Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests

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Summary Variability in short root morphology of the three main tree species of Europe's boreal forest (Norway spruce (Picea abies L. Karst.), Scots pine (Pinus sylvestris L.) and silver birch (Betula pendula Roth)) was investigated in four stands along a latitudinal gradient from northern Finland to southern Estonia. Silver birch and Scots pine were present in three stands and Norway spruce was present in all stands. For three fertile Norway spruce stands, fine root biomass and number of root tips per stand area or unit basal area were assessed from north to south. Principal component analysis indicated that short root morphology was significantly affected by tree species and site, which together explained 34.7% of the total variability. The range of variation in mean specific root area (SRA) was 51–74, 60–70 and 84–124 m² kg⁻¹ for Norway spruce, Scots pine and silver birch, respectively, and the corresponding ranges for specific root length were 37–47, 40–48 and 87–97 m g⁻¹. The range of variation in root tissue density (RTD) was 127–158 and 81–156 kg m⁻³, respectively. Sensitivity of short root morphology to site conditions decreased in the order: Norway spruce > silver birch > Scots pine. Short root SRA increased with site fertility in all species. In Norway spruce, fine root biomass and number of root tips per m² decreased from north to south. The differences in morphological parameters among sites were significant but smaller than the site differences in fine root biomass and number of root tips.

Keywords: adaptive strategies, Betula pendula, fine root biomass, Picea abies, Pinus sylvestris, specific root length.

Introduction

Fine roots play a key role in the boreal forest ecosystem, where they constitute a major carbon sink. Mycorrhizal roots, hereafter referred to as short roots, lack secondary thickening, are morphologically distinct from other fine roots and are usually less than 2 mm in diameter (Vogt and Persson 1991). They form the most active part of the fine root system. Short roots adapt according to soil conditions both anatomically and morphologically (Robinson and Rorison 1983, Ostonen et al. 1999, Lõhmus et al. 2006a, 2006b, Ostonen et al. 2006). Studies that have examined short root morphology in relation to species or soil conditions include Lõhmus et al. (1989), Eissenstat (1991), Ostonen et al. (1999), Comas et al. (2002), Comas and Eissenstat (2004), Leuschner et al. (2004), Lõhmus et al. (2006a, 2006b) and Ostonen et al. (2006). Interrelations between root structure and growth strategies have been investigated by Wilson et al. (1999) and Wahl and Ryser (2000).

At both the individual root and entire root system levels, functional morphological characteristics that have been studied include specific root area (SRA), specific root length (SRL) and root tissue density (RTD). Size-related short root morphological characteristics (diameter, length, mass and volume) have been examined to compare root systems of different species. These morphological parameters, especially SRL, and to a lesser extent SRA, have been used as indices of root benefit to root cost, assuming that resource acquisition is proportional to length or surface area and that root cost (construction and maintenance) is proportional to mass (Lõhmus et al. 1989, Eissenstat and Yanai 1997, Pregitzer et al. 2002). Specific root area is reported to be higher and RTD lower in highly productive Norway spruce stands on fertile well-drained soils. The larger the SRA and the smaller the RTD, the higher the allocation of assimilates to short roots (Ostonen et al. 1999).

Trees adapt to nutrient-poor soils by increasing either the mass and length of fine roots (extensive adaptation) or the nutrient uptake efficiency of fine roots or associated microorganisms, or both (intensive adaptation) (Lõhmus et al. 2006a, 2006b). Extensive adaptation accords with the general assumption that net primary production allocation to roots is enhanced under conditions of low nutrient availability (Keyes and Grier 1981, Vogt et al. 1987, Helmsaari et al. 2006).

We analyzed short root morphology of the three main tree species of Europe's boreal forest (Norway spruce (Picea abies...
L. Karst.), Scots pine (Pinus sylvestris L.) and silver birch (Betula pendula Roth) growing along a latitudinal gradient from northern Finland to southern Estonia. The importance of extensive adaptation was estimated from fine root biomass and the number of root tips (apices) per stand or unit basal area, whereas the importance of intensive adaptation was assessed on the basis of morphological parameters. To clarify the possible effect of soil conditions on short root morphology, both a high-fertility and a low-fertility site in Estonia were included in the study; the sites in Finland were of high fertility. The main objectives were to analyze: (1) the effects of tree species and site conditions on short root morphology of Scots pine, Norway spruce and silver birch along a latitudinal gradient in the boreal zone; and (2) the relative contributions of intensive and extensive mechanisms of fine root adaptations in Norway spruce.

Material and methods

The study was carried out at four locations (Table 1), two in Finland (Kivalo, Sahalahti) and two in Estonia (Voore, Kuusnõmme). Finland lies within the boreal forest zone, whereas Estonia is in the transitional zone between boreal and temperate forest. Dominant tree species in both countries are Scots pine (Pinus sylvestris), Norway spruce (Picea abies) and silver birch (Betula pendula).

Stand characteristics

At Kivalo, we investigated three adjacent stands, each dominated by a different species, silver birch (Scots pine or Norway spruce). Sahalahti is a pure Norway spruce stand. Voore and Kuusnõmme are mixed forest stands. The canopy composition and forest site type at each location are given in Table 1. Stand productivity at Kivalo, Sahalahti and Voore is high. The productivity of the Kuusnõmme stand is restricted by high pH (Table 2) (Frey and Frey 1995), temporary flooding in spring and autumn and midsummer drought. The Voore and Kuusnõmme stands are located at similar latitudes, but the Kuusnõmme stand, which is located close to the western coast of the island Saaremaa, has a higher annual mean temperature and a longer growing season (Table 3).

The high fertility Norway spruce forest sites (Kivalo, Sahalahti and Voore) differ considerably in mean annual temperature, mean annual temperature sum > 5 °C and growing season length (Table 3). The site of the low fertility stand at Kuusnõmme has a longer growing season, higher temperatures and less rain than the other stands.

Root sampling

Short root morphology of each study species was investigated at Kivalo, Voore, Kuusnõmme and, for Norway spruce, Sahalahti. Short root morphology and fine root biomass were investigated in Norway spruce at Kivalo, Sahalahti and Voore.

Short root characteristics

Short roots were sampled from all stands during September and October 2004. Ten root samples per species were collected with a spade from the humus and 20-cm-deep mineral soil layers at random locations. Two or three random short root subsamples were taken from each sample. The number of short root tips in each set of 20–30 subsamples for each tree species ranged from 234 to 949. The number of root tips in subsamples was 2–3 times higher for silver birch than for the conifers. The short root samples were washed with tap water, cleaned with a soft brush and the root tips counted with the aid of a microscope. The presence of ectomycorrhizal infection was recorded.

Short root morphological characteristics

Short root diameter, length and projected area were measured with WinRHIZO Pro 2003b (Regent Instruments Inc., Qué-

<table>
<thead>
<tr>
<th>Forest location and site type</th>
<th>Age (years)</th>
<th>Species</th>
<th>Stand composition</th>
<th>Basal area (m² ha⁻¹)</th>
<th>Height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kivalo, Finland (66°20′ N, 26°40′ E)</td>
<td>74</td>
<td>Betula pendula</td>
<td>10B</td>
<td>21.3</td>
<td>15.5</td>
</tr>
<tr>
<td>Hylcomonium–Vaccinium myrtillus</td>
<td></td>
<td>Pinus sylvestris</td>
<td>9P + 1B</td>
<td>22.0</td>
<td>14.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Picea abies</td>
<td>8S + 2B + 1P</td>
<td>28.4</td>
<td>14.6</td>
</tr>
<tr>
<td>Sahalahti, Finland (61°26′ N, 24°24′ E)</td>
<td>69</td>
<td>Picea abies</td>
<td>10S</td>
<td>28.4</td>
<td>22.8</td>
</tr>
<tr>
<td>Oxalis–Vaccinium myrtillus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Voore, Estonia (58°42′ N, 26°45′ E)</td>
<td>65</td>
<td>Betula pendula</td>
<td>10S + 1B + 1P</td>
<td>50</td>
<td>28.1</td>
</tr>
<tr>
<td>Oxalis</td>
<td></td>
<td>Pinus sylvestris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Picea abies</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kuusnõmme, Estonia (58°19′ N, 21°59′ E)</td>
<td>90†</td>
<td>Betula pendula</td>
<td>5P + 5S + 1B</td>
<td>11.8†</td>
<td>11†</td>
</tr>
<tr>
<td>Calamagrostis</td>
<td></td>
<td>Pinus sylvestris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Picea abies</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
bec, QC). For mean root tip volume \((V)\), we first calculated the volume of short roots in the sample \((V_S, \text{mm}^3)\):

\[
V_S = 0.25\pi D^2 \sum_{i=1}^{n} L_i
\]

(1)

where \(D\) = mean root tip diameter, \(L_i\) = length of a short root tip and \(n\) = the number of short-root tips. We then divided \(V_S\) by the number of root tips in the sample to obtain \(V\).

Root tissue density (kg m\(^{-3}\)), SRA, (m\(^2\) kg\(^{-1}\)) and SRL (m g\(^{-1}\)) were calculated as \(M/V\), \(S/M\) and \(L/M\), respectively, where \(S\), \(M\) and \(L\) are mean root tip surface area, dry mass and length, respectively. The method for determining SRA, SRL and RTD are given in detail by Lõhmus et al. (1989) and Ostonen et al. (1999). Root tip frequency was expressed as root tips mg\(^{-1}\) or root tips per unit length (RTFl).

**Fine root biomass**

To determine fine root biomass, Norway spruce root samples were taken in August 1996 from Voore (Ostonen et al. 2005) and in August 1999 from Kivalo and Sahalahti. The Kivalo and Sahalahti Norway spruce stands each contained three 25 x 25 m sample plots; at Voore there were two plots (Ostonen et al. 2005). Twelve root cores were taken from Kivalo and Sahalahti with a cylindrical soil corer (diameter 40 mm). The cores were divided into organic layer, and 0–5, 5–10 and 10–20-cm mineral soil layers. Roots were washed free of soil then sorted into living and dead and the number of living root tips counted with the aid of a microscope. Roots were considered alive if the exposed stele was shiny and resilient (Vogt and Persson 1991). Root samples were dried at 70 °C for 48 h and weighed. The ash content of the fine roots was determined to estimate mineral soil contamination and the fine root biomass values were corrected accordingly. Because no significant differences between plots were found, data for the plots were pooled by study area.

**Statistical methods**

The normality of short root variables of different tree species was tested using the Shapiro-Wilk test. Significant differences were determined using the Student’s t-test for paired samples. P-values < 0.05 were considered significant.
Results

Short root morphology was significantly affected by tree species and forest site (Table 4; Figures 1A and 2). According to the PCA, tree species and site together explained 34.7% of the total variation in short root morphology. The first two axes accounted for 76.9% of the variation in short root morphology across species and sites (Figure 1B). From Figure 1B, it is apparent that two groups of short root characteristics were identified: size-related parameters (L, M, V and D) and derived functional root parameters (SRA, SRL, RTD, RTFm and RTF).

Effect of tree species on short root morphology

According to the PCA, tree species explained 25% of the total variability in short root morphology within sites. On the first axis, PCA differentiation between silver birch and the conifers (Figure 1A), the greatest difference in short root morphology among species was between silver birch and Norway spruce.

Within a site, the pattern of variation in short root morphology was similar for all species. However, multiple comparison of means analysis revealed significant differences between species (Table 4). The ranges of variation in mean short root SRA, SRL and RTD for Norway spruce were 51–74 m² kg⁻¹, 47–57 m g⁻¹ and 127–158 kg m⁻³, respectively; for silver birch the corresponding values were 68–78 m² kg⁻¹, 40–47 m g⁻¹ and 126–156 kg m⁻³. Hence SRA and SRL were smaller and RTD larger for conifers than for silver birch. However, the effect of tree species on RTD was insignificant at the low fertility Kuusnõmme site.

Effects of site fertility and climatic conditions on short root morphology were examined by rank correlation analysis (gamma correlation). To calculate gamma correlation coefficients, an ordinal scale variable representing site fertility according to the mean height of stands was defined; the highest value was found in the youngest stand, Voore (Table 1).

The dataset of short root parameters was subjected to principal component analysis (PCA) based on a correlation matrix with the software package ADE-4 (Thioulouse et al. 1997). In PCA, new orthogonal variables (latent variables or principal components) are obtained by maximizing the variance of the data. The number of latent variables (factors) is much lower than the number of original variables, so that the data can be visualized in a low-dimensional space. Before PCA analysis, short root parameter values were log-transformed.

Effect of tree species among species was between silver birch and Norway spruce. However, the effect of tree species on RTD was insignificant at the low fertility Kuusnõmme site.

Table 4. Mean short root morphological characteristics (± standard errors) within different stands for Norway spruce (Picea abies), Scots pine (Pinus sylvestris) and silver birch (Betula pendula). Letters denote significant differences between species within a site and between sites within a species (Tukey's test; P < 0.05). All mass measurements were dry mass. Abbreviations: SRA = specific root area; SRL = specific root length; RTD = root tissue density; RTFm = root tip frequency per unit dry mass; RTF = root tip frequency; n = mean diameter; L = mean length; M = mean dry mass; and V = mean volume.

<table>
<thead>
<tr>
<th>Area</th>
<th>Species</th>
<th>SRA (m² kg⁻¹)</th>
<th>SRL (m g⁻¹)</th>
<th>RTD (kg m⁻³)</th>
<th>RTFm (m² kg⁻¹)</th>
<th>RTF (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kivio</td>
<td>Picea abies</td>
<td>67.4 (± 2.6) a</td>
<td>46.0 (± 2.9) az</td>
<td>132 (± 5) ab</td>
<td>2.4 (± 0.1) ay</td>
<td>2.4 (± 0.1) b</td>
</tr>
<tr>
<td></td>
<td>Pinus sylvestris</td>
<td>68.1 (± 2.5) a</td>
<td>47.8 (± 3.2) az</td>
<td>127 (± 4) ab</td>
<td>2.4 (± 0.1) ay</td>
<td>1.6 (± 0.1) a</td>
</tr>
<tr>
<td></td>
<td>Betula pendula</td>
<td>121.7 (± 6.5) b</td>
<td>50.5 (± 5.4) az</td>
<td>113 (± 6) ab</td>
<td>2.3 (± 0.1) ay</td>
<td>1.5 (± 0.1) a</td>
</tr>
<tr>
<td>Vooore</td>
<td>Picea abies</td>
<td>69.6 (± 4.9) a</td>
<td>48.3 (± 3.9) az</td>
<td>132 (± 5) ab</td>
<td>2.4 (± 0.1) ay</td>
<td>1.6 (± 0.1) a</td>
</tr>
<tr>
<td></td>
<td>Pinus sylvestris</td>
<td>121.7 (± 6.5) b</td>
<td>50.5 (± 5.4) az</td>
<td>113 (± 6) ab</td>
<td>2.3 (± 0.1) ay</td>
<td>1.5 (± 0.1) a</td>
</tr>
<tr>
<td></td>
<td>Betula pendula</td>
<td>123.6 (± 7.0) by</td>
<td>96.7 (± 7.3) az</td>
<td>129 (± 5) ab</td>
<td>2.6 (± 0.1) ay</td>
<td>1.5 (± 0.1) a</td>
</tr>
<tr>
<td>Kuusnõmme</td>
<td>Picea abies</td>
<td>50.5 (± 1.6) a</td>
<td>x 36.6 (± 1.6) az</td>
<td>129 (± 5) ab</td>
<td>2.4 (± 0.1) by</td>
<td>1.5 (± 0.1) a</td>
</tr>
<tr>
<td></td>
<td>Pinus sylvestris</td>
<td>59.2 (± 4.0) a</td>
<td>48.3 (± 3.9) az</td>
<td>132 (± 5) ab</td>
<td>2.4 (± 0.1) ay</td>
<td>1.6 (± 0.1) a</td>
</tr>
<tr>
<td></td>
<td>Betula pendula</td>
<td>84.2 (± 5.8) bx</td>
<td>79.9 (± 6.5) az</td>
<td>158 (± 10) ay</td>
<td>182 (± 6.1) ax</td>
<td>1.5 (± 0.1) a</td>
</tr>
<tr>
<td>Sahalahti</td>
<td>Picea abies</td>
<td>66.5 (± 2.0) y</td>
<td>44.3 (± 1.6) xyz</td>
<td>129 (± 5) ab</td>
<td>2.4 (± 0.1) by</td>
<td>1.5 (± 0.1) a</td>
</tr>
</tbody>
</table>
Root tip frequency per unit dry mass was significantly higher (2.0–2.5 times) in silver birch than in Norway spruce and Scots pine (Figure 2, Table 4). The size-related morphological characteristics differed in patterns of variation from the functional characteristics (Table 4). Although short roots of Norway spruce and Scots pine were significantly thicker than those of silver birch, there was no significant difference between Scots pine and Norway spruce. Mean length, mass and volume of root tips decreased in the order: Norway spruce > Scots pine = silver birch (Table 4).

Effect of site conditions on short root morphology

In the absence of species effects, site explained 9.7% of the total variation in short root morphology. The PCA grouped the species at the low-productivity Kuusnõmme site together, as shown in the upper part of Figure 1A, indicating that the effect of site was related to the second PCA axis. Parameters SRA and SRL were smaller and RTD was larger for all species at the low fertility site (Kuusnõmme) than at the more fertile sites (Table 4 and Figure 2).

Short root morphological sensitivity and reaction to site soil conditions varied between species based on the multivariate Hotelling $T^2$ test (Table 5). The effect of site conditions on short root morphology was most evident in Norway spruce, for which the largest number of significant differences between sites was found, and was non-existent in Scots pine. The largest number of differences in short root morphology was found between Kuusnõmme (low fertility site) and the other stands (high fertility sites).

Gamma correlation coefficients were calculated to assess the relationships between site fertility and short root morphology. We used mean height of the stands as an integrated measure of site fertility. An ordinal scale variable was defined to rank the sites. Site fertility decreased in the order: Voore > Sahalahti > Kivalo > Kuusnõmme, reflecting the inverse relationship between stand age and tree height among study sites. The Voore stand is the youngest, but has the greatest mean tree height; the Kuusnõmme stand is the oldest, but has the lowest mean tree height (Table 1). Specific root area was the only morphological parameter for which there were significant gamma correlations in all species ($R$ varied between $-0.31$ and $-0.35$; $P < 0.01$).

For silver birch and Norway spruce, $D$ increased ($R = 0.3$, $P < 0.001$ in both cases) and RTD decreased ($R = -0.4$, $P < 0.001$ in both cases) with site fertility, whereas the effects of site fertility on $D$ and RTD were insignificant for Scots pine. Specific root length increased with site fertility in Norway spruce and Scots pine; however the correlations were extremely weak ($R = -0.18$ and $R = -0.26$ ($P < 0.05$ in both cases) in Norway spruce and Scots pine, respectively).

Effects of annual temperature sum and precipitation on Norway spruce fine roots

We compared short root morphology and fine root biomass at the three high fertility Norway spruce stands, Kivalo, Sahalahti and Voore, located from north to south in the boreal forest zone (Tables 4 and 6). Effects of mean annual temperature sum $> 5 ^\circ$C were examined by rank correlation analysis. Mean
Table 5. Sensitivity of short-root morphological characteristics of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*) to site conditions. Hotelling $T^2$ test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; and ns, not significant.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stand</th>
<th>Silver birch</th>
<th>Norway spruce</th>
<th>Scots pine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Voore</td>
<td>Sahalahti</td>
<td>Voore</td>
</tr>
<tr>
<td>Silver birch</td>
<td>Kivalo</td>
<td>ns</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Voore</td>
<td>***</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>Norway spruce</td>
<td>Kivalo</td>
<td>**</td>
<td>*</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>Sahalahti</td>
<td>ns</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>Voore</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Scots pine</td>
<td>Kivalo</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>Voore</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

Annual temperature sum > 5 °C and precipitation were the selected climate variables (Table 3). Significant but weak gamma correlations with mean annual temperature sum were found for $D$, RTD, $L$, $M$ and RTF; annual precipitation in 2004 was significantly correlated with RTD, $D$ and $V$ (Table 7). No significant effects of mean temperature sum and annual precipitation were found for SRA or SRL. At higher latitudes with a lower temperature sum, short roots tended to be thinner and longer. Both RTD and $M$ decreased from north to south. Annual precipitation mainly affected $V$, which increased with water availability.

Climatic differences among forest sites strongly affected fine root biomass and root tip numbers. Both $M$ and root tip number decreased from north to south, and up to tenfold differences in these parameters were observed between sites at different latitudes (for the morphological parameters the differences were up to twofold; Tables 4 and 6). Mean root tip numbers for the Kivalo, Sahalahti and Voore sites were $16 \times 10^5$, $1.6 \times 10^6$ and $0.45 \times 10^6$ m$^{-2}$, respectively. Values for mean number of root tips m$^{-2}$ of basal area, which provides a better comparison among stands differing in density, were $56 \times 10^5$, $5.6 \times 10^5$ and $0.9 \times 10^5$ for Kivalo, Sahalahti and Voore, respectively.

**Discussion**

The size-related morphological characteristics of short roots depend on the root branching pattern of the species. Although Scots pine is more similar in root functional patterns to Norway spruce, $L$ of Scots pine is more similar to that of silver birch, reflecting the dichotomous branching of Scots pine short roots. Tyree et al. (1998) found that, among functional characteristics, water and nutrient uptake per unit root mass increases with SRA if area-related uptake rates remain unchanged. Analogously, Eisenstat (1992) reported that species with high SRL invest their root biomass more effectively than species with low SRL. Root tissue density can be considered a characteristic of root functional status, because it is closely associated with physiological activity (Ostonen et al. 1999, Wahl and Ryser 2000). Trees can increase root surface area by producing thinner roots that have a larger SRA for a given investment of carbon. Increases in SRA, SRL and RTF permit a tree species to increase the volume of soil explored per unit biomass invested in fine roots. Curt and Prevosto (2003) reported that Scots pine has a relatively coarse fine root system, whereas silver birch has thin and densely branched roots that provide an efficient foraging system.

Among the short root characteristics, SRA was the only parameter to decrease with site quality in all study species. A similar tendency was found in a comparison of seven Norway spruce stands assigned to different site quality classes but with similar climatic conditions (Ostonen et al. 1999). We found that RTD of short roots tended to decrease with increasing site fertility, which corroborates our earlier study showing that short roots of Norway spruce stands in productive habitats had a low RTD, whereas a high RTD was typical of stands growing in unproductive environments (Ostonen et al. 1999). Similarly, we observed a decrease in RTD from north to south within the high productivity Norway spruce stands (Kivalo, Sahalahti and Voore).

The PCA showed that site conditions explained only 9.7% of the total variability in short root morphology. The second PCA axis is likely associated with overall site fertility, which is determined by both abiotic and biotic factors.

Functional morphological parameters reflect the intensive adaptation strategy of short roots. We linked the morphological parameters of short roots with fine root biomass or root tip number to analyze the effects of environmental conditions on fine root system function in more detail and to assess the relative contribution of the extensive adaptation strategy. Analyses of fine root biomass, number of tips m$^{-2}$ and short root morphology in the three Norway spruce stands located at different latitudes in the boreal forest zone demonstrated that the trees used both extensive and intensive strategies to adjust water and mineral nutrient uptake capacities. The effects of latitude on fine root biomass and number of tips per stand or unit of basal area were greater than on morphological characteristics. In the three Norway spruce stands, latitude resulted in differences of up to a factor of three in fine root biomass and up to a factor of ten in number of root tips per stand or per unit basal area, whereas latitude resulted in differences up to only a factor of two in the morphological characteristics.

The biomass of Norway spruce fine roots (diameter < 2 mm) ranges from 600 to 5750 kg ha$^{-1}$ for stands in Europe.
Abbreviations: RTD = root tissue density; RTFm = short root tip frequency per unit dry mass; D = short root diameter; L = short root length; M = short root dry mass and V = short root volume.

We draw three main conclusions from our study. First, the significant difference in short root morphology between coniferous and deciduous trees was confirmed: short roots of Norway spruce and Scots pine were thicker and their root tissue density was higher than the respective measures in silver birch. Consequently, specific root length and specific root area of short roots were greater for silver birch than for Norway spruce or Scots pine. Second, the pattern of short root morphological characteristics along a latitudinal gradient was generally similar for all investigated species. The effect of site fertility on short root parameters, as a result of abiotic and biotic factors, decreased in the order: Norway spruce > silver birch > Scots pine. Third, for the fine root system of Norway spruce, the extensive adaptation strategy (higher fine root biomass and number of root tips per stand or per unit basal area) is the primary mechanism and the intensive strategy (morphological adaptations) the secondary mechanism for coping with harsh conditions.

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References


