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Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands

HELJÄ-SISKO HELMISAARI,[1,2] JOHN DEROME,[3] PEKKA NÖJD[1] and MIKKO KUKKOLA[1]

[1] *Finnish Forest Research Institute, Vantaa Research Unit, P.O.Box 18, FI-01301 Vantaa, Finland*

[2] *Corresponding author (helja-sisko.helmisaari@metla.fi)*

[3] *Finnish Forest Research Institute, Rovaniemi Research Unit, P.O. Box 16, FI-96301 Rovaniemi, Finland*

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Summary Variations in fine root biomass of trees and understory in 16 stands throughout Finland were examined and relationships to site and stand characteristics determined. Norway spruce fine root biomass varied between 184 and 370 g m^{-2}, and that of Scots pine ranged between 149 and 386 g m^{-2}. In northern Finland, understory roots and rhizomes (< 2 mm diameter) accounted for up to 50% of the stand total fine root biomass. Therefore, the fine root biomass of trees plus understory was larger in northern Finland in stands of both tree species, resulting in a negative relationship between fine root biomass and the temperature sum and a positive relationship between fine root biomass and the carbon:nitrogen ratio of the soil organic layer. The foliage:fine root ratio varied between 2.1 and 6.4 for Norway spruce and between 0.8 and 2.2 for Scots pine. The ratio decreased for both Norway spruce and Scots pine from south to north, as well as from fertile to more infertile site types. The foliage:fine root ratio of Norway spruce was related to basal area and stem surface area. The strong positive correlations of these three parameters with fine root nitrogen concentration implies that more fine roots are needed to maintain a certain amount of foliage when nutrient availability is low. No significant relationships were found between stand parameters and fine root biomass at the stand level, but the relationships considerably improved when both fine root biomass and stand parameters were calculated for the mean tree in the stand. When the northern and southern sites were analyzed separately, fine root biomass per tree of both species was significantly correlated with basal area and stem surface area per tree. Basal area, stem surface area and stand density can be estimated accurately and easily. Thus, our results may have value in predicting fine root biomass at the tree and stand level in boreal Norway spruce and Scots pine forests.

Keywords: boreal forest, carbon allocation, Picea abies, Pinus sylvestris, understory.

Introduction

Roots of trees and understory vegetation contain considerable stores of carbon and nutrients and therefore play an important role in the carbon and nutrient dynamics of forest ecosystems. However, there is insufficient quantitative information available about their contribution to the carbon and nutrient budgets (Gower et al. 1994, Bartelink 1998, Trumbore and Gaudinski 2003, Majdi and Andersson 2004).

Knowledge of root biomass and its dynamics is essential for a detailed understanding of carbon allocation and storage in terrestrial ecosystems (Cairns et al. 1997). Direct assessment of root biomass is laborious and costly, and therefore cannot be employed in large surveys. As a result, the development of models for predicting root biomass has been a research target for several decades. Allometric biomass functions for coarse roots have been developed for different species, sites and geographical regions (Santantonio et al. 1977, Nielsen 1990, Kapeluck and Van Lear 1995). Recently, Bolte et al. (2004) and Petersson and Ståhl (2006) developed allometric functions for roots > 2 mm in diameter in German and Swedish stands of *Fagus sylvatica* L., *Picea abies* L. Karst., *Pinus sylvestris* L., *Betula pendula* Roth. and *Betula pubescens* Ehrh.

It has proved difficult to develop allometric functions for fine roots. Distinguishing among roots of different species and between living and dead roots is the initial challenge. In developing allometric functions, there is also the challenge of assigning fine roots to individual trees. Further difficulties arise because the growth and development of fine roots closely reflect the heterogeneity of the soil environment, and because fine root turnover can be rapid, resulting in large temporal and spatial variations in fine root biomass.

Santantonio (1989) reported a linear relationship between fine root and foliage biomass in several conifer species; however, many other studies have shown that this relationship is highly variable (cf. Vanninen and Mäkelä 1999). Foliage biomass is usually estimated by modeling, but models have not been developed for all species or regions. To date, only a few studies have attempted to establish relationships between fine root biomass and more easily measured stand variables (e.g. Santantonio 1989, Vogt et al. 1996, Cairns et al. 1997, Vanninen and Mäkelä 1999, Li et al. 2003, Chen et al. 2004, Ammer and Wagner 2005).

Cairns et al. (1997) showed that aboveground biomass density and stand age and latitude are the most important predictors of root biomass density. However, none of the tested aboveground biomass variables (density, latitude, temperature, precipitation, temperature/precipitation ratios, tree type, soil texture and age) had a substantial effect on the root:shoot ratio.

Site fertility has been shown to affect the fine root:needle biomass ratio of Scots pine (Vanninen and Mäkelä 1999). Vanninen and Mäkelä (1999) found that basal area was a good predictor of fine root biomass of Scots pine stands when the data were stratified according to site quality. However, the site quality classifications used in individual countries vary, making it difficult to compare the results of different studies.

Most studies of fine roots in forests have concentrated on tree fine roots, and the roots and rhizomes of the understory vegetation have often been neglected. Although the understory vegetation represents a relatively minor component of the whole biomass of boreal forest ecosystems, it plays an important role in annual biomass production and carbon and nutrient cycling, especially at northern latitudes (Chapin 1980*a*, Helmisaari 1995, Olsrud and Christensen 2004).

Quantification of fine roots is required to estimate their roles as carbon stores and sources of the soil litter input. If the relationships between fine roots and more easily measurable variables could be identified, it would make an important contribution to carbon modeling and reporting. We studied fine root biomass in 16 stands throughout Finland representing a range of site fertilities and stand characteristics. Our study considered understory as well as tree belowground biomass. The specific aims were to: (1) describe the variation in Norway spruce, Scots pine and understory fine root biomass on different sites; and (2) determine whether there are relationships between fine root biomass and site and stand factors.

Materials and methods

Experimental stands

We studied eight Norway spruce (*Picea abies* L. Karst.) and eight Scots pine (*Pinus sylvestris* L.) dominated stands in Finland (Figure 1). The stands belong to the intensive monitoring network of the EU/Forest Focus and UN-ECE/ICP Forests Level II monitoring programmes (International Cooperative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests).

The stands are located in different parts of Finland and represent relatively different climates (Table 1), site types (Table 2) and stages of stand development (Table 3). The stands in southern Finland are located in the humid continental region and those in northern Finland in the sub-arctic climatic region. In this study, the stands located below latitude 64° N were considered to be in southern Finland, and those to the north of this latitude in northern Finland. The long-term (1961–1990) mean annual effective temperature sum (threshold +5 °C) varied between 660 and 1290 d.d. (degree days), and mean annual precipitation between 420 and 630 mm. In addition to latitude, altitude has an effect on the summer temperature and temperature sum (Sjörs et al. 2004).

All the stands are in the boreal vegetation zone. The site types vary from fertile herb-rich *Oxalis–Myrtillus* (OMT) types to nutrient-poor xeric *Calluna* (CT) and *Empetrum–Calluna* (ECT) types. The soil types are mostly podzols, except for the relatively fertile sites at Punkaharju and Juupajoki that are cambisols and arenosols. The soils include till, sandy loam and loamy sand (Table 2). The thickness of the organic layer varies between 5 and 10 cm in the Norway spruce stands and between 2 and 5 cm in the Scots pine stands. The organic layer is, on average, about 2 cm thicker in the stands in southern Finland compared with those in northern Finland (Table 2). The Norway spruce stands are located on till soils with a stoniness varying between 5 and 49% (mean value 23%) of the soil volume (0–30 cm mineral soil layer, Table 2). Most of the Scots pine stands are on sandy sorted soils, with a stoniness of between 0.5 and 9% (mean 3%) (Table 2). The stoniness was measured at 60 locations in each stand and calculated according to Viro (1952).

Twelve of the stands are in managed forests and have been thinned at various stages of development. However, four of the stands are relatively natural old-growth forests in nature conservation areas. In general, the stands in northern Finland have been managed less intensively than the stands in southern Finland. All stands have reached canopy closure. At the time of the study, ages of the six relatively even-aged managed Norway spruce stands varied between 55 and 140 years, and the mean age of the largest trees in the two uneven-aged natural stands was 170 years. Ages of the seven, relatively even-aged, managed Scots pine stands varied between 55 and 200 years,

Figure 1. Location of the Norway spruce (▲) and Scots pine (○) stands.

Table 1. Location and climate of the stands. Temperature sum and precipitation are for the period 1961–1990. Temperature sum equals the sum of differences between daily mean temperatures and the threshold of +5 °C.

Stand	Latitude (N)	Longitude (E)	Elevation (m)	Annual mean temperature sum (°C)	Annual mean precipitation (mm)
Norway spruce					
Tammela	60° 38′	23° 48′	143	1253	625
Evo	61° 14′	25° 04′	165	1209	601
Punkaharju	61° 48′	29° 19′	88	1289	594
Juupajoki	61° 51′	24° 18′	177	1140	615
Uusikaarlepyy	63° 33′	22° 29′	3	1131	492
Oulanka	66° 18′	29° 30′	270	774	554
Kivalo	66° 20′	26° 38′	252	825	539
Pallasjärvi	67° 60′	24° 14′	300	683	480
Scots pine					
Tammela	60° 37′	23° 50′	120	1275	627
Miehikkälä	60° 42′	27° 50′	48	1351	629
Punkaharju	61° 46′	29° 20′	99	1280	593
Juupajoki	61° 52′	24° 13′	154	1163	614
Lieksa	63° 09′	30° 42′	168	1066	623
Ylikiiminki	64° 58′	26° 23′	90	1030	524
Kivalo	66° 21′	26° 44′	145	885	537
Sevettijärvi	69° 35′	28° 54′	105	658	419

and the mean age of the one uneven-aged natural stand was 130 years (Table 3). Stand age is higher in northern Finland than in southern Finland because of the longer rotation period in the north.

Stand characteristics and tree biomass

Each stand contained three sub-plots, 30 × 30 m in size, and a surrounding buffer zone. Stand measurements were made on all three sub plots in each stand. Tree species, diameter (at 1.3 m above ground level), tree height and crown length were measured on all trees in the plot with a breast height diameter of at least 4.5 cm. Taper curve functions of Laasasenaho (1982) were used to estimate stem volume. The KPL program (Heinonen 1994) was used to calculate the characteristics of the individual trees and to transform them into stand-level estimates.

Table 2. Site and soil characteristics of the stands (Rautjärvi et al. 2002). Biotic region is according to Sjörs et al. (2004). Site type 1 is according to Cajander (1949), and type 2 is according to Sjörs et al. (2004). An asterisk (*) denotes a soil structure of sorted glaciofluvial deposits.

Stand	Site type 1	Site type 2	Biotic region	Soil type	Soil structure	Stones (%)	Organic layer cm	Organic layer N (%)	Organic layer C/N
Norway spruce									
Tammela	MT	Mesic	Southern boreal	Haplic podzol	Till	18.4	8	12.6	30.6
Evo	OMT	Herb-rich	Southern boreal	Cambic podzol	Sandy loam	49	5	9.7	27.4
Punkaharju	OMT	Herb-rich	Southern boreal	Cambic arenosol	Till	17.9	8	13.7	28
Juupajoki	OMT	Herb-rich	Middle boreal	Dystric cambisol	Till	32.3	5	13	28.4
Uusikaarlepyy	OMT	Herb-rich	Southern boreal	Cambic podzol	Till	5.2	10	16	27
Oulanka	HMT	Mesic	Northern boreal	Haplic podzol	Sandy loam	17.3	6	7	46.7
Kivalo	HMT	Mesic	Northern boreal	Ferric podzol	Till	16	5	10.4	43.9
Pallasjärvi	HMT	Mesic	Northern boreal	Ferric podzol	Till	24.6	5	8.5	46.7
Scots pine									
Tammela	VT	Sub-xeric	Southern boreal	Haplic podzol	*	5.5	4	10.8	32.8
Miehikkälä	CT	Xeric	Southern boreal	Ferric podzol	Till	6.3	4	10.2	40.9
Punkaharju	VT	Sub-xeric	Southern boreal	Ferric podzol	Till	8.8	5	7.9	42.2
Juupajoki	VT	Sub-xeric	Middle boreal	Ferric podzol	Till	2.2	5	12.5	36.1
Lieksa	EVT	Xeric	Middle boreal	Haplic podzol	Loamy sand	0.5	5	8.6	52.7
Ylikiiminki	ECT	Xeric	Middle boreal	Ferric podzol	Till	0.5	3	7.5	43.7
Kivalo	EMT	Sub-xeric	Northern boreal	Cambic podzol	Till	0.5	3	8.7	44.7
Sevettijärvi	UVET	Sub-xeric	Northern boreal	Ferric podzol	Sandy loam	0.5	2	10.4	42.2

Table 3. Stand characteristics in spring 2000. Mean diameter at breast height (DBH) is weighted with basal area, mean height is arithmetic, and stem volume is with bark. Stand characteristics other than density are given for all trees in the stands. Site index (H100) is dominant height at age 100 years. Fine root nitrogen (N) is for the living Norway spruce and Scots pine fine roots in the organic layer.

Stand	Stem no. (ha^{-1})					Stand age (years)	Mean DBH (cm)	Mean height (m)	Site index (H100) (m)	Basal area ($m^2\ ha^{-1}$)	Stem		Volume growth ($m^3\ ha^{-1}\ year^{-1}$)	Tree fine root N (%)
	Birch	Pine	Spruce	Other	All						Surface area ($m^2\ ha^{-1}$)	Volume ($m^3\ ha^{-1}$)		
Norway spruce														
Tammela	41	67	544	26	678	60	23.9	20.0	30.2	27.6	4979	273	8.9	0.82
Evo	228	8	769	290	1295	170	30.2	18.5	22.6	54.1	6595	650	4.2	0.88
Punkaharju			374	4	378	70	31.5	26.1	34.7	28.5	6291	348	8.8	1.02
Juupajoki	48	19	770	30	867	80	24.3	19.8	28.0	33.2	7261	339	10.4	1.07
Uusikaarlepyy			944	26	970	55	22.7	18.9	27.3	34.8	7776	334	13.9	0.99
Oulanka	108	88	1267	279	1742	170	22.9	8.8	15.5	25.6	2384	176	2.7	0.58
Kivalo	11	4	1644	4	1663	70	14.8	9.6	17.3	21.6	3898	117	3.1	0.75
Pallasjärvi			1096	11	1107	140	17.2	7.5	10.0	13.0	2280	66	1.8	0.62
Scots pine														
Tammela	19	581		4	604	60	22.2	19.2	25.5	21.9	4491	203	10.5	1.01
Miehikkälä		407		8	415	120	23.6	19.4	19.5	16.8	3832	159	4.3	0.7
Punkaharju		948		8	956	80	20.8	21.4	26.0	29.4	7496	306	11.1	0.71
Juupajoki		378			378	80	25.7	21.1	23.6	17.9	3866	182	3.8	0.88
Lieksa	65	377		146	588	130	31.8	16.9	23.1	28.8	4510	311	8.5	0.45
Ylikiiminki		548			548	90	18.3	12.7	15.9	12.5	2194	83	2.2	0.8
Kivalo		1748			1748	55	13.3	11.1	17.9	21.3	4698	127	6.0	0.79
Sevettijärvi	10	355		5	370	200	24.4	10.1	8.1	13.4	1866	75	1.2	0.82

Stem surface area was calculated by determining the taper curve of each stem and then dividing the stem into 10-cm long sections. The surface area of each section was calculated based on a cylindrical approximation.

Needle biomass estimates for individual trees were calculated with the functions of Marklund (1987, 1988), which in most cases describe the biomass components (stem wood, living and dead branches, bark, needles) as a function of tree species, diameter and height. However, the functions describing needle biomass for Norway spruce and Scots pine also include crown length as an additional explanatory variable. The needle mass function for Scots pine also includes the latitudinal coordinate.

Fine and small root biomass

Fine root samples for biomass and nutrient determinations were taken over 3 weeks (July 20–August 12, 1998) to facilitate comparisons between sites. From each stand, 12 root cores were taken with a cylindrical soil corer (diameter 40 mm). The cores were divided into sections comprising the organic layer and the 0–5, 5–10, 10–20 and 20–30-cm mineral soil layers. Roots were separated from the soil by washing. The roots were sorted into living and dead based on color, elasticity and toughness (Persson 1983), and further into Scots pine, Norway spruce, birch and other broad-leaved species roots and understory (mainly dwarf shrubs and grasses) roots and rhizomes based on microscopic morphology and color. Roots less than 2 mm in diameter were denoted as fine roots (Persson 1983, Vogt et al. 1983), and they included mycorrhizal short root tips. Roots with a diameter of 2–5 mm were also sorted, and they were classified as small roots.

Root samples were dried at 70 °C for 48 h, weighed and milled. Total nitrogen was determined with a CHN analyzer (Leco). Ash content of fine roots was determined to estimate the extent to which mineral soil, still remaining on the fine roots after washing, affected the dry mass values. The ash content was always less than 6%.

Root cores were taken from the buffer zone along the four sides of one of the sub plots where conditions were assumed to be representative of the whole stand. The managed stands were homogeneous, but in the few unmanaged stands, trees were unevenly distributed so 12 cores may have been insufficient to provide a representative sample.

Fine root biomass in each of the volumetric mineral soil samples was corrected for the presence of stones based on the stoniness index (Viro 1952, Tamminen 1991).

Results

Variation in tree and understory fine root biomass

Mean fine root biomasses of Norway spruce (261 ± 57 g m^{-2}) and Scots pine (243 ± 88 g m^{-2}) were of the same magnitude, but with greater variation in the Scots pine stands. Fine root biomass varied between 184 and 370 g m^{-2} in Norway spruce (Figure 2a) and between 149 and 386 g m^{-2} in Scots pine (Figure 2b). Total fine root biomass of all tree species plus the total biomass of understory roots and rhizomes (< 2 mm diameter) varied between 207 and 552 g m^{-2} in the Norway spruce stands (Figure 2a) and between 230 and 493 g m^{-2} in the Scots pine stands (Figure 2b). Fine root biomass plus small root (< 5 mm diameter) biomass varied between 380 and 1160 g m^{-2} (data not shown).

Total fine root biomass of the Norway spruce stands was nearly twice as high in northern Finland as in southern Finland (Figure 2a), because of the relatively high proportion of understory roots and rhizomes in northern Finland (16–43% of the total fine root biomass) compared with southern Finland (1–14%). Birch fine roots in the northern stands at Kivalo and Pallasjärvi were primarily roots of the dwarf birch (*Betula nana* L.), which is a dwarf shrub and was therefore omitted from the tree stand measurements (Table 3). When the values for birch roots were added to the understory root compartment, understory roots accounted for one half of the fine root biomass in Pallasjärvi. The Scots pine stands in southern Finland had a relatively high understory belowground biomass (ranging between 12 and 47% of the total; Figure 2b).

Dead fine roots as a proportion of the total of living plus dead roots varied between 30 and 50% for tree fine roots. This proportion was greater (but not significantly) in southern than in northern Finland for both tree and understory roots (Figure 3). There were fewer dead understory roots than dead tree roots.

Norway spruce and Scots pine had relatively and absolutely

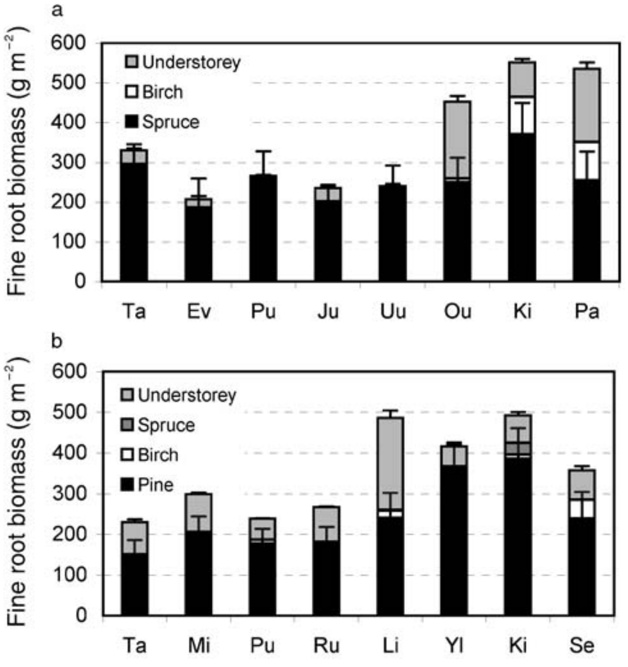

Figure 2. Living tree (all species on the site) and understory fine roots in the organic layer + upper 30-cm mineral soil layer in (a) Norway spruce and (b) Scots pine stands. Stands on the x-axis are in ascending order of latitude (Table 1), the last three stands in both figures are stands in northern Finland. Standard deviation within stands (n = 8 root cores per stand) is shown for Norway spruce, Scots pine and understory fine roots.

more fine roots in the organic layer in northern than in southern Finland. Scots pine had more fine roots in the mineral soil in northern than in southern Finland. The depth distribution of fine roots differed by species only slightly in southern Finland, whereas in northern Finland, Norway spruce fine roots were more superficially distributed than those of Scots pine (Figure 4). Understory roots and rhizomes were more superficially distributed than tree fine roots. A majority (67 ±19%) of all the dwarf shrub and grass roots was located in the organic layer. For trees, the corresponding value was 45 ±14%.

There was a significant ($P < 0.01$) relationship between fine root biomass and the temperature sum ($r^2 = 0.80$) in Scots pine, but not for Norway spruce ($r^2 = 0.29$). However, there was a significant relationship between the biomass of all the fine roots (including understory fine roots) in the Norway spruce and Scots pine stands and the temperature sum (Figure 5a), as well as with the carbon:nitrogen (C:N) ratio of the organic layer (Figure 5b). For stands of both tree species, the relationships between total fine root biomass and the C:N ratio of the soil organic layer were also significant (Norway spruce: $y = 14.61x - 156.96$, $r^2 = 0.90$, $P < 0.001$; Scots pine: $y = 14.58x - 262.68$, $r^2 = 0.66$, $P < 0.05$).

Fine root biomass and stand characteristics

The ratio of stand needle biomass to fine root biomass varied between 2.1 and 6.4 for Norway spruce, and between 0.8 and 2.2 for Scots pine. There was a decreasing trend in the ratio for both Norway spruce and Scots pine on moving from south to north, as well as from fertile to more infertile site types (Figure 6a). The ratio was smaller in the Norway spruce stands in northern (2.1–3.4) than in southern (3.6–6.4) Finland (Figure 6b).

In Norway spruce, the stand foliage:fine root biomass ratio was related to basal area (Figure 7a) and stem surface area (Figure 7b), and all three parameters were significantly correlated with the fine root N concentration (Figures 8a–c). The Scots pine foliage:fine root biomass ratio was unrelated to basal area, stem surface area or fine root N concentration, but there was a significant relationship between foliage:fine root biomass ratio and stand age in southern Finland ($y = 0.0057x + 0.167$, $r^2 = 0.87$, $n = 5$ stands). The fine root N concentration of both species was strongly correlated with the C:N ratio of the organic layer ($y = -0.018x + 1.50$, $r^2 = 0.77$).

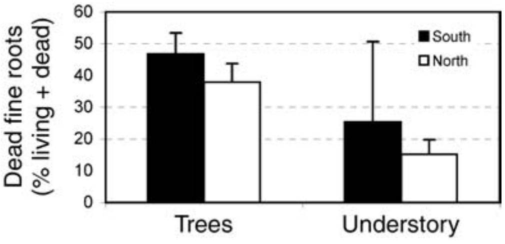

Figure 3. Dead fine roots of trees (all species on the site) and understory, expressed as a percentage of total live and dead fine roots, in Norway spruce and Scots pine stands in southern and northern Finland (five stands of each tree species in southern Finland and three stands of each tree species in northern Finland; Table 1).

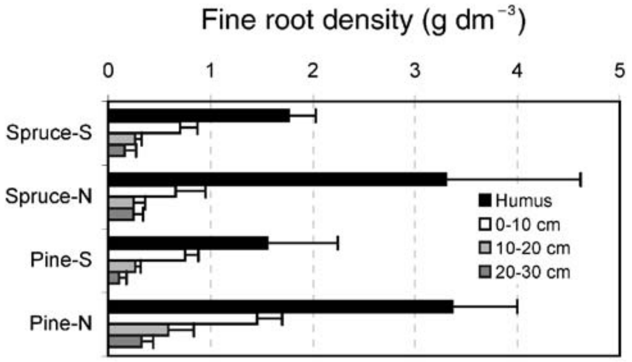

Figure 4. Mean Norway spruce and Scots pine fine root density in different soil layers (Humus = organic layer; 0–10 cm, 10–20 cm and 20–30 cm are mineral soil layers) in southern (S) and northern (N) Finland. Error bars are standard deviations between stands (five stands of each species in southern Finland and three stands of each species in northern Finland).

Commonly used variables describing stand structure, e.g., number of stems ($r^2 = 0.25$ and 0.29 for Norway spruce and Scots pine, respectively), needle mass ($r^2 = 0.00$ and 0.18), basal area ($r^2 = 0.16$ and 0.12) or the stem surface area ($r^2 = 0.21$ and 0.12), showed no significant correlations with fine root biomass at the stand level. In contrast, significant correlations were found when we recalculated the parameters for the mean tree in the stand by dividing the stand-level values by stem number (Chen et al. 2004).

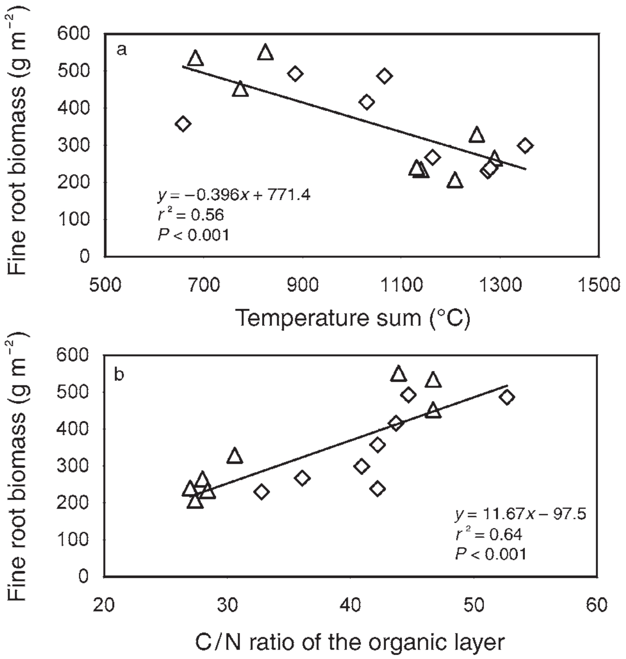

Figure 5. Relationships of tree (all species on the site) and understory fine roots with (a) temperature sum (Table 1) and (b) C/N ratio of the organic layer (Table 2) in Norway spruce (△) and Scots pine (◇) stands ($n = 16$ stands).

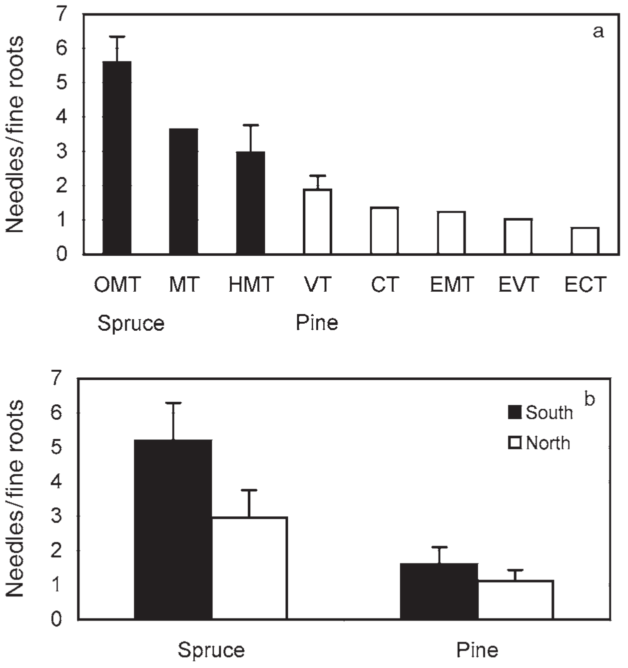

Figure 6. Stand-level foliage:fine root biomass ratios for Norway spruce and Scots pine (a) according to tree species and site types (Table 2) (filled bars = spruce, open bars = pine) and (b) according to tree species in southern and northern Finland. Bars are standard deviations between stands: OMT = 4 stands, HMT and VT = 3 stands each, and all other site types were represented by 1 stand only; five stands of each tree species in southern Finland and three stands of each tree species in northern Finland. The site type UVET (needle:fine root ratio = 1.38) is missing from Figure 6a, as it is the northernmost stand close to the timberline. Site types are according to Cajander (1949).

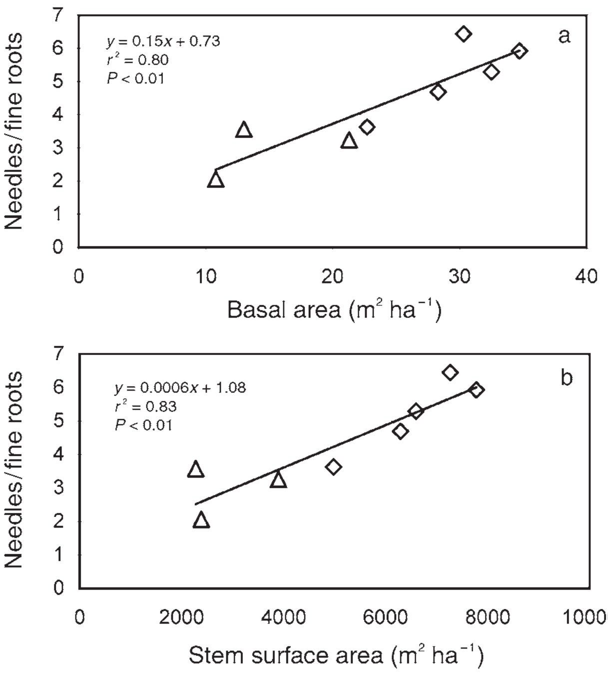

Figure 7. Relationships between stand-level Norway spruce foliage:fine root biomass ratio and (a) basal area and (b) stem surface area ($n = 8$ stands). Symbols: △ = stands in northern Finland; and ◇ = stands in southern Finland.

When data were grouped according to tree species, linear relationships could not be established between fine root biomass tree^{-1} and basal area tree^{-1}. For both species, the range of basal area tree^{-1} was very different in northern Finland from that in southern Finland (Figures 9a and 9b). As a result, when the northern and southern sites were analyzed separately, fine root biomass tree^{-1} of both species significantly correlated with basal area tree^{-1} (Figures 10a and 10b).

In Figure 10a, we included data for young stands recalculated at the tree level from Helmisaari and Hallbäcken (1999; a Norway spruce stand at Heinola, southern Finland) and Helmisaari et al. (2002; three Scots pine stands in southern Finland). Data from our study gave a similar relationship ($y = 92.52x$) to that shown in Figure 10a, but with a lower r^2 value of 0.67 ($P < 0.01$). In Figure 10b, we included data recalculated at the tree level from Helmisaari and Hallbäcken (1999; two Norway spruce stands in northern Finland). Data from our study gave a slightly better relationship ($y = 204.94$, $r^2 = 0.81$, $P < 0.001$) than that shown in Figure 10b, and showed a correlation between fine root biomass tree^{-1} and the stem surface area tree^{-1} (southern Finland $r^2 = 0.62$; northern Finland $r^2 = 0.82$, data not shown).

Understory rhizome and root biomass (< 5 mm diameter) was significantly related to the aboveground percentage cover of the understory species groups, especially the dwarf shrub cover (Figure 11). When the tree species were analyzed separately, understory belowground biomass in the Scots pine stands was best related to the cover of vascular plants ($r^2 = 0.65$, $P < 0.05$), whereas in the Norway spruce stands the relationship with the dwarf shrub cover gave the best result ($r^2 = 0.89$, $P < 0.001$).

Discussion

Fine root biomass and site characteristics

Mean tree fine root biomass values in our study were in the same range as those previously reported for Scots pine and Norway spruce in boreal forests (e.g., Helmisaari and Hallbäcken 1999, Vanninen and Mäkelä 1999, Makkonen and Helmisaari 2001, Claus and George 2005). In the study by Vanninen and Mäkelä (1999), Scots pine fine root biomass varied between 118 and 412 g m^{-2} in 23- to 178-year-old Scots pine stands in southern Finland, which is comparable to our range of 230–493 g m^{-2} in 55- to 200-year-old stands. Our spruce fine root biomass values of 184–370 g m^{-2} were lower than the range reported in Sweden (145–656 g m^{-2}) by Persson et al. (1995) and Majdi and Persson (1995).

Scots pine had more fine roots in northern Finland than in southern Finland, whereas there were no clear differences between north and south Finland for Norway spruce. Two of the Norway spruce stands in northern Finland were in unmanaged, relatively pristine (Oulanka) or relatively unmanaged (Pallas-

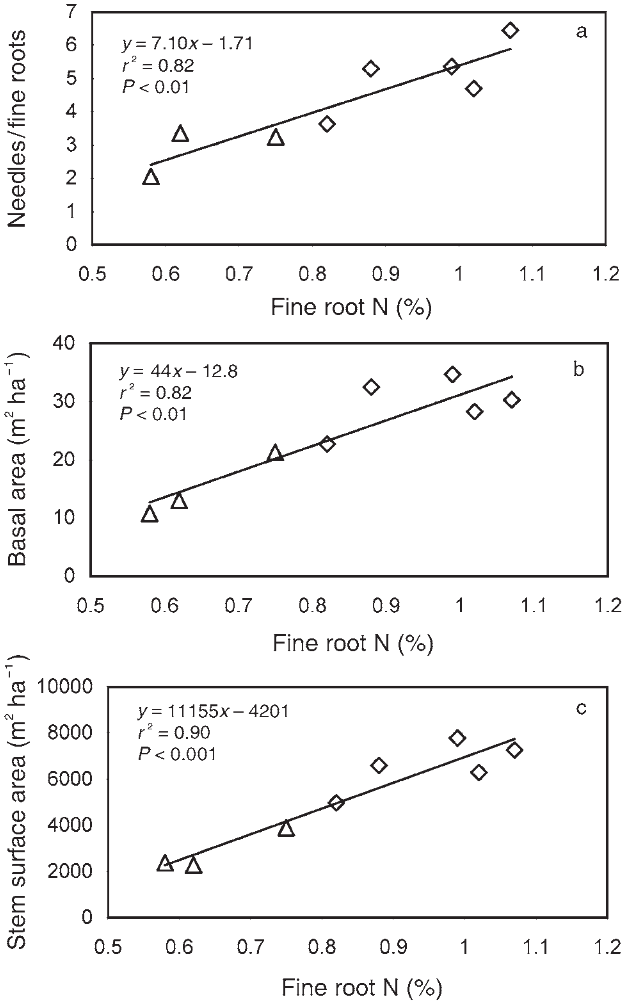

Figure 8. Relationships between stand-level (a) Norway spruce foliage:fine root biomass ratio, (b) basal area and (c) stem surface area and fine root nitrogen (N) concentration (n = 8 stands). Symbols: △ = stands in northern Finland; and ◇ = stands in southern Finland.

järvi) forests with a well-developed understory root system. Thus, belowground competition with the understory vegetation may have adversely affected Norway spruce fine root biomass in the northern stands.

The study stands were well past canopy closure, and understory belowground biomass did not correlate with any of the stand variables. Because most of the understory roots were of dwarf shrub, the understory rhizome and fine root biomass was highest in the Norway spruce stands growing on the northern *Hylocomium–Myrtillus* (HMT) site type where low stand density and the narrow crown form of Norway spruce allows light to penetrate to the forest floor. The understory rhizome and fine root biomass in the Scots pine stands was more evenly distributed over the sites, except in the case of the unmanaged stand at Lieksa in eastern Finland, where understory belowground biomass was especially high.

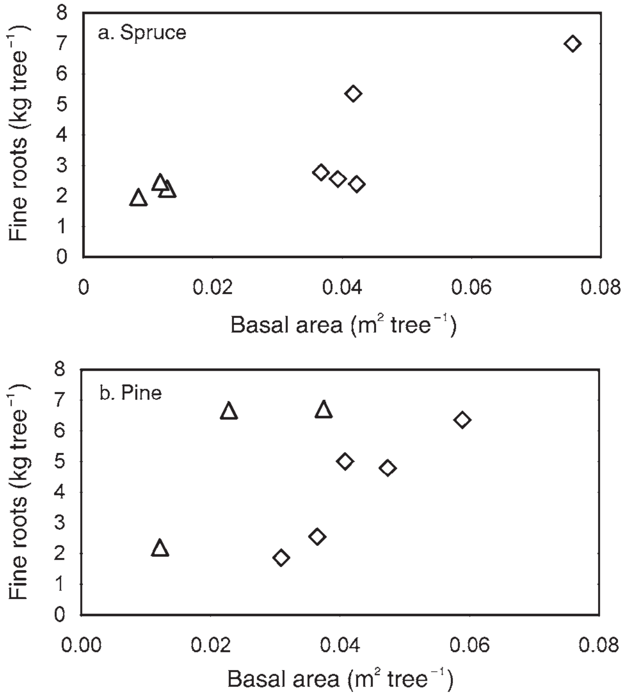

Figure 9. Relationship between fine roots and basal area for (a) Norway spruce and (b) Scots pine (n = 8 stands for each species). Symbols: △ = stands in northern Finland; and ◇ = stands in southern Finland.

Most of the understory belowground biomass consisted of dwarf shrub rhizomes, which explains the strong relationship with the dwarf shrub aboveground cover. The relationship was strongest in the Norway spruce stands. The vegetation in the southern spruce stands on fertile site types is characterized by herbs (Salemaa and Korpela 2000), which have a high aboveground cover but a small fine root biomass. However, the Scots pine fine root biomass was best related to the cover of vascular plants, including not only dwarf shrubs but also grasses that have a well-developed belowground root system.

Muukkonen et al. (2006) developed models for predicting understory aboveground biomass based on percent cover. Their biomass data for field layer aboveground vegetation gathered from 23 stands in upland soils showed a similar range (0–250 g m^{-2}) as our root and rhizome biomass data from southern Finland showed for the understory belowground (2 to 280 g m^{-2}). The linear relationships between understory aboveground biomass and percent cover (Muukkonen et al. 2006) compared with ours on belowground biomass show that there may be more belowground than aboveground understory biomass even in southern Finland. Old stands from northern Finland were not represented in the study by Muukkonen et al. (2006).

Because of the abundant understory, total fine root biomass was larger in northern Finland in stands of both tree species, resulting in a negative relationship between fine root biomass and temperature sum. However, the northern and southern Finland stands formed two clusters, within which there was no relationship between fine root biomass and temperature sum. This means that temperature sum alone is not a sensitive vari-

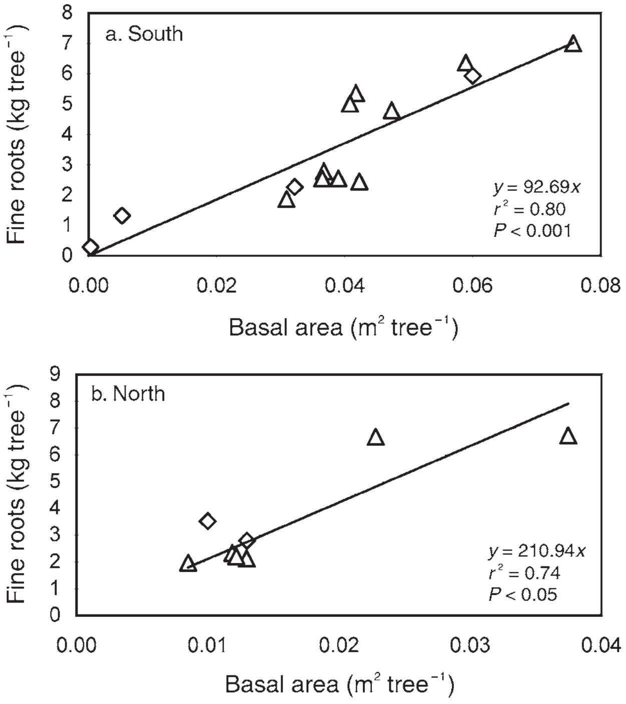

Figure 10. Relationships between fine roots and basal area for Norway spruce and Scots pine in (a) southern Finland (n = 14 stands) based on data from this study (△) and Helmisaari and Hallbäcken (1999) and Helmisaari et al. (2002) (◇) and in (b) northern Finland (n = 8 stands) based on data from this study (△) and Helmisaari and Hallbäcken (1999) (◇).

able across sites within southern or northern Finland.

There was a positive relationship between fine root biomass and the C:N ratio of the organic layer. The C:N ratio was higher in the Norway spruce stands in northern Finland (44–47) than in southern Finland (27–31). In the Scots pine stands, the differences in C:N ratio between northern (42–45) and southern Finland (33–53) were smaller because Scots pine grows naturally on less fertile sites. According to a survey by Tamminen (2000), the organic layer C:N ratio averages 46.6 in the least fertile and 24.3 in the most fertile site type group in Finland.

The low percentage of dead fine roots in northern Finland (< 45% of all roots for trees and < 20% for the understory) may be related to the longevity of fine roots and rhizomes, or to differences in the decomposition rate, which is, however, lower in the north and significantly related to climate parameters (Kurka et al. 2000). The longevity of fine roots in the north could be related to the optimization of nutrient uptake with as low carbon costs as possible for fine root production. Chapin (1980*b*) hypothesized that the maintenance of long-lived, high-density fine root systems may be more adaptive in nutrient-poor soils and that fine root turnover rates are higher in fertile soils. According to Janssens et al. (2002), increased root longevity is favored under nutrient-poor conditions because of the need to avoid nutrient losses through root mortality.

The depth distribution of the fine roots of both tree species

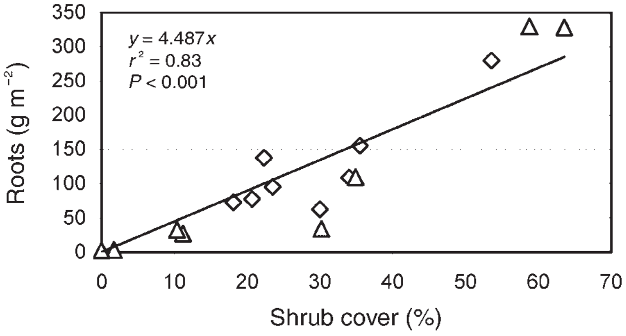

Figure 11. Relationship between understory root biomass (roots < 5 mm) and shrub cover in Norway spruce (△) and Scots pine (◇) stands (n = 16 stands).

was more superficial in northern Finland than in southern Finland, particularly in Norway spruce. In northern Finland, especially on the HMT site type, nitrogen availability, soil temperature and oxygen availability decrease more sharply on moving into deeper mineral layers than in southern Finland, which may contribute to the superficial fine root distribution in the north.

The fine root biomasses in our study were measured in the 2–10-cm-thick organic layer and the underlying 30-cm-thick mineral soil layer. Taking Norway spruce and Scots pine together, the proportion of fine root biomass in the deepest layer (20–30 cm mineral soil) was only 7.5 ± 4.1% of the whole core. Quantities of fine root biomass beyond the maximum sampling depth of the organic layer plus 30 cm mineral soil were likely, therefore, to have been insignificant.

We sampled fine roots during the period of seasonal maximum fine root biomass for Scots pine in Finland (Makkonen and Helmisaari 1998). Other studies, e.g., those of Vanninen and Mäkelä (1999) and Ostonen et al. (2005), report only small temporal variation in Scots pine and Norway spruce fine root biomass during the growing season. There is also annual variation in fine root biomass, especially during periods with extreme weather conditions, e.g., drought (Makkonen and Helmisaari 1998). There was no drought in summer 1998 in Finland.

Fine root biomass and stand characteristics

Needle biomass relative to fine root biomass was lower in northern Finland than in southern Finland, and on less fertile sites compared with fertile sites. In Scots pine, this was mainly because of the larger fine root biomass in the north, but for Norway spruce, it was a reflection of the smaller needle biomass of the narrow-canopy trees in the north. This means that, based on site nutrient availability, trees may optimize their resource allocation strategies between photosynthesizing needles and fine roots. If nutrient availability is low (because of low soil fertility or a short growing season, or both), there is increased biomass allocation belowground. Laboratory studies have also shown that plants with a low N supply develop a low shoot: root ratio (Ericsson 1995).

The published range of root:shoot ratios is broad (Santantonio 1989, Olsthoorn 1991, Haynes and Gower 1995, Hendricks and Bianchi 1995). Our fine root:foliage ratios of 0.46–0.74 for Scots pine on *Vaccinium* (VT) and *Calluna* (CT) site types in southern Finland were within the range reported for Scots pine stands on CT site type (0.46–0.81) by Vanninen and Mäkelä (1999). The lower fine root:foliage ratios for Norway spruce (0.15–0.48) and the more superficial rooting pattern compared with Scots pine is consistent with the greater sensitivity of Norway spruce to drought.

The foliage:fine root ratio of Norway spruce was related to basal area and stem surface area. The strong positive correlation of these three parameters with fine root nitrogen concentration implies that more fine roots are needed to maintain a certain amount of foliage when nutrient availability is low (cf. Keyes and Grier 1981, Vogt et al. 1983, 1985, 1987, Gower et al. 1992, Vanninen and Mäkelä 1999). The strong correlations between fine root N concentration and basal area, stem surface area and C:N ratio of the organic layer suggest that fine root N is strongly related to N availability at the site. In Finland, N is the main nutrient restricting growth on upland soils (Mälkönen et al. 1990).

The foliage:fine root ratio of Scots pine did not correlate with basal area, stem surface area or fine root N concentration. Both fine root N concentration and foliage:fine root ratio at the individual sites had a narrower range than in Norway spruce. Scots pine has the capacity for efficient retranslocation and can satisfy a large part of its nutrient requirements through this process (Helmisaari 1992*a*, 1992*b*), which partly explains why Scots pine biomass allocation is less dependent on soil nutrient availability.

Processes related to fine root biomass, such as resource allocation and nutrient and water uptake, should be investigated on an average tree basis, rather than by comparing stands with a varying number of trees. No significant stand-level relationships were found between stand parameters and fine root biomass, whereas the relationships were apparent when both fine root biomass and stand parameters were calculated for an average tree in the stand. Our stands were all past canopy closure, and most were even-aged with only one canopy layer. Thus, average tree parameters calculated by dividing the parameters by the stand density were considered to be representative of the trees in the stands. We were able to use this approach because we sorted the understory and tree roots separately, which is rarely done (Kurz et al. 1996, Cairns et al. 1997).

Our foliage:fine root ratios demonstrate that estimates of fine root biomass of the mean tree in a stand can be made from stand-level needle biomass and stand density only. Needle biomass first has to be estimated with biomass models, which may introduce an additional source of error. Also, part of the variation in needle biomasses will be lost when biomass functions are used based on mean needle mass. We used the biomass functions of Marklund (1987, 1988), which are based on material from Sweden, which is climatically similar to Finland; however, the northernmost plots in our study are located at high latitudes not represented by material in the study of Marklund (1987, 1988). Thus, the needle biomass estimates for those plots are less reliable. Also, the function for Scots pine needle biomass uses stand location as an independent variable, whereas the functions for Norway spruce do not. Because the geographical range of our Norway spruce plots is large (from latitude 60° to 68° N), this is a potential source of bias.

Because of the difficulties and sources of error in estimating needle biomass, other tree dimensions may prove to be more useful for predicting fine root biomass. Most of the equations predicting coarse root biomass on the basis of stand measurements include tree diameter as one of the factors (Santantonio et al. 1977, Bolte et al. 2004). Our results suggest a strong positive correlation between fine root biomass and basal area and stem surface area per average tree. In southern Scots pine and Norway spruce stands, an average tree with a similar fine root biomass as in northern Finland had more than twice the basal area. Therefore, the best relationships were those calculated separately for northern and southern Finland, independently of tree species. Based on data from the literature, Chen et al. (2004) found statistically significant correlations between fine root biomass tree^{-1} and stem diameter at the ground surface for boreal and temperate forests. The standard error of the estimation was high in their study because the data represented studies that employed different methods, sampling times and root sample depths.

Our study was focused on the boreal region, and we used the same methods, sampling period and root sample depths for all stands. We found significant relationships between fine root biomass and needle:fine root biomass ratio and stand parameters. Because basal area, stem surface area and stand density can be estimated accurately and easily, our results may have value in predicting fine root biomass at the tree level and, further, at the stand level in boreal Norway spruce and Scots pine forests.

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