Oxalis–Myrtillus*	374	386.7	33.1	27.1	99	75	526	Cambic arenosol
Evo (19)	*Oxalis–Myrtillus*	1254	658.1	30.9	26.3	69	175	616	Cambic podzol
Tammela (12)	*Myrtillus*	663	309.4	25.2	21.6	84	65	584	Haplic podzol
Scots pine									
Kivalo (6)	*Empetrum–Myrtillus*	1755	167.3	14.4	13.3	100	60	587	Carbic podzol
Lieksa (20)	*Empetrum–Vaccinium*	588	298.1	31.9	22.8	97	135	580	Haplic podzol
Juupajoki (10)	*Vaccinium*	378	210.6	27.2	22.4	100	85	629	Ferric podzol
Punkaharju (16)	*Vaccinium*	959	358.6	22.1	22.8	100	85	526	Ferric podzol
Tammela (13)	*Vaccinium*	604	254.5	24.0	21.1	97	65	619	Haplic podzol
Miehikkälä (18)	*Calluna*	415	177.8	24.9	20.2	100	125	600	Ferric podzol

[1)] Cajander 1926, 1949, [2)] Derome *et al.* 2007, [3)] Lindroos *et al.* 2006; mean 1996–2003, [4)] FAO 1990.

tions (length 5 cm) of the main branches and four annual shoots of collateral branches were randomly selected from each sector. The sections from the main branches of the same tree, as well as the samples of the collateral branches, were pooled separately and analyzed by tree. In addition, a number of dead branches were taken from each felled tree and combined to form a bulk sample for the plot. The samples were stored in a freezer before pre-treatment in the laboratory.

Determination of the above-ground tree biomass

Estimates of biomass components (stemwood, bark, living and dead branches, needles) were calculated using the functions of Marklund (1987, 1988). The individual functions T-6, T-10, T-14, T-19, T-22, G-5, G-7, G-12, G-17 and G-20 from Marklund (1988) were applied. The allometric functions predict the logarithm of the dry weight of each biomass component of individual trees using tree species, breast-height diameter and tree height as explanatory variables. These variables have been measured on all trees on the Finnish UN-ECE/ICP Forests plots (with a diameter exceeding 4.5 cm). The functions predicting needle biomass include crown length as an additional explanatory variable and the function for Scots pine also the latitudinal coordinate. The biomass per hectare for each component was obtained as the sum of the estimates for the individual trees. The total above-ground tree biomass per hectare was calculated as the sum of the biomass of stemwood, bark, living and dead branches and needles.

Chemical analyses

Samples of the individual tree biomass components (stemwood, bark, living branches, dead branches) were dried at a temperature of 40 °C, and the litterfall and needle samples at a temperature of 60 °C. The dried samples were milled and wet digested using microwave-assisted digestion in a mixture of $HNO_3 + H_2O_2$. The concentrations of Ca, K, Mg, Mn, P, S, Fe and Zn in the solution were determined by inductively coupled plasma atomic emission spectrometry (ICP-AES). The total N concentration was determined with a CHN analyser (LECO). The size of the subsample for wet digestion was 0.5 g and for CHN analysis 0.1–0.3 g.

Data processing and statistical analysis

Annual mean nutrient concentrations in litterfall were calculated by weighting the concentrations in each fraction by the corresponding mass of the litterfall fraction. Litter production (dry mass per unit area) was calculated by dividing the amount of litter collected by all the traps on the plot by the combined surface area of the traps. Nutrient return in litterfall was calculated by multiplying the nutrient concentrations by the monthly litter production. The nutrient concentrations of living needle were calculated as the means of the plot mean concentrations of current and previous year's needles. Nutrient concentrations of the above-ground tree biomass are means for each tree compartment on the plot. The sap- and heartwood in the stem disc was separated and analyzed separately whenever possible. However, in this study we have used the mean concentrations in the sap- and heartwood (stemwood). The nutrient concentrations in the living branches are means of the concentrations in the main branches and collateral shoots. The nutrient pools of different above-ground tree compartments were calculated by multiplying the nutrient concentration by the mass of the corresponding tree compartment.

In order to estimate the proportions of the above-ground tree biomass and nutrient pool that are annually returned to the soil as litterfall, the turnover rate percent was calculated:

$$\mathrm{TR_B} = \frac{N_{\mathrm{LF}}}{N_{\mathrm{AGT}}} \times 100 \qquad (1)$$

where $\mathrm{TR_B}$ = biomass-incorporated nutrient turnover rate (%), N_{LF} = nutrient amount in annual litterfall (kg ha^{-1} yr^{-1}), and N_{AGT} = nutrient pool in the above-ground tree biomass (kg ha^{-1}).

In order to estimate the proportions of living needle biomass and nutrient pool that are annually returned to the soil as needles in litterfall, the turnover rate percentage was calculated:

$$TR_N = \frac{N_{NLF}}{N_{LN}} \times 100 \quad (2)$$

where TR_N = needle-mass-incorporated nutrient turnover rate (%), N_{NLF} = nutrient amount in litter needles (kg ha^{-1} yr^{-1}), and N_{NLN} = nutrient pool in living needles (kg ha^{-1}).

The two-sample *t*-test was used to determine the statistical significance of the differences in the concentrations in litterfall or above-ground tree compartments between the spruce and pine stands. Pearson product-moment correlations were used to analyse the relationship between total litterfall and above-ground tree biomass. Statistical analyses were performed using the SYSTAT® software package (SYSTAT® 1998).

Results and discussion

Nutrient concentrations

Litterfall

In general, the nutrient concentrations in the spruce litterfall tended to be higher than those in pine, which is consistent with earlier studies (e.g. Johansson 1984, 1995) (Tables 2 and 3, Appendices 1 and 2). In fact the concentrations of all other nutrients except K, P and Zn were significantly higher ($p < 0.05$) in spruce litter than in pine litter (Table 4), which is obviously related to the greater interception capacity of spruce over pine.

Nutrient concentrations varied between the fractions, the highest concentrations frequently occurring in the brown or green broadleaf fraction. However, the amount of broadleaf litter was so small that its importance on these conifer-dominated plots is assumed to be minor. Elevated nutrient concentrations in the litter of broadleaf tree species compared to conifers have also been reported in other studies (e.g. Johansson 1995). Iron was the only nutrient with the highest concentration in the miscellaneous fraction on both the spruce and pine plots. This finding is in agreement with Finér's (1996) study in a Scots pine stand.

Slight latitude-related trends were found in the nutrient concentrations of the two most abun-

Table 2. Annual mass and mass-weighted litterfall concentrations by litter fraction on the Scots pine plots. (na = not available).

		Scots pine: senescent needles	Scots pine: green needles	Miscellaneous	Brown leaves	Green leaves	Norway spruce: senescent and green needles
Number of plots		6	6	6	4	1	1
Mass (g m^{-2})	mean	120.13	5.01	94.44	5.55	0.31	0.48
	min–max	76.85–184.42	1.18–10.64	38.52–139.45	0.30–12.64		
N (%)	mean	0.49	1.12	0.77	0.69	na	0.71
	min–max	0.44–0.56	0.97–1.26	0.61–0.90	0.55–0.89		
Ca (mg g^{-1})	mean	4.74	2.95	2.44	9.94	7.25	7.70
	min–max	3.63–5.74	2.47–3.50	1.97–3.40	7.82–13.30		
K (mg g^{-1})	mean	1.08	4.59	1.03	3.09	5.55	1.17
	min–max	0.87–1.25	4.24–5.07	0.88–1.14	2.36–3.71		
Mg (mg g^{-1})	mean	0.47	0.79	0.35	2.56	2.09	0.56
	min–max	0.42–0.58	0.72–0.90	0.30–0.41	1.52–3.92		
Mn (mg g^{-1})	mean	0.95	0.62	0.12	1.05	1.01	1.42
	min–max	0.63–1.43	0.38–0.91	0.06–0.16	0.60–1.60		
P (mg g^{-1})	mean	0.37	1.25	0.66	1.37	1.81	0.84
	min–max	0.31–0.42	1.10–1.36	0.52–0.84	0.83–1.72		
S (mg g^{-1})	mean	0.45	0.79	0.58	0.56	1.32	0.62
	min–max	0.42–0.48	0.73–0.85	0.44–0.67	0.48–0.70		
Zn (mg g^{-1})	mean	0.05	0.04	0.05	0.15	0.16	0.04
	min–max	0.04–0.06	0.03–0.04	0.03–0.08	0.10–0.18		
Fe (mg g^{-1})	mean	0.07	0.08	0.24	0.08	0.07	0.06
	min–max	0.05–0.09	0.05–0.12	0.19–0.34	0.06–0.09		

Table 3. Annual mass and mass-weighted litterfall concentrations by litter fraction on the Norway spruce plots.

		Norway spruce needles (senescent and green needles)	Miscellaneous	Scots pine senescent needles	Brown leaves	Scots pine green needles	Green leaves	Cones	Branches
Number of plots		7	7	4	5	3	1	1	1
Mass (g m^{-2})	mean	179.32	102.53	7.87	15.91	0.48	2.39	40.48	1.29
	min–max	56.6–327.81	23.56–154.03	0.39–14.92	1.12–68.00	0.14–0.72			
N (%)	mean	0.82	1.21	0.51	0.97	1.17	2.11	0.88	1.44
	min–max	0.69–1.03	0.97–1.63	0.38–0.63	0.78–1.53	1.09–1.23			
Ca (mg g^{-1})	mean	10.41	3.09	4.08	9.90	2.38	6.66	0.29	4.24
	min–max	5.64–15.26	1.83–4.26	3.01–4.92	7.48–11.46	1.60–3.06			
K (mg g^{-1})	mean	2.05	2.47	1.22	4.10	4.19	7.73	3.62	1.80
	min–max	1.23–3.45	1.71–3.46	1.09–1.37	2.93–6.93	3.52–4.80			
Mg (mg g^{-1})	mean	0.89	0.76	0.48	2.71	0.67	2.69	0.76	0.67
	min–max	0.57–1.15	0.67–0.96	0.38–0.54	2.11–3.14	0.49–0.86			
Mn (mg g^{-1})	mean	1.38	0.39	0.59	1.54	0.45	0.90	0.06	0.23
	min–max	0.55–1.98	0.21–0.62	0.24–0.89	0.86–2.54	0.31–0.62			
P (mg g^{-1})	mean	0.77	1.14	0.33	1.29	1.09	1.67	0.64	0.84
	min–max	0.58–0.98	0.86–1.40	0.24–0.40	0.51–2.04	0.96–1.19			
S (mg g^{-1})	mean	0.70	0.97	0.47	0.76	0.74	1.30	0.68	1.07
	min–max	0.61–084	0.73–1.24	0.42–0.52	0.61–1.03	0.62–0.85			
Zn (mg g^{-1})	mean	0.05	0.09	0.03	0.12	0.03	0.09	0.02	0.09
	min–max	0.01–0.10	0.04–0.15	0.02–0.04	0.08–0.18	0.03–0.04			
Fe (mg g^{-1})	mean	0.04	0.39	0.11	0.09	0.07	0.07	0.03	0.37
	min–max	0.04–0.06	0.26–0.54	0.07–0.18	0.06–0.14	0.05–0.10			

dant fractions (brown/green needles and miscellaneous). The most obvious trend was for the Mn and S concentrations in both the spruce and pine stands. The Mn concentrations increased toward the north, while the S concentration showed a corresponding decrease. The northwards decreasing S trend in the needle and miscellaneous litter fractions followed the general S deposition trend reported in Finland (e.g. Ukonmaanaho *et al*. 1998, Ukonmaanaho & Starr 2002, Lindroos *et al*. 2006). The highest nutrient concentration in litterfall frequently occurred on the Uusikaarlepyy plot (No. 23). This plot is located on an acid sulphate soil and receives an input of $MgSO_4$ from the sea (Gulf of Bothnia) and, in addition, there is a fur farm in the vicinity of the plot. Therefore, the tree canopy on the plot is also exposed to ammonia (NH_3) emissions from the fur farm (Ferm *et al*.1990, Lindroos *et al*. 2007). All these factors undoubtedly contribute to the relatively high S, N and Mg concentrations in litterfall on the Uusikaarlepyy plot.

Above-ground tree compartments

The mean concentrations of most of the nutrients in the individual above-ground tree biomass compartments were higher on the spruce than on the pine plots (Table 5). This is in agreement with the differences observed in the nutrient concentrations of the litterfall (Tables 2 and 3). However, only the Ca concentration was significantly higher ($p < 0.05$) in all the above-ground tree compartments of spruce than of pine, which is most probably related to the fact that most of the spruce plots are located on more fertile sites. The concentrations of Fe and Mg in stemwood, and N and Zn in living needles, were significantly higher ($p < 0.05$) in pine than in spruce. The concentrations of most of the nutrients were the highest in living needles, and decreased in the following order: bark > living branches > dead branches > stemwood. Similar results have been reported by Mälkönen (1974) and Rothpfeffer and Karltun (2007).

Table 4. Annual average mineral nutrient concentrations of all litterfall fractions for Scots pine stands (n = 127) and for Norway spruce stands (n = 149).

Element	Scots pine	Norway spruce	Significance
N (%)	0.79	0.98	***
Ca (mg g^{-1})	4.17	6.16	***
K (mg g^{-1})	2.30	2.68	
Mg (mg g^{-1})	0.74	1.07	***
Mn (mg g^{-1})	0.66	0.90	***
P (mg g^{-1})	0.86	0.94	
S (mg g^{-1})	0.61	0.77	***
Zn(mg g^{-1})	0.06	0.07	
Fe (mg g^{-1})	0.12	0.17	**

Statistically significant difference in litterfall concentrations between Scots pine and Norway are indicated as follows: **$p < 0.01$, ***$p < 0.001$.

Of the individual nutrients, the N concentrations were the highest in both tree species and in all tree compartments, ranging from 0.10% (stemwood) to 1.37% (living needles) (Table 5; for more details *see* Appendices 3 and 4). Calcium was especially enriched in the bark, where the average concentration was as high as 12.71 mg g^{-1} in the spruce stands. In the other tree compartments the Ca concentration was considerably lower, especially in stemwood (< 1 mg g^{-1}). The Zn concentrations in the bark clearly varied between the two tree species: the mean Zn concentration in spruce was significantly higher ($p < 0.05$) (0.135 mg g^{-1}) than that in pine (0.017 mg g^{-1}). These results are consistent with earlier reported Zn concentrations for the bark of Norway spruce in Sweden (Rothpfeffer and Karltun 2007), and the bark of Scots pine in Finland (Saarsalmi *et al*. 2006): 0.185 mg g^{-1} and 0.007–0.009 mg g^{-1}, respectively. The Zn concentration in the bark of spruce was considerably higher than in the other tree compartments, and even higher than that in living needles. This finding is in agreement with the studies of Rothpfeffer and Karltun (2007) and Österås and Greger (2003).

The nutrient concentrations in the above-ground tree compartments, excluding living branches and needles, showed only a weak relationship with the latitude of the plot (Appendices 3 and 4). For pine, the Mg and Mn concentrations in living branches increased on moving from south to north. In contrast, the needle concentrations of most of the nutrients decreased towards the north, particularly the S concentration, reflecting the general S deposition trend in Finland. Although the outer bark has been used as an indicator of the air pollution load (Lippo *et al*. 1995, Poikolainen 1997), there was no clear trend in the S concentration in the bark on the pine plots. On the spruce plots there were no clear differences in the concentrations of the individual tree compartments between the plots, apart from the S concentration in living needles, which showed a slightly decreasing trend towards the north (when the Uusikaarlepyy plot, No. 23, was excluded). The Uusikaarlepyy plot had the highest concentrations of most nutrients on the spruce plots. However, the concentration of Ca was lower on this plot than on the other spruce plots. Ferm *et al*. (1990) also reported lower Ca concentrations in the foliage near a fur farm in Finland. Some studies have shown that high concentrations of NH_4^+ in the soil lead to a decrease in the Ca concentrations of plants (e.g. Cox and Reisenauer 1973, McNulty *et al*. 1991, NIVA 1996).

Stand and litter biomass and the nutrients incorporated in litterfall and above-ground tree compartments

Litterfall mass

The total annual litter production varied considerably between the years and plots (Fig. 2), which is normal in forest ecosystems. On the spruce plots, the mean annual litter production ranged from 651 to 4912 kg ha^{-1} (average for all spruce plots 2986 kg ha^{-1}), whereas for pine it ranged from 1325 to 3402 kg ha^{-1} (average 2225 kg ha^{-1}). The average annual litter production in the spruce stands is in good agreement with the average, estimated long-term litter production in spruce stands of 2400 kg ha^{-1} yr^{-1}, which was based on 18 spruce stands in different parts of Finland (Saarsalmi *et al*. 2007). However, the average annual litter production in the pine stands was greater than that obtained in a study on 32 pine stands in Finland, where the average annual

Table 5. Nutrient concentrations of the different biomass compartments on the Scots pine (n = 6) and Norway spruce (n = 7) plots.

		Stemwood		Living branches		Needles		Bark		Dead branches	
Species		pine	spruce	pine	spruce	pine	spruce	pine	spruce	pine	spruce
Biomass (kg ha^{-1})	mean	91500	108400	9800	27000	3300	11600	6400	8200	2400	3000
	SD	30460	54200	1230	8050	1010	1410	2120	2710	660	1440
N (%)	mean	0.10	0.12*	0.59	0.58	1.37*	1.23	0.37	0.42*	0.23	0.21
	SD	0.036	0.046	0.057	0.068	0.161	0.125	0.054	0.044	0.030	0.068
Ca (mg g^{-1})	mean	0.60	0.75***	2.20	4.36***	2.89	5.00**	4.61	12.71***	1.15	4.66**
	SD	0.039	0.118	0.096	0.778	0.480	0.858	0.581	1.667	0.345	2.137
K (mg g^{-1})	mean	0.32	0.41**	2.74	2.86	5.28	5.74	0.91	2.16***	0.17	0.41*
	SD	0.032	0.088	0.192	0.318	0.327	0.802	0.222	0.428	0.120	0.229
Mg (mg g^{-1})	mean	0.13***	0.10	0.62	0.56	0.98	1.23**	0.25	0.63***	0.22	0.29
	SD	0.014	0.018	0.070	0.043	0.115	0.184	0.062	0.143	0.093	0.075
Mn (mg g^{-1})	mean	0.08	0.07	0.19	0.31***	0.62	0.84	0.10	0.53***	0.11	0.24*
	SD	0.012	0.028	0.039	0.128	0.125	0.288	0.025	0.193	0.043	0.110
P (mg g^{-1})	mean	0.02	0.02	0.56	0.57	1.41	1.45	0.21	0.40***	0.02	0.07**
	SD	0.003	0.009	0.053	0.092	0.153	0.170	0.057	0.082	0.006	0.029
S (mg g^{-1})	mean	0.035	0.040*	0.344	0.335	0.852	0.807	0.218	0.284***	0.110	0.139
	SD	0.004	0.005	0.024	0.032	0.088	0.080	0.034	0.021	0.038	0.070
Zn (mg g^{-1})	mean	0.007	0.009	0.026	0.057***	0.049*	0.036	0.017	0.135***	0.013	0.048**
	SD	0.001	0.003	0.004	0.016	0.004	0.014	0.004	0.034	0.003	0.019
Fe (mg g^{-1})	mean	0.021**	0.009	0.041	0.044	0.035	0.032	0.038	0.030	0.014	0.014
	SD	0.015	0.003	0.011	0.016	0.007	0.006	0.019	0.017	0.005	0.006

Statistically significant difference in concentrations of different biomass compartments between Scots pine and Norway are indicated as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

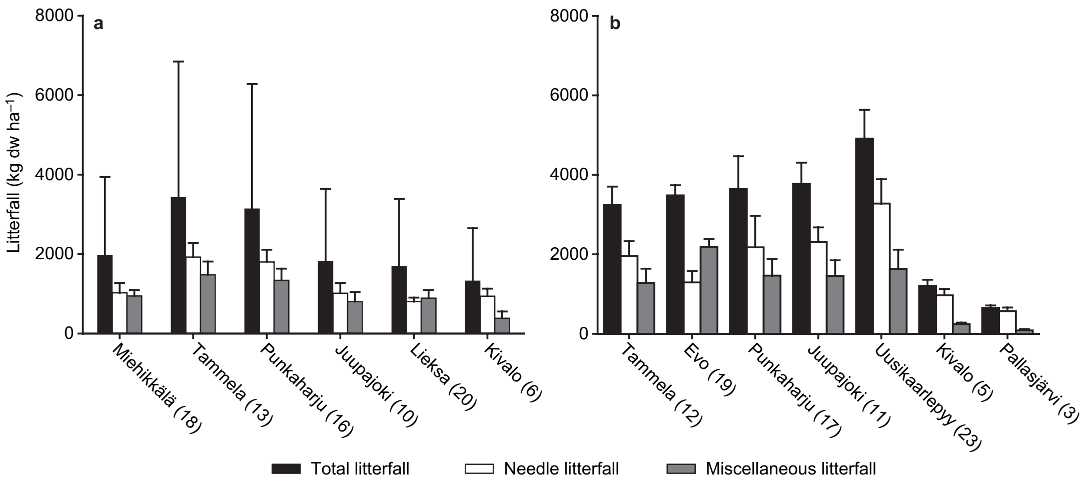

Fig. 2. Mean (+ SD) annual litterfall mass of (**a**) Scots pine, and (**b**) Norway spruce.

litter production was 1100 kg ha^{-1} yr^{-1} (Starr *et al.* 2005). The considerably lower average litter production obtained for these 32 plots may be related to the fact that most of the plots were located at higher latitudes and on sites of lower fertility than our plots. A number of studies have indicated that tree stands on fertile sites produce more litter than those growing on infertile sites (Alberktson 1988, Vose and Allen 1991). The litter production in Scots pine stands in Sweden has been reported to vary between 740–4200 kg ha^{-1} yr^{-1} (Breymeyer *et al.* 1996) and between 590–3160 kg ha^{-1} yr^{-1} (Flower-Ellis 1985). These results are more consistent with our findings.

Needles represented a considerably higher proportion of the annual litter production than the miscellaneous fraction on the plots located in managed forests (Fig. 2). However, the litterfall traps used in this study did not collect other litterfall fractions, such as large dead branches, as efficiently as needles and this might have had an effect on the results. The variation in needle litter production was considerable between the plots and years. The average proportion of needle litter produced during the study period varied from 37% (Evo, No. 19) to 87% (Uusikaarlepyy, No. 23) out of the total litter production on the spruce plots, and from 47% (Lieksa, No. 20) to 71% (Tammela, No. 13) on the pine plots. On the average, the proportion of needle litterfall was slightly higher on the spruce plots (60%) than on the pine plots (56%). In a long-term study in 34 pine stands in Finland, the annual needle litter production ranged from 49% to 75% of the total stand litterfall (Starr *et al.* 2005). Correspondingly, in a study of 18 spruce stands in Finland, needle litter production accounted for an average of 70% (range 52%–94%) of the total litter production (Saarsalmi *et al.* 2007). Similar results have also been reported by Mälkönen (1974), Helmisaari (1992) and Finér (1996), for Scots pine stands.

The proportions of the individual litter fractions followed an opposite pattern on the plots located in the non-managed stands (Evo, No. 19; Lieksa, No. 20) (Fig. 2). The amount of miscellaneous litter was higher than that of needle litter in these natural or semi-natural, old growth forests (Kokko *et al.* 2002). The amount of branches, bark and cones in litterfall increases with stand age (Mälkönen 1974, Flower-Ellis 1985, Finér 1996) although, according to Finér (1996), the contribution of the other litterfall fractions is smaller than that of needle litterfall also in old stands. However, our results did not support Finér's finding. The larger amount of miscellaneous litter in these non-managed old growth forests is probably due to the higher amount of decaying branches, bark, cones and other woody debris, as well as epiphytic lichens, than in managed forests. Therefore, for example, storms result in greater inputs of miscellaneous litter, such as branches and broken twigs, than in managed forests. Similar results have been reported by Edmonds and Murray (2002) for temperate old-growth forest ecosystems.

Total litter production decreased from south to north (Fig. 2). This clear, decreasing gradient was, especially in the pine stands, related to the stand characteristics and climate, as well as to the longer needle retention time. The highest amount of annual spruce litterfall occurred on the Uusikaarlepyy plot (No. 23) (4912 kg ha^{-1} yr^{-1}). This plot is located near a fur farm, and the NH_3 emissions from the farm might have had a fertilizing effect on the surrounding forests. This is also supported by the fact that the above-ground tree biomass was, except for Evo (No. 19), the highest on the Uusikaarlepyy plot. Thus, it is obvious that the high amount of litterfall at Uusikaarlepyy reflects the high forest productivity of the site. Total above-ground tree biomass and total litterfall correlated strongly with each other in the spruce stands ($r^2 = 0.86$, $n = 7$), but not in the pine stands ($r^2 = 0.53$, $n = 6$).

Nutrient return to the forest floor through litterfall

The annual nutrient return to the forest floor through litterfall was much higher on the spruce plots than on the pine plots (Tables 6 and 7), but

Table 6. Annual nutrient return (kg ha^{-1}) to the forest soil through the litterfall by litter fraction on the Scots pine plots during 1996–2003. Plots are arranged from north to south.

Plot	Compartment	*n*		N	Ca	K	Mg	Mn	P	S	Zn	Fe
6	Needles	8	mean	4.17	4.86	0.85	0.43	0.87	0.40	0.40	0.05	0.06
			SD	0.756	0.909	0.215	0.087	0.159	0.082	0.078	0.010	0.008
	Miscellaneous	8	mean	2.28	0.73	0.37	0.12	0.03	0.25	0.16	0.01	0.06
			SD	0.793	0.293	0.312	0.056	0.015	0.084	0.056	0.004	0.013
	Total	8	mean	6.44	5.60	1.23	0.55	0.90	0.65	0.56	0.06	0.12
			SD	1.259	1.135	0.407	0.106	0.168	0.149	0.106	0.012	0.020
20	Needles	5	mean	4.39	3.25	0.97	0.47	0.84	0.31	0.37	0.04	0.04
			SD	0.557	0.525	0.121	0.053	0.113	0.050	0.059	0.005	0.006
	Miscellaneous	5	mean	6.70	3.52	1.09	0.49	0.20	0.62	0.51	0.04	0.16
			SD	2.009	0.847	0.303	0.107	0.041	0.188	0.155	0.008	0.040
	Total	5	mean	11.08	6.77	2.06	0.96	1.05	0.93	0.88	0.08	0.21
			SD	2.287	1.157	0.354	0.131	0.111	0.229	0.192	0.008	0.041
10	Needles	8	mean	5.12	3.62	1.12	0.49	0.73	0.41	0.47	0.04	0.08
			SD	1.365	0.842	0.258	0.139	0.177	0.103	0.117	0.011	0.017
	Miscellaneous	8	mean	7.33	1.59	0.91	0.32	0.08	0.69	0.55	0.05	0.23
			SD	2.350	0.501	0.339	0.132	0.032	0.233	0.193	0.038	0.100
	Total	8	mean	12.45	5.21	2.03	0.81	0.81	1.10	1.02	0.09	0.31
			SD	2.894	1.111	0.514	0.224	0.190	0.290	0.256	0.029	0.110
16	Needles	5	mean	9.01	10.12	2.37	0.86	2.52	0.74	0.89	0.10	0.09
			SD	1.709	2.068	0.521	0.151	0.438	0.071	0.132	0.019	0.012
	Miscellaneous	5	mean	10.29	3.41	1.49	0.46	0.18	0.90	0.83	0.04	0.27
			SD	1.594	0.530	0.359	0.113	0.047	0.113	0.107	0.008	0.028
	Total	5	mean	19.29	13.53	3.85	1.32	2.70	1.64	1.73	0.14	0.36
			SD	2.943	2.302	0.710	0.202	0.432	0.113	0.190	0.025	0.025
13	Needles	8	mean	11.46	9.53	2.50	0.86	1.68	0.85	0.96	0.10	0.16
			SD	2.987	1.867	0.583	0.190	0.274	0.240	0.227	0.018	0.075
	Miscellaneous	8	mean	12.21	3.92	1.89	0.75	0.35	1.07	0.92	0.13	0.36
			SD	2.890	1.275	0.516	0.209	0.124	0.264	0.219	0.090	0.067
	Total	8	mean	23.67	13.44	4.39	1.61	2.03	1.92	1.88	0.22	0.52
			SD	5.391	2.592	0.983	0.360	0.328	0.461	0.400	0.102	0.083
18	Needles	2	mean	5.10	4.79	1.45	0.44	0.64	0.35	0.46	0.06	0.09
			SD	0.893	1.028	0.668	0.138	0.146	0.077	0.099	0.015	0.035
	Miscellaneous	2	mean	6.97	2.29	0.90	0.28	0.06	0.49	0.52	0.03	0.31
			SD	0.604	0.241	0.153	0.030	0.006	0.033	0.045	0.005	0.031
	Total	2	mean	12.07	7.07	2.35	0.73	0.70	0.83	0.98	0.10	0.40
			SD	0.289	0.787	0.514	0.109	0.141	0.044	0.054	0.021	0.065

the location of a plot also had a strong effect. On both the spruce and pine plots the annual nutrient return tended to be smaller in the north of the country than in the south. This was obviously related to litter production on the plots. However, for most nutrients the annual return on the spruce plot at Uusikaarlepyy (No. 23) was more than 100% greater than the average for the other spruce plots; this was presumably related to the specific conditions on the Uusikaarlepyy plot, as discussed earlier. The amount of N, Ca and K returned annually in litterfall to the soil was greater than that of the other nutrients, irrespective of the forest site type (Tables 6 and 7). This is in line with the findings of many other studies (Cole and Rapp 1981, Rapp *et al*. 1999, Edmonds and Murray 2002).

The average annual return of N on the spruce

Table 7. Annual nutrient return (kg ha^{-1}) to the forest soil through the litterfall by litter fraction on the Norway spruce plots during 1996–2003. Plots are arranged from north to south.

Plot	Compartment	*n*		N	Ca	K	Mg	Mn	P	S	Zn	Fe
3	Needles	2	mean	3.94	8.70	0.70	0.45	0.88	0.44	0.35	0.06	0.02
			SD	1.078	2.094	0.127	0.074	0.177	0.070	0.073	0.014	0.001
	Miscellaneous	2	mean	0.99	0.33	0.15	0.06	0.05	0.10	0.08	0.01	0.03
			SD	0.382	0.081	0.062	0.024	0.012	0.041	0.030	0.002	0.007
	Total	2	mean	4.94	9.03	0.84	0.51	0.93	0.55	0.42	0.07	0.05
			SD	0.696	2.014	0.065	0.050	0.165	0.029	0.043	0.012	0.005
5	Needles	8	mean	7.32	11.05	1.65	0.55	1.92	0.76	0.65	0.08	0.04
			SD	1.693	2.134	0.289	0.094	0.386	0.140	0.114	0.015	0.010
	Miscellaneous	8	mean	2.32	0.58	0.57	0.18	0.14	0.27	0.17	0.02	0.06
			SD	0.355	0.177	0.273	0.046	0.040	0.059	0.024	0.004	0.022
	Total	8	mean	9.65	11.63	2.23	0.73	2.06	1.02	0.83	0.10	0.10
			SD	1.541	2.063	0.343	0.086	0.375	0.098	0.105	0.014	0.022
23	Needles	5	mean	33.50	18.71	11.18	3.79	1.82	3.05	2.74	0.09	0.14
			SD	5.085	4.842	1.697	0.730	0.451	0.444	0.520	0.019	0.030
	Miscellaneous	5	mean	25.00	4.44	5.93	1.57	0.34	2.21	1.91	0.11	0.58
			SD	8.167	1.854	2.642	0.499	0.128	0.796	0.625	0.040	0.185
	Total	5	mean	58.51	23.15	17.10	5.35	2.16	5.25	4.66	0.19	0.72
			SD	9.005	5.718	3.144	0.781	0.492	0.907	0.833	0.048	0.193
11	Needles	8	mean	19.76	23.23	5.02	1.78	4.29	2.26	1.59	0.10	0.09
			SD	3.589	5.087	0.907	0.337	1.021	0.404	0.278	0.022	0.014
	Miscellaneous	8	mean	17.50	5.67	3.47	1.08	0.95	1.83	1.53	0.23	0.65
			SD	4.651	2.014	1.226	0.351	0.315	0.601	0.427	0.217	0.176
	Total	8	mean	37.25	28.90	8.49	2.86	5.24	4.09	3.11	0.33	0.74
			SD	6.028	5.674	1.475	0.513	1.111	0.713	0.548	0.219	0.174
17	Needles	5	mean	16.81	17.45	3.96	2.42	2.82	1.23	1.55	0.03	0.09
			SD	6.65	7.235	1.10	0.920	1.174	0.372	0.498	0.009	0.030
	Miscellaneous	5	mean	15.68	2.76	4.24	1.08	0.314	1.49	1.36	0.06	0.49
			SD	6.06	1.096	1.397	0.371	0.125	0.654	0.534	0.019	0.198
	Total	5	mean	32.49	20.21	8.21	3.49	3.14	2.72	2.91	0.09	0.58
			SD	8.30	7.48	1.42	0.95	1.22	0.69	0.71	0.021	0.207
19	Needles	5	mean	10.42	16.13	2.80	1.22	1.89	0.74	0.89	0.03	0.05
			SD	2.541	4.166	0.467	0.312	0.569	0.115	0.162	0.006	0.009
	Miscellaneous	5	mean	22.47	13.62	5.73	3.27	1.51	1.59	1.85	0.14	0.62
			SD	3.330	0.909	1.312	0.305	0.100	0.285	0.214	0.010	0.093
	Total	5	mean	32.89	29.76	8.53	4.49	3.40	2.33	2.74	0.17	0.67
			SD	3.092	4.050	1.135	0.345	0.572	0.226	0.161	0.011	0.088
12	Needles	8	mean	16.34	20.15	3.35	1.86	2.04	1.53	1.39	0.06	0.11
			SD	2.916	4.297	0.670	0.452	0.504	0.239	0.229	0.013	0.016
	Miscellaneous	8	mean	14.68	3.80	3.02	1.04	0.32	1.35	1.20	0.13	0.59
			SD	3.704	1.143	1.054	0.296	0.099	0.435	0.299	0.076	0.142
	Total	8	mean	31.02	23.96	6.38	2.89	2.36	2.88	2.59	0.19	0.71
			SD	4.858	4.439	1.184	0.508	0.513	0.471	0.356	0.077	0.138

plots was 30 kg ha^{-1} yr^{-1} and on the pine plots about one half of this value. Corresponding results for Scots pine plots have been reported by e.g. Finér (1996). The atmospheric input of N in 2004, for instance, was less than that of litterfall: on the average 4 kg ha^{-1} on the pine plots and 3 kg ha^{-1} on the spruce plots (Lindroos *et al*. 2007). Because the growth and productivity of boreal forest ecosystems is limited by the availability of N (e.g. Mälkönen *et al*. 1990), the N input to the soil via litterfall is of great importance for the N status of a site. However, the N in litter first has to be released through decomposition and mineralization of the litter, while the N in atmospheric deposition is usually immediately available for plant uptake as it is almost completely in a soluble form (Parker 1983). The annual N requirements in mature Scots pine stands in Finland have been estimated to be 26 kg ha^{-1} (Helmisaari 1992). In our pine stands, litterfall could therefore account for approximately one half of the N requirements for new annual biomass production. However, litterfall and deposition most probably cannot satisfy all the N requirements in these pine stands. An important part of the N requirement (30%–50%) is provided by internal N retranslocation, i.e. N is translocated from aging and senescing tissues back to the trunk and needles during senescence (Helmisaari 1992). The annual return of Ca in litterfall was, on the average, 21 kg ha^{-1} yr^{-1} on the spruce plots and 9 kg ha^{-1} yr^{-1} on the pine plots. Similar values for the annual Ca return have been reported, for example, in black spruce forests and plantations in Canada (Gordon *et al*. 2000). On our plots, the annual deposition of Ca in throughfall (in 2004, Lindroos *et al*. 2007) was considerably lower than that in the annual litterfall, deposition being on the average 2 kg ha^{-1} yr^{-1} for both the spruce and pine plots (Lindroos *et al*. 2007). Litterfall is a more important pathway for N, Ca, P, Mg, Fe, Mn and Zn to the forest floor, while throughfall is more important for K and S (Parker 1983, Morrison 1991, Ukonmaanaho and Starr 2001, 2002). Our results indicated that a significant proportion of the annual Ca requirements in the pine stands could be supplied by the litterfall input, because in mature Scots pine stands in Finland they are estimated to be 8 kg ha^{-1} (Helmisaari 1992). The average return of K through litterfall was 7 kg ha^{-1} yr^{-1} on the spruce plots and 3 kg ha^{-1} yr^{-1} on the pine plots, while throughfall was 9 and 4 kg ha^{-1} yr^{-1}, respectively (Lindroos *et al*. 2007). Only on the Uusikaarlepyy plot (Nr. 23) was the annual return of K in litterfall slightly higher than that in throughfall. These results support the conclusion that litterfall plays a less important role in the return of K to the forest floor as compared with that in throughfall. However, the study of Ukonmaanaho and Starr (2001) showed that significant amounts of K, S and Na are leached from the litterfall while still in the traps. The mean annual return of the other nutrients in litterfall was much smaller than that of N, Ca and K: 2 kg ha^{-1} yr^{-1} for Mg, S, Mn and P, 0.4 kg ha^{-1} yr^{-1} for Fe, and 0.1 kg ha^{-1} yr^{-1} for Zn (average values for both spruce and pine). These inputs are similar to those reported in other studies (e.g. Edmonds and Murray 2002, Ukonmaanaho and Starr 2002).

Above-ground tree biomass and nutrient pools

The total amount of above-ground tree biomass varied between 83 600 kg ha^{-1} and 174 900 kg ha^{-1} on the pine plots, and from 53 300 kg ha^{-1} to 220 300 kg ha^{-1} on the spruce plots, being on the average higher on the spruce plots (Table 8). Figure 3 shows the distribution of different tree biomass components of the pine and spruce stands (average) predicted by Marklund's model (1987, 1988). The amount of stemwood biomass was surprisingly similar for both species (pine 81%, spruce 69%), but the amount of living branches and needles was higher in the spruce than in the pine stands. This is obviously related to the species-specific structure of these tree species. As a result, mature spruce stands produce more logging residues in connection with final felling, and are of greater interest for bioenergy production favoured by the current energy policy in Finland.

The total mass of the above-ground tree compartments in the spruce stands was greater on the southern plots (Nos. 12, 13, 17, 19, 23) than on the northern ones (Nos. 3, 5), but there were no clear trends on the pine plots (Table 8). Proportionally, the needle biomass was the highest on

Fig. 3. Distribution of different tree biomass compartments of Scots pine and Norway spruce. Estimates of biomass components were calculated using the functions of Marklund (1987, 1988).

the northernmost spruce plots at Kivalo (No. 5) and Pallasjärvi (No. 3). Similarly, the proportionally highest needle biomass for pine occurred on the Kivalo plot (No. 6). An opposite trend was found for needle litter production: needle litter production in both the pine and spruce stands was the lowest on the northernmost plots at Kivalo (Nos. 5 and 6) and at Pallasjärvi (No. 3) (Fig. 2). Both the highest needle biomass and the lowest needle litter production on the northernmost plots were related to the longer needle retention time in the north.

The nutrient pools in the above-ground tree compartments were, on the average, almost 2- to 3-fold larger in the spruce stands than in the pine stands (Tables 9 and 10), although the difference in the total biomass was smaller. The major nutrient pools in the spruce and pine stands were those of N, Ca and K. Most of the N pool (91% in spruce and 87% in pine) was in the living branches, needles and stemwood (Tables 9 and 10, Fig. 4). Finér *et al*. (2003) reported that Norway spruce has relatively more N in the foliage and branches than Scots pine in Finland. The N pool was the largest on the Uusikaarlepyy plot (No. 23), presumably due to NH_3 emissions from nearby fur farms. The increased availability of NH_4^+ accelerates its uptake and accumulation in different above-ground tree compartments. On the spruce plots over 30% and on the pine plots over 27% of the Ca pool was located in the bark and dead branches. In our study the bark was not separated into outer bark and inner phloem sections, and therefore the bark also includes the living phloem, through which most of the mineral nutrients and metabolites are transported. The high proportion of the Ca in perennial plant tissues is due to its central role in the formation

Table 8. Above ground tree biomass (kg ha^{-1}) by compartment.

Plot	Stemwood	Living branches	Living needles	Bark	Dead branches	Total
Scots pine						
6	60300	8800	4700	7200	2600	83600
10	82600	8900	2500	5000	1900	100900
13	97100	10300	3700	7100	2500	120700
16	146000	11400	4200	9800	3500	174900
18	67600	8500	2700	5000	1800	85600
20	95300	11000	2200	4000	1900	114400
Norway spruce						
3	25600	13900	9300	3800	700	53300
5	46000	21700	13000	6300	1400	88400
11	128800	31000	12400	10100	3600	185900
12	98600	24000	10800	8200	2700	144300
17	153900	27800	11600	8500	4000	205800
19	165600	31500	10600	8100	4500	220300
23	140500	39000	13200	12300	4000	209000

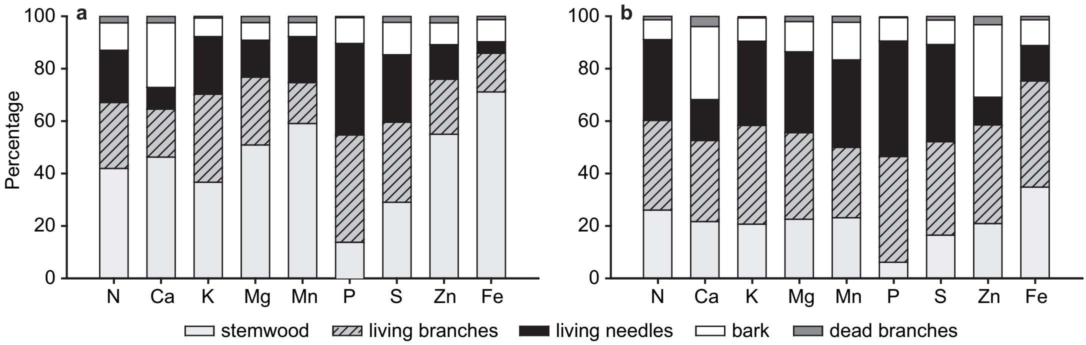

Fig. 4. Relative nutrient pool in different above-ground tree compartments on (**a**) Scots pine, and (**b**) Norway spruce plots. Estimates of biomass components were calculated using the functions of Marklund (1987, 1988).

Table 9. Nutrients (kg ha^{-1}) incorporated in the above-ground tree compartments of the Scots pine plots (from north to south).

Plot	Compartment	N	Ca	K	Mg	Mn	P	S	Zn	Fe
6	Stemwood	75.38	37.14	21.41	9.12	4.99	1.23	2.18	0.40	2.76
	Living branches	47.26	20.18	25.73	6.44	2.09	4.40	2.87	0.23	0.55
	Needles	54.29	12.76	23.38	4.78	2.49	5.91	3.60	0.22	0.20
	Bark	27.35	34.48	8.67	2.48	0.77	2.09	1.63	0.11	0.46
	Dead branches	5.79	3.21	0.40	0.51	0.30	0.08	0.28	0.04	0.02
	Total	210.08	107.77	79.60	23.33	10.63	13.71	10.56	1.00	3.99
20	Stemwood	58.76	52.90	27.86	10.36	6.17	1.64	3.08	0.76	2.68
	Living branches	60.21	25.40	30.73	6.76	2.31	6.33	3.96	0.34	0.43
	Needles	25.83	5.01	10.49	2.03	1.37	2.58	1.59	0.10	0.05
	Bark	12.44	20.14	3.42	0.94	0.48	0.64	0.84	0.09	0.23
	Dead branches	3.77	1.45	0.14	0.17	0.13	0.02	0.33	0.03	0.03
	Total	161.00	104.91	72.64	20.25	10.46	11.21	9.79	1.32	3.43
10	Stemwood	91.74	46.56	22.85	10.36	6.40	1.79	3.03	0.64	0.59
	Living branches	52.95	19.13	25.20	5.95	1.72	5.47	3.12	0.23	0.35
	Needles	37.44	6.81	13.14	2.93	1.73	3.83	2.27	0.13	0.10
	Bark	19.20	23.86	3.86	1.14	0.48	1.00	1.08	0.08	0.12
	Dead branches	4.04	2.83	0.26	0.63	0.29	0.04	0.16	0.03	0.03
	Total	205.36	99.20	65.31	21.01	10.62	12.13	9.67	1.11	1.18
16	Stemwood	148.88	85.42	51.29	19.53	12.48	2.99	4.76	0.89	3.87
	Living branches	60.69	23.95	26.93	6.36	2.18	5.62	3.45	0.24	0.41
	Needles	59.85	12.13	22.47	3.94	3.31	5.94	3.61	0.18	0.11
	Bark	31.89	38.68	5.70	1.58	0.85	1.39	1.57	0.10	0.18
	Dead branches	9.86	5.42	1.42	1.13	0.59	0.10	0.29	0.04	0.06
	Total	311.17	165.60	107.81	32.53	19.41	16.04	13.68	1.46	4.63
13	Stemwood	153.49	62.87	30.16	12.64	8.31	2.31	4.11	0.68	1.02
	Living branches	67.19	21.42	28.73	5.81	1.80	6.34	3.72	0.24	0.32
	Needles	57.88	13.86	20.71	3.79	2.47	5.94	3.60	0.18	0.15
	Bark	32.72	37.55	7.13	2.00	0.94	1.81	1.87	0.13	0.19
	Dead branches	6.33	3.06	0.34	0.56	0.25	0.07	0.20	0.02	0.02
	Total	317.60	138.76	87.07	24.80	13.77	16.46	13.50	1.25	1.70
18	Stemwood	47.29	43.17	22.57	9.07	3.90	1.19	2.08	0.64	0.69
	Living branches	56.04	19.08	23.15	4.78	1.03	4.77	3.07	0.25	0.36
	Needles	37.67	7.89	15.08	2.15	1.16	3.85	2.34	0.15	0.10
	Bark	19.17	19.58	5.26	1.20	0.31	1.02	1.17	0.09	0.20
	Dead branches	4.00	1.30	0.18	0.28	0.11	0.03	0.25	0.02	0.03
	Total	164.16	91.02	66.23	17.48	6.52	10.85	8.91	1.15	1.38

of structural compounds such as pectates in the cell walls. Therefore large amounts of Ca are found in the dead parts of tree compartment (Johnson 1992). In contrast, the proportions of K and P in the dead branches were < 1%, indicating their translocation to the living parts of the tree or loss by leaching. The Ca pool was the highest on the Evo plot (No. 19), where the total above-ground tree biomass was also the highest. Calcium accumulation is known to be related to an increased biomass and increased stand age. On the Evo plot, the age of the dominant trees is estimated to be 175 years (Table 1). More than 80% of the pool of most of the other nutrients was in the living part of the biomass (needles, branches, stem), which is to be expected because these nutrients play an essential role in the vital functioning of trees.

Table 10. Nutrients (kg ha^{-1}) incorporated in the above-ground tree compartments of the Norway Spruce plots (from north to south).

Plot	Compartment	N	Ca	K	Mg	Mn	P	S	Zn	Fe
3	Stemwood	41.48	22.85	12.46	3.24	2.76	1.03	1.21	0.31	0.29
	Living branches	86.10	77.35	37.98	8.01	6.54	8.88	5.00	1.01	0.78
	Needles	95.75	57.90	48.33	11.65	7.97	14.33	7.04	0.52	0.35
	Bark	12.88	46.30	6.82	2.04	2.63	1.15	0.96	0.64	0.06
	Dead branches	1.56	4.31	0.32	0.22	0.26	0.06	0.20	0.06	0.01
	Total	237.77	208.71	105.91	25.16	20.16	25.46	14.41	2.54	1.50
5	Stemwood	52.91	37.34	20.18	4.60	4.78	1.16	1.86	0.52	0.29
	Living branches	118.27	102.62	58.08	11.44	10.42	12.14	7.64	1.67	1.09
	Needles	143.24	71.77	71.72	13.54	17.18	18.43	9.58	0.71	0.36
	Bark	23.90	87.00	11.47	3.58	4.67	2.17	1.67	1.04	0.14
	Dead branches	4.11	5.06	0.41	0.24	0.31	0.11	0.22	0.08	0.03
	Total	342.43	303.78	161.87	33.40	37.36	34.01	20.98	4.01	1.91
23	Stemwood	150.37	88.17	73.37	17.05	7.85	3.88	5.89	1.30	0.82
	Living branches	251.35	122.44	123.33	24.86	8.14	23.51	14.70	2.23	1.18
	Needles	179.63	57.30	95.29	19.85	7.56	20.73	12.90	0.40	0.45
	Bark	55.50	122.30	31.84	9.94	5.02	5.81	3.83	1.75	0.57
	Dead branches	9.51	10.27	3.50	1.46	0.72	0.35	0.42	0.16	0.04
	Total	646.37	400.47	327.34	73.15	29.29	54.27	37.74	5.84	3.07
11	Stemwood	157.10	92.08	42.94	11.16	12.22	2.25	4.57	1.16	1.05
	Living branches	208.21	127.75	98.72	17.72	12.16	21.73	10.38	1.84	1.09
	Needles	156.01	54.81	76.62	13.56	14.08	21.39	9.75	0.43	0.32
	Bark	43.42	123.86	28.88	7.03	7.91	5.00	2.75	1.61	0.18
	Dead branches	10.44	20.01	1.61	1.40	1.51	0.36	0.49	0.23	0.06
	Total	575.18	418.52	248.77	50.86	47.88	50.73	27.95	5.26	2.70
17	Stemwood	250.80	105.98	60.58	15.15	8.00	4.29	6.69	0.87	1.70
	Living branches	150.64	115.95	76.22	16.01	6.37	16.45	8.75	1.06	0.77
	Needles	155.61	43.25	58.02	14.71	8.60	15.72	9.33	0.20	0.31
	Bark	36.24	108.71	18.56	5.32	3.29	3.81	2.49	0.79	0.22
	Dead branches	5.63	12.22	0.96	0.94	0.66	0.20	0.41	0.10	0.04
	Total	598.91	386.11	214.34	52.13	26.92	40.48	27.67	3.03	3.04
19	Stemwood	49.67	150.83	68.21	12.82	7.35	2.74	5.72	0.79	1.03
	Living branches	149.58	153.99	99.37	16.06	6.66	13.56	8.85	1.13	1.05
	Needles	136.76	56.96	63.88	11.17	7.39	13.26	8.43	0.34	0.42
	Bark	33.32	125.14	13.90	3.20	2.73	2.38	2.45	0.66	0.51
	Dead branches	8.12	38.25	1.77	1.28	0.79	0.18	0.49	0.13	0.04
	Total	377.45	525.18	247.12	44.54	24.92	32.11	25.94	3.05	3.05
12	Stemwood	143.92	62.52	25.95	9.26	4.91	1.34	3.40	0.83	1.46
	Living branches	142.37	94.29	56.42	12.79	4.94	11.60	7.73	1.41	1.72
	Needles	130.53	58.66	55.22	15.42	5.96	13.93	8.64	0.31	0.37
	Bark	38.67	103.25	17.70	6.32	3.26	3.43	2.38	1.11	0.19
	Dead branches	3.27	8.98	0.54	0.82	0.39	0.07	0.21	0.12	0.02
	Total	458.76	327.70	155.82	44.59	19.47	30.37	22.35	3.78	3.75

Proportion of biomass and nutrient pool annually returned to the forest floor in litterfall (turnover rate)

Above-ground tree biomass/total litterfall

In order to quantify the proportions of the above-ground tree biomass and nutrient pools that annually returned to the forest floor in the form of litterfall, we calculated the nutrient turnover rate for the pine and spruce stands (Table 11). As, on the average, about 2% of the above-ground tree biomass was returned annually to the forest floor as litterfall in both the spruce and pine stands, the differences between the nutrient turnover rates was mainly caused by differences in the nutrient concentrations. The mean turnover rate for both tree species was at a similar level (Table 11), but slightly higher for the individual nutrients in the pine stands than in the spruce stands, apart from Mg. This indicated that nutrient cycling via litterfall was faster in the pine stands. The higher Mg turnover rate in the spruce stands may be a sign of less efficient Mg retranslocation than in pine, and may also imply that spruce is more susceptible to Mg deficiency. Reduced Mg uptake has been suggested as one of the reasons for forest decline in central Europe in the 1980s (e.g. Oren *et al*. 1988, Palomäki and Rautio 1995). The turnover rates obtained in our study were comparable to the turnover rates reported for evergreen oak forests in France, where the turnover rates were 9% for N, 5% for P, 8% for K, 4% for Ca and 9% for Mg (Rapp *et al*. 1999). In contrast, the turnover rates in a similar study in deciduous oak forests were greater (Rapp *et al*. 1999). The N and S turnover rates decreased on moving northwards, especially in the case of pine. This decreasing trend appeared to be related more to the latitude and annual amount of litterfall than to the site fertility. The needle retention time in the northern parts of Finland is longer, and therefore the needle litter production is correspondingly less. Another reason could be the long interval between litter sampling, especially during the long winter period in the north, which may have affected the amount and especially the nutrient concentrations of the litter.

Living needles/senescent needles

We also estimated the proportions of the living needle biomass and nutrient pool that are returned to the forest floor in the form of senescent needles (= needles in litterfall) (Table 12). The mass and concentrations of the living needles were higher than those of senescent needles, apart from Ca, Fe, Mn and Zn (Tables 2, 3 and 5). These results are comparable with those for other studies, in which the concentrations of these relatively immobile nutrients (Ca, Mn, Zn and Fe) are reported to be greater in senescent needles than in living needles (e.g. Finér 1996).

Table 11. Annual turnover rates (%) of biomass and nutrients (above-ground tree compartments/litterfall).

Species	Plot	Biomass	N	Ca	K	Mg	Mn	P	S	Zn	Fe
Scots pine	6	1.6	3.1	5.2	1.5	2.4	8.5	4.8	5.3	6.0	3.1
	20	1.5	6.9	6.5	2.8	4.8	10.0	8.3	9.0	6.3	6.0
	10	1.8	6.1	5.2	3.1	3.9	7.6	9.0	10.5	7.9	26.6
	16	1.8	6.2	8.2	3.6	4.0	13.9	10.2	12.6	9.5	7.7
	13	2.8	7.5	9.7	5.0	6.5	14.7	11.6	13.9	17.7	30.6
	18	2.3	7.3	7.8	3.6	4.2	10.7	7.7	11.0	8.4	29.1
	mean	2.0	6.2	7.1	3.3	4.3	10.9	8.6	10.4	9.3	17.2
Norway spruce	3	1.2	2.1	4.3	0.8	2.0	4.6	2.1	2.9	2.8	3.2
	5	1.4	2.8	3.8	1.4	2.2	5.5	3.0	3.9	2.5	5.4
	23	2.4	9.1	5.8	5.2	7.3	7.4	9.7	12.3	2.3	23.5
	11	2.0	6.5	6.9	3.4	5.6	10.9	8.1	11.1	6.2	27.4
	17	1.8	5.4	5.2	3.8	6.7	11.7	6.7	10.5	3.0	19.2
	19	1.6	8.7	5.7	3.5	10.1	13.6	7.3	10.5	5.7	21.9
	12	2.2	6.8	7.3	4.1	6.5	12.1	9.5	11.6	4.9	18.8
	mean	1.8	5.9	5.6	3.2	5.8	9.4	6.6	9.0	3.5	17.1

Larger amounts of needles ended up on the forest floor as senescent needles on the spruce (1793 kg ha^{-1}) than on the pine plots (1251 kg ha^{-1}), although the proportion of senescent needles in relation to the living needle mass of the trees was higher in the pine stands (38%) than in the spruce stands (15%). This means that, for example, an average of 15 kg ha^{-1} yr^{-1} of needle N was recycled back to the soil on the spruce plots, but only 7 kg ha^{-1} yr^{-1} on the pine plots, which undoubtedly has an effect on the nutrient status of the soil. In the needles of both the pine and spruce stands the turnover rate of N, K and P, which are the most mobile nutrients, was less than 16%, indicating that over 85% of these nutrients have been translocated back into the trunk or living needles. In contrast, the turnover rate of the least mobile nutrients (Ca, Mn and Fe) was over 55% in the pine stands, while in the spruce stands notably less, but still over 20%. The results imply that, in pine stands, proportionally more of the immobile nutrients in needles return to the forest floor through the senescent needles than in spruce stands. Similar results have been reported by Mälkönen (1974), Nambiar and Fife (1987) and Helmisaari (1992).

Conclusions

Our results showed, overall, that the average litterfall and above-ground tree mass were greater in the seven Norway spruce stands than in the six Scots pine ones. Similarly, the element concentrations tended to be higher in the spruce stands. We could not find very clear latitude-related nutrient trends in litterfall. However, probably the most obvious trend was for the S concentration, which decreased towards the north in the needles and miscellaneous fraction in both the pine and spruce stands. Similarly, there was also a slightly northwards-decreasing S concentration trend in living needles.

On the average, about 2% of the above-ground tree biomass returned to the forest floor as litterfall on both the spruce and pine plots, although quantitatively more in the spruce than in the pine stands. The stands in north Finland tended to return smaller amounts of nutrients to the forest floor than those in the south, which is obviously related to the lower litter production on the plots in the north. The pool of most of the nutrients in the above-ground tree biomass was 2- to 3-fold higher in the spruce than in the pine stands, the pools of N, Ca and K being the largest. The N, Ca, and K inputs to the forest floor through litterfall were also the largest. For example, in the pine stands the litterfall inputs to the soil could account for a significant proportion of the annual Ca requirements for the annual production of new biomass. Nutrient return via litterfall on the spruce plot at Uusikaarlepyy (No.

Table 12. Annual turnover rates (%) of needle biomass and nutrients (living needle–litterfall needles).

	Plot	Needle mass	N	Ca	K	Mg	Mn	P	S	Zn	Fe
Scots pine	6	20.1	7.7	38.1	3.7	9	34.9	6.8	11	21.3	29.8
	20	37.1	17	64.8	9.2	23.4	61.6	12.2	23.4	44.4	85.4
	10	39.8	13.7	53.1	8.5	16.8	42.4	10.6	20.7	30.5	83.7
	16	43.2	15.1	83.4	10.5	21.9	75.9	12.5	24.7	52.3	79.1
	13	52.1	19.8	68.8	12.1	22.7	67.9	14.3	26.6	52.1	111.4
	18	38.4	13.5	60.7	9.6	20.6	54.8	9	19.6	41.1	88.8
	mean	38.4	14.4	61.4	8.9	19.1	56.3	10.9	21.0	40.3	79.7
Norway spruce	3	6.1	4.1	15.0	1.4	3.8	11.1	3.1	4.9	11.4	6.6
	5	7.4	5.1	15.4	2.3	4.1	11.2	4.1	6.8	11.2	12.1
	23	24.9	18.7	32.6	11.7	19.1	24.1	14.7	21.3	22.3	30.1
	11	18.6	12.7	42.4	6.6	13.1	30.5	10.6	16.3	23.2	28.4
	17	18.7	10.8	40.3	6.8	16.4	32.8	7.8	16.6	15.2	29.6
	19	12.2	7.6	28.3	4.4	10.9	25.5	5.6	10.5	8.9	12.1
	12	18.1	12.5	34.4	6.1	12.1	34.2	11.0	16.2	19.3	30.0
	mean	15.1	10.2	29.8	5.6	11.4	24.2	8.1	13.2	15.9	21.3

23) was often more than 100% greater than that on the other spruce plots. Its location near a fur farm, the proximity of the sea and the acid sulphate soil, undoubtedly contributed to the high litterfall fluxes on this plot.

The calculated turnover rates showed that the Mg turnover rate was higher in the spruce than in the pine stands, which may imply its less efficient retranslocation in the spruce stands. The turnover rates of the other nutrients were slightly higher in the pine stands, indicating faster nutrient cycling via litterfall in the pine stands. The N and S turnover rates appeared to decrease on moving towards the north, especially in the case of pine. This decreasing trend seemed to be related more to the latitude and annual litter production than to site fertility. Larger amounts of needles ended up on the forest floor as senescent needles in the spruce stands than in the pine stands. This means that, for example, an average of 15 kg ha^{-1} yr^{-1} of needle N was recycled back to the soil on the spruce plots, but only 7 kg ha^{-1} yr^{-1} on the pine plots. The turnover rates of the most mobile nutrients (N, K, P) in needles were much lower than those of the relatively immobile nutrients (Ca, Mn, Fe), indicating that the most mobile nutrients had already been translocated from senescent needles into the trunk and old living needles, while the least mobile nutrients accumulated in the oldest tissues and ended up on the forest floor in senescent needles.

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Appendix 1. Annual mass-weighted litterfall nutrient concentrations (mg g^{-1}) by litter fraction on the Scots pine plots from north to south (n.a. = not analysed).

Plot	Fraction	*n*		N (%)	Ca	K	Mg	Mn	P	S	Zn	Fe
6	1	8	mean	0.44	5.22	0.87	0.46	0.93	0.42	0.42	0.05	0.06
			SD	0.061	0.251	0.189	0.050	0.059	0.063	0.021	0.002	0.011
	2	8	mean	0.97	3.26	4.24	0.78	0.60	1.30	0.73	0.04	0.10
			SD	0.258	0.156	0.395	0.020	0.027	0.117	0.046	0.001	0.081
	12	8	mean	0.61	2.05	0.88	0.32	0.09	0.68	0.44	0.04	0.19
			SD	0.101	0.776	0.292	0.030	0.036	0.104	0.061	0.005	0.056
20	1	5	mean	0.52	4.10	1.05	0.58	1.07	0.36	0.45	0.05	0.06
			SD	0.043	0.158	0.124	0.019	0.052	0.036	0.029	0.002	0.002
	2	5	mean	1.06	2.56	4.50	0.90	0.69	1.10	0.74	0.04	0.05
			SD	–	0.108	0.273	0.019	0.024	0.061	0.046	0.002	0.008
	12	5	mean	0.75	3.40	0.97	0.34	0.16	0.57	0.58	0.04	0.19
			SD	0.099	0.175	0.062	0.029	0.038	0.105	0.047	0.002	0.015
	15	5	mean	0.68	8.84	3.46	2.41	0.85	1.72	0.51	0.10	0.07
			SD	0.074	0.546	0.430	0.270	0.098	0.048	0.048	0.013	0.010
10	1	8	mean	0.48	3.63	1.02	0.47	0.73	0.38	0.45	0.04	0.08
			SD	0.025	0.134	0.189	0.043	0.033	0.028	0.016	0.004	0.007
	2	8	mean	1.14	2.47	4.37	0.79	0.51	1.24	0.78	0.03	0.09
			SD	0.160	0.207	0.284	0.081	0.024	0.054	0.027	0.002	0.055
	12	8	mean	0.90	1.97	1.10	0.38	0.10	0.84	0.67	0.07	0.28
			SD	0.198	0.215	0.147	0.070	0.023	0.197	0.142	0.077	0.068
16	1	5	mean	0.45	5.74	1.10	0.46	1.43	0.36	0.47	0.05	0.05
			SD	0.027	0.277	0.210	0.015	0.066	0.027	0.015	0.002	0.005
	2	5	mean	1.22	3.50	4.67	0.82	0.91	1.30	0.85	0.04	0.05
			SD	0.065	0.152	0.203	0.043	0.047	0.046	0.028	0.002	0.004
	12	5	mean	0.78	2.59	1.11	0.34	0.14	0.68	0.64	0.03	0.21
			SD	0.065	0.353	0.095	0.020	0.017	0.088	0.074	0.003	0.035
	15	1	mean	0.65	13.30	2.83	3.92	1.17	1.54	0.56	0.16	0.06
13	1	8	mean	0.56	5.02	1.16	0.43	0.89	0.40	0.48	0.05	0.08
			SD	0.064	0.276	0.202	0.028	0.064	0.041	0.025	0.002	0.030
	2	8	mean	1.26	3.19	4.69	0.72	0.62	1.36	0.83	0.04	0.12
			SD	0.085	0.234	0.231	0.043	0.049	0.082	0.032	0.002	0.107
	12	8	mean	0.82	2.23	1.14	0.41	0.16	0.69	0.62	0.08	0.25
			SD	0.065	0.125	0.124	0.051	0.029	0.127	0.052	0.079	0.032
	13	3	mean	0.71	7.70	1.17	0.56	1.42	0.84	0.62	0.04	0.06
			SD	0.212	2.281	0.491	0.198	0.595	0.087	0.119	0.005	0.021
	14	1	mean	n.a.	7.25	5.55	2.09	1.01	1.81	1.32	0.16	0.07
	15	5	mean	0.89	9.81	3.71	2.38	1.60	1.39	0.70	0.18	0.08
			SD	0.118	0.588	0.473	0.219	0.141	0.267	0.097	0.020	0.023
18	1	2	mean	0.48	4.76	1.25	0.42	0.63	0.31	0.44	0.06	0.09
			SD	0.043	0.154	0.332	0.031	0.011	0.009	0.015	0.000	0.012
	2	2	mean	1.08	2.74	5.07	0.75	0.38	1.22	0.78	0.04	0.07
			SD	0.177	0.163	0.185	0.027	0.016	0.036	0.022	0.002	0.002
	12	2	mean	0.74	2.41	0.95	0.30	0.06	0.52	0.55	0.04	0.34
			SD	0.055	0.118	0.009	0.013	0.002	0.048	0.041	0.011	0.086
	15	2	mean	0.55	7.82	2.36	1.52	0.60	0.83	0.48	0.17	0.09
			SD	0.146	0.424	1.226	0.017	0.089	0.207	0.038	0.007	0.016

1 = senescent needles (Scots pine), 2 = green needles (Scots pine), 12 = miscellaneous, 13 = senescent and green needles (Norway spruce), 14 = green broadleaves, 15 = brown broadleaves.

Appendix 2. Annual mass-weighted litterfall nutrient concentrations (mg g^{-1}) by litter fraction on the Norway spruce plots from north to south.

Plot	Fraction	*n*		N (%)	Ca	K	Mg	Mn	P	S	Zn	Fe
3	12	2	mean	1.18	3.97	1.71	0.73	0.593	1.24	0.90	0.13	0.31
			SD	0.010	0.536	0.092	0.016	0.078	0.020	0.016	0.022	0.038
	13	2	mean	0.69	15.26	1.23	0.79	1.554	0.78	0.61	0.10	0.04
			SD	0.077	1.198	0.023	0.002	0.059	0.004	0.029	0.008	0.004
5	12	8	mean	0.97	2.30	2.26	0.67	0.556	1.07	0.73	0.08	0.26
			SD	0.134	0.785	0.748	0.089	0.174	0.161	0.086	0.004	0.092
	13	8	mean	0.75	11.39	1.71	0.57	1.975	0.79	0.67	0.08	0.04
			SD	0.100	0.773	0.211	0.023	0.189	0.090	0.028	0.004	0.009
	15	2	mean	0.80	7.48	2.93	2.11	1.904	2.04	0.61	0.10	0.06
			SD	0.162	1.417	1.230	0.433	0.386	0.619	0.065	0.040	0.022
23	1	5	mean	0.38	4.03	1.37	0.54	0.235	0.24	0.42	0.02	0.18
			SD	–*	0.217	0.261	0.070	0.030	0.021	0.019	0.002	0.193
	5	1	mean	0.88	0.29	3.62	0.76	0.062	0.64	0.68	0.02	0.03
	7	1	mean	1.44	4.24	1.80	0.67	0.231	0.84	1.07	0.09	0.37
	12	5	mean	1.63	2.87	3.46	0.96	0.217	1.40	1.24	0.07	0.42
			SD	0.269	0.460	0.835	0.060	0.030	0.098	0.188	0.010	0.149
	13	5	mean	1.03	5.64	3.45	1.15	0.551	0.94	0.84	0.03	0.04
			SD	0.067	0.450	0.450	0.025	0.041	0.098	0.038	0.002	0.004
	15	2	mean	1.53	9.21	6.93	3.11	1.000	1.25	1.03	0.18	0.14
			SD	0.103	0.179	3.610	0.249	0.014	0.234	0.107	0.044	0.084
11	1	8	mean	0.52	3.01	1.26	0.38	0.749	0.38	0.47	0.03	0.09
			SD	0.048	0.126	0.153	0.033	0.053	0.064	0.034	0.002	0.051
	2	8	mean	1.09	1.60	3.52	0.49	0.419	0.96	0.62	0.03	0.05
			SD	0.440	0.915	2.086	0.287	0.244	0.559	0.349	0.015	0.040
	12	8	mean	1.24	3.79	2.39	0.73	0.621	1.28	1.08	0.15	0.47
			SD	0.123	0.421	0.360	0.046	0.057	0.161	0.081	0.113	0.079
	13	8	mean	0.85	9.97	2.17	0.77	1.839	0.98	0.68	0.04	0.04
			SD	0.038	0.628	0.126	0.032	0.145	0.055	0.029	0.003	0.007
	15	4	mean	0.87	11.46	3.06	2.30	2.540	1.70	0.75	0.13	0.08
			SD	0.225	0.560	0.627	0.373	0.231	0.262	0.063	0.012	0.020
17	12	5	mean	1.04	1.83	2.89	0.72	0.209	0.98	0.90	0.04	0.33
			SD	0.206	0.470	0.235	0.083	0.063	0.225	0.166	0.004	0.091
	13	5	mean	0.78	7.91	1.86	1.10	1.278	0.58	0.72	0.01	0.04
			SD	0.029	0.469	0.162	0.036	0.089	0.037	0.029	0.001	0.005
19	1	5	mean	0.53	4.92	1.16	0.52	0.885	0.29	0.47	0.04	0.07
			SD	0.110	0.380	0.088	0.042	0.065	0.026	0.026	0.001	0.004
	2	5	mean	1.19	3.06	4.80	0.86	0.624	1.19	0.85	0.04	0.05
			SD	0.296	0.389	0.552	0.113	0.113	0.165	0.116	0.003	0.012
	12	5	mean	1.18	4.26	2.17	0.74	0.311	0.86	0.97	0.06	0.42
			SD	0.074	0.271	0.564	0.061	0.035	0.096	0.029	0.003	0.063
	13	5	mean	0.80	12.41	2.19	0.94	1.443	0.58	0.69	0.02	0.04
			SD	0.064	0.546	0.216	0.051	0.107	0.071	0.042	0.003	0.003
	14	5	mean	2.11	6.66	7.73	2.69	0.896	1.67	1.30	0.09	0.07
			SD	0.392	1.056	1.400	0.185	0.180	0.582	0.212	0.013	0.012
	15	5	mean	0.78	10.36	3.49	3.14	1.383	0.51	0.66	0.08	0.08
			SD	0.053	0.892	0.486	0.248	0.119	0.077	0.038	0.009	0.006
12	1	8	mean	0.63	4.38	1.09	0.49	0.495	0.40	0.52	0.04	0.11
			SD	0.206	0.310	0.255	0.036	0.054	0.089	0.041	0.002	0.056
	2	4	mean	1.23	2.48	4.24	0.68	0.310	1.13	0.76	0.03	0.10
			SD	0.095	0.729	1.397	0.216	0.093	0.351	0.233	0.008	0.092
	12	8	mean	1.22	2.63	2.39	0.79	0.215	1.13	0.99	0.10	0.54
			SD	0.142	0.296	0.379	0.080	0.029	0.209	0.104	0.048	0.209
	13	8	mean	0.84	10.27	1.72	0.94	1.034	0.79	0.72	0.03	0.06
			SD	0.060	0.487	0.117	0.056	0.060	0.041	0.024	0.002	0.010
	15	5	mean	0.87	11.02	4.10	2.89	0.861	0.95	0.75	0.11	0.12
			SD	0.130	0.790	1.222	0.134	0.086	0.107	0.085	0.017	0.022

1 = Senescent (Scots pine), 2 = green needles (Scots pine), 5 = cones, 7 = branches, 12 = miscellaneous, 13 = needles (Norway spruce), 14 = green broadleaves, 15 = senescent broadleaves. * Only one N analysis.

Appendix 3. Nutrient concentrations (mg g^{-1}) of different biomass compartments of Scots pine plots (mean). Plots are arranged from north to south.

Plot	Compartment	*n*		N (%)	Ca	K	Mg	Mn	P	S	Zn	Fe
6	Stemwood	5	mean	0.13	0.62	0.36	0.15	0.08	0.02	0.04	0.007	0.046
			SD	0.038	0.059	0.029	0.018	0.012	0.005	0.004	0.001	0.015
	Living branches	10	mean	0.54	2.29	2.92	0.73	0.24	0.50	0.33	0.026	0.062
			SD	0.246	0.722	1.793	0.369	0.105	0.346	0.204	0.010	0.062
	Needles	2	mean	1.16	2.73	5.00	1.02	0.53	1.26	0.77	0.047	0.042
			SD	0.074	0.948	0.548	0.125	0.198	0.092	0.007	0.009	0.001
	Bark	5	mean	0.38	4.79	1.20	0.35	0.11	0.29	0.23	0.015	0.064
			SD	0.051	1.151	0.190	0.056	0.01	0.037	0.014	0.015	0.029
	Dead branches	1	mean	0.22	1.22	0.15	0.19	0.11	0.03	0.11	0.016	0.009
20	Stemwood	3	mean	0.06	0.56	0.29	0.11	0.06	0.02	0.03	0.008	0.028
			SD	0.013	0.039	0.045	0.006	0.025	0.003	0.004	0.002	0.012
	Living branches	6	mean	0.55	2.31	2.79	0.61	0.21	0.57	0.36	0.031	0.039
			SD	0.366	0.653	2.031	0.288	0.087	0.500	0.295	0.011	0.037
	Needles	2	mean	1.19	2.32	4.85	0.94	0.63	1.19	0.73	0.045	0.024
			SD	0.023	1.047	0.691	0.077	0.264	0.106	0.004	0.011	0.004
	Bark	3	mean	0.31	5.02	0.85	0.23	0.12	0.16	0.21	0.023	0.058
			SD	0.050	1.833	0.145	0.026	0.048	0.033	0.037	0.004	0.052
	Dead branches	1	mean	0.20	0.77	0.07	0.09	0.07	0.01	0.18	0.014	0.018
10	Stemwood	5	mean	0.11	0.56	0.28	0.13	0.08	0.02	0.04	0.008	0.007
			SD	0.022	0.062	0.031	0.016	0.023	0.002	0.002	0.003	0.002
	Living branches	10	mean	0.60	2.15	2.83	0.67	0.19	0.61	0.35	0.026	0.039
			SD	0.355	0.659	1.970	0.325	0.058	0.492	0.263	0.013	0.033
	Needles	2	mean	1.47	2.67	5.16	1.15	0.68	1.50	0.89	0.050	0.038
			SD	0.007	0.856	0.404	0.185	0.203	0.064	0.035	0.008	0.010
	Bark	5	mean	0.38	4.75	0.77	0.23	0.10	0.20	0.22	0.016	0.024
			SD	0.039	1.874	0.194	0.087	0.026	0.066	0.025	0.007	0.005
	Dead branches	1	mean	0.21	1.47	0.14	0.33	0.15	0.02	0.08	0.015	0.014
16	Stemwood	5	mean	0.10	0.59	0.35	0.13	0.09	0.02	0.03	0.006	0.027
			SD	0.013	0.072	0.053	0.006	0.008	0.002	0.002	0.001	0.025
	Living branches	10	mean	0.53	2.11	2.37	0.56	0.19	0.49	0.30	0.021	0.036
			SD	0.335	0.893	1.419	0.215	0.048	0.374	0.213	0.010	0.029
	Needles	2	mean	1.43	2.91	5.39	0.94	0.79	1.42	0.86	0.044	0.028
			SD	0.033	1.245	0.281	0.082	0.328	0.035	0.054	0.013	0.004
	Bark	5	mean	0.32	3.93	0.58	0.16	0.09	0.14	0.16	0.010	0.018
			SD	0.039	1.344	0.124	0.045	0.026	0.038	0.018	0.004	0.009
	Dead branches	1	mean	0.28	1.54	0.40	0.32	0.17	0.03	0.08	0.011	0.018
13	Stemwood	5	mean	0.16	0.65	0.31	0.13	0.09	0.02	0.04	0.007	0.011
			SD	0.022	0.043	0.026	0.028	0.028	0.002	0.006	0.002	0.005
	Living branches	10	mean	0.65	2.08	2.79	0.56	0.18	0.62	0.36	0.023	0.031
			SD	0.318	0.881	1.613	0.260	0.073	0.430	0.229	0.010	0.021
	Needles	2	mean	1.57	3.75	5.61	1.03	0.67	1.61	0.98	0.050	0.040
			SD	0.070	1.294	0.502	0.124	0.224	0.078	0.013	0.007	0.008
	Bark	5	mean	0.46	5.30	1.01	0.28	0.13	0.26	0.26	0.018	0.027
			SD	0.065	1.779	0.444	0.146	0.088	0.120	0.060	0.010	0.005
	Dead branches	1	mean	0.25	1.21	0.14	0.22	0.10	0.03	0.08	0.009	0.007
18	Stemwood	5	mean	0.07	0.64	0.33	0.13	0.06	0.02	0.03	0.009	0.010
			SD	0.030	0.075	0.034	0.017	0.017	0.003	0.001	0.002	0.006
	Living branches	10	mean	0.66	2.24	2.71	0.56	0.12	0.56	0.36	0.029	0.042
			SD	0.428	0.811	1.841	0.236	0.036	0.466	0.273	0.013	0.033
	Needles	2	mean	1.41	2.96	5.65	0.81	0.44	1.44	0.88	0.056	0.039
			SD	0.026	1.245	0.356	0.142	0.188	0.078	0.035	0.014	0.009
	Bark	5	mean	0.38	3.88	1.04	0.24	0.06	0.20	0.23	0.018	0.039
			SD	0.026	0.768	0.251	0.066	0.021	0.053	0.024	0.005	0.010
	Dead branches	1	mean	0.22	0.71	0.10	0.16	0.06	0.02	0.14	0.012	0.017

Appendix 4. Nutrient concentrations (mg g^{-1}) of different biomass compartments of Norway spruce plots (mean). Plots are plots arranged from north to south.

Plot	Compartment	*n*		N (%)	Ca	K	Mg	Mn	P	S	Zn	Fe
3	Stemwood	5	mean	0.16	0.89	0.49	0.13	0.11	0.04	0.05	0.012	0.011
			SD	0.066	0.123	0.115	0.012	0.033	0.020	0.006	0.004	0.004
	Living branches	10	mean	0.62	5.57	2.74	0.58	0.47	0.64	0.36	0.073	0.056
			SD	0.388	1.394	1.918	0.252	0.094	0.483	0.220	0.012	0.068
	Needles	2	mean	1.03	6.20	5.18	1.25	0.85	1.53	0.75	0.056	0.037
			SD	0.056	2.942	1.113	0.013	0.356	0.134	0.003	0.017	0.008
	Bark	5	mean	0.34	12.22	1.80	0.54	0.69	0.30	0.25	0.168	0.015
			SD	0.038	3.514	0.290	0.113	0.209	0.049	0.027	0.060	0.001
	Dead branches	1	mean	0.22	6.09	0.45	0.31	0.37	0.09	0.29	0.078	0.021
5	Stemwood	5	mean	0.12	0.81	0.44	0.10	0.10	0.03	0.04	0.011	0.006
			SD	0.050	0.141	0.162	0.041	0.013	0.003	0.004	0.002	0.001
	Living branches	10	mean	0.54	4.72	2.67	0.53	0.48	0.56	0.35	0.077	0.050
			SD	0.282	0.640	1.871	0.235	0.182	0.355	0.190	0.018	0.024
	Needles	2	mean	1.10	5.50	5.50	1.04	1.32	1.41	0.73	0.054	0.027
			SD	0.107	2.432	0.795	0.098	0.463	0.141	0.001	0.013	0.004
	Bark	5	mean	0.38	13.76	1.81	0.57	0.74	0.34	0.26	0.164	0.021
			SD	0.026	2.628	0.282	0.122	0.194	0.076	0.016	0.039	0.004
	Dead branches	1	mean	0.29	3.57	0.29	0.17	0.22	0.08	0.16	0.054	0.022
23	Stemwood	5	mean	0.11	0.63	0.52	0.12	0.06	0.03	0.04	0.009	0.006
			SD	0.027	0.057	0.116	0.026	0.010	0.008	0.004	0.001	0.001
	Living branches	10	mean	0.65	3.14	3.16	0.64	0.21	0.60	0.38	0.057	0.030
			SD	0.431	0.563	2.265	0.260	0.099	0.456	0.258	0.013	0.019
	Needles	2	mean	1.36	4.35	7.24	1.51	0.57	1.57	0.98	0.031	0.034
			SD	0.132	1.577	2.003	0.022	0.120	0.332	0.063	0.001	0.006
	Bark	5	mean	0.45	9.92	2.58	0.81	0.41	0.47	0.31	0.142	0.046
			SD	0.046	1.653	0.375	0.075	0.098	0.064	0.012	0.018	0.030
	Dead branches	1	mean	0.24	2.59	0.88	0.37	0.18	0.09	0.11	0.041	0.011
11	Stemwood	5	mean	0.12	0.72	0.33	0.09	0.09	0.02	0.04	0.009	0.008
			SD	0.043	0.040	0.029	0.014	0.016	0.004	0.001	0.001	0.002
	Living branches	10	mean	0.67	4.12	3.19	0.57	0.39	0.70	0.34	0.059	0.035
			SD	0.428	0.865	2.193	0.271	0.118	0.541	0.219	0.013	0.021
	Needles	2	mean	1.26	4.41	6.17	1.09	1.13	1.72	0.79	0.035	0.026
			SD	0.112	1.252	1.788	0.148	0.237	0.283	0.073	0.004	0.001
	Bark	5	mean	0.43	12.21	2.85	0.69	0.78	0.49	0.27	0.158	0.018
			SD	0.051	3.310	0.124	0.089	0.092	0.055	0.018	0.023	0.003
	Dead branches	1	mean	0.29	5.56	0.45	0.39	0.42	0.10	0.14	0.063	0.016
17	Stemwood	5	mean	0.16	0.69	0.39	0.10	0.05	0.03	0.04	0.006	0.011
			SD	0.038	0.039	0.126	0.004	0.015	0.005	0.006	0.001	0.004
	Living branches	10	mean	0.54	4.17	2.74	0.58	0.23	0.59	0.31	0.038	0.028
			SD	0.403	0.854	2.177	0.279	0.089	0.508	0.232	0.009	0.016
	Needles	2	mean	1.34	3.72	4.99	1.27	0.74	1.35	0.80	0.017	0.026
			SD	0.105	0.948	1.317	0.149	0.086	0.318	0.034	0.004	0.000
	Bark	5	mean	0.43	12.84	2.19	0.63	0.39	0.45	0.29	0.094	0.026
			SD	0.029	2.977	0.347	0.059	0.138	0.036	0.034	0.025	0.014
	Dead branches	1	mean	0.14	3.04	0.24	0.23	0.16	0.05	0.10	0.026	0.010
19	Stemwood	1	mean	0.03	0.91	0.41	0.08	0.04	0.02	0.03	0.005	0.006
	Living branches	2	mean	0.48	4.89	3.16	0.51	0.21	0.43	0.28	0.036	0.033
			SD	0.502	0.764	3.217	0.305	0.054	0.433	0.249	0.011	0.037
	Needles	2	mean	1.29	5.38	6.03	1.06	0.70	1.25	0.80	0.032	0.039
			SD	0.107	1.775	1.535	0.090	0.150	0.290	0.058	0.002	0.007
	Bark	1	mean	0.41	15.40	1.71	0.39	0.34	0.29	0.30	0.082	0.062
	Dead branches	1	mean	0.18	8.48	0.39	0.28	0.18	0.04	0.11	0.029	0.009
12	Stemwood	5	mean	0.15	0.63	0.26	0.09	0.05	0.01	0.03	0.008	0.015
			SD	0.044	0.045	0.033	0.022	0.011	0.005	0.003	0.001	0.010
	Living branches	10	mean	0.59	3.93	2.35	0.53	0.21	0.48	0.32	0.059	0.072
			SD	0.395	0.886	1.597	0.223	0.084	0.375	0.223	0.017	0.054
	Needles	2	mean	1.21	5.42	5.10	1.43	0.55	1.29	0.80	0.029	0.034
			SD	0.144	1.803	1.685	0.038	0.106	0.339	0.103	0.003	0.004
	Bark	5	mean	0.47	12.60	2.16	0.77	0.40	0.42	0.29	0.136	0.023
			SD	0.062	3.715	0.342	0.155	0.169	0.066	0.031	0.035	0.005
	Dead branches	1	mean	0.12	3.30	0.20	0.30	0.15	0.02	0.08	0.044	0.007