Quantity, vertical distribution and morphology of fine roots in Norway spruce stands with different stem density

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Abstract: In the study, the influence of stand density on quantitative and morphological parameters of fine roots with the diameter less than 2 mm was analysed. The results confirmed the differences of the fine root distributions and the total fine root mass between stands with different density. The Norway spruce stand with lower stem density has a lower overall fine root mass but, at the same time, a higher fine root mass regarding the single tree. In the litter (Ol, Of-horizons), the fine roots are present only in the plot with higher density. The cumulative proportion of fine root biomass in the layer 0–10 cm reaches 67% in the plot with lower density and 78% in the plot with higher density. In the lower density plot, a lower proportion of fine roots in the diameter class under 0.25 mm was found in all analysed parameters. Specific root length, root surface area and root tissue density reflect the different diameter structure of fine roots in the surveyed plots. We suppose the stand density significantly affects the fine root system, especially by the change of moisture regime in the litter and in the upper parts of the A-horizon. Despite the high fine root dynamics of single trees, the Norway spruce stand with the lower stem density is not able to effectively utilize the entire soil space.

Keywords: fine roots, *Picea abies*, root mass, specific root length, stand density

Abbreviations: RTD, root tissue density; SRL, specific root length; SSA, specific root surface area

Introduction

Quantitative parameters of belowground biomass are influenced by the complex of various factors. Cairns et al. (1997) report, that aboveground biomass density alone accounted for 83% of the variation in root biomass density. After accounting for aboveground biomass density, age and latitudinal zone also significantly improved the predictive utility of root biomass density. Even though their research concerned the biomass of all roots, similar patterns are valid also for the fine root category, i.e. the roots with the diameter less than 2 mm.

Although fine root biomass contributes relatively little to total tree biomass (Norby and Jackson 2000), fine roots are major contributors to carbon inputs because of their rapid turnover. In forests, belowground net primary productivity accounts of 30–50% of total net primary production according to Gill and Jackson (2000). Makkonen and Helmisaari (1999) found that the proportion of the total tree biomass represented by fine roots and mycorrhizas is in average 10–20%, whereas their growth and maintenance use a major part, perhaps as much as 67–70%, of total net primary production. Welke et al. (2003) report that the fine roots represent 8–73% of annual net primary production of western forest ecosystems. Vogt et al. (1996) estimate the usual proportion of fine root biomass under 5% of total tree biomass.

Fine roots are often abundant in the organic horizon. Tingey et al. (2000), Jackson et al. (1996) mention that in forests about 50–80% of roots are found in the upper 30 cm of soil. Also for the category of fine roots, clear vertical gradients were found (Claus and George 2005, Baker et al. 2001). The upper soil layer is characterized by the high availability of water and nutrients, especially of nitrogen in available forms as well as by the activity of microorganisms (Hertel 1999, Konôpka and Takáčová 2010, Zhou and Shangguan 2007). The difference between various ecosystems or soils, respectively, concerns the depth, where the vast majority of the fine roots is concentrated. According to Meinen et al. (2009), who analysed the horizontal and vertical distribution of

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fine roots in beech stands with various admixture of the other broadleaved species, the changing proportion of the admixture of other tree species had no significant influence on its values.

Dead roots make up 50–80% of the fine root biomass (Usman et al. 1999). According to Welke et al. (2003) the annual loss of fine roots in forest ecosystems ranges from 40% to 92% of standing crop. Due to the high turnover, the contribution of the fine roots to the increase of the organic matter in soil is 2–5 times higher than that of the aboveground parts. Thus the pool of organic matter and nutrients released upon decomposition of fine roots could compensate the adverse effect of harvesting.

Not surprisingly, the diameter class of fine roots in forests had a strong role in determining the fine root turnover. Gill and Jackson (2000) found out, that as the diameter class increased, the root turnover decreased. Therefore, besides the fine root total biomass and necromass, the distribution of the fine roots according to the average diameter plays an important role as well. Furthermore, the biomass alone is not indicative of the functional potential of the root system as an absorbing organ (Børja et al. 2008). Morphological plasticity of fine roots has been proposed as a mechanism by which plants react to variation in soil nutrient supply. By the change of the morphological parameters, e.g. specific root length (SRL), specific root surface area (SSA) or root tissue density (RTD), the tree is able to significantly influence the extent of the occupied soil bulk and subsequently to modify some physical features in the rhizosphere.

Silvicultural interventions in forest stand impact not only its aboveground part (the increase of crown volumes, mean tree diameter and mechanical stability of trees) but also the entire root system, including the fine roots. Fine root production should be especially sensitive to the amount of new biomass needed for mechanical support of the crown because fine roots are the distal end of the carbohydrate source-sink network (Dean 2000). According to Helmisaari et al. (2006), commonly used variables describing the stand structure (volume, basal area, number of stems, needle biomass) did not show any notable correlations with the fine root biomass of the Norway spruce at the stand level. In contrast, considerably better correlations were found when the parameters were calculated for an average tree by dividing the stand values by the stem number. When the northern and southern sites of Finland were analysed separately, the fine root biomasses per tree of spruce correlated well with e.g. the basal area per tree. Several of the relationships found at the stand and tree level can be used for predicting fine root biomass and the amount of carbon it contains.

The most important task of tending the Norway spruce stands is the promoting of static stability of individual stems as well as of the whole stand. The direct consequence of decreasing stem density and increasing space for the crown growth of remained trees is the increase of their basal area. Finér et al. (2007) report that the fine root biomass per tree increased with basal area per tree in spruce stands in the temperate zone.

Fine roots of the trees distinctively influence the humus content in the soil and the soil porosity, while both of these characteristics have a crucial impact on the soil hydrolimits. In the forests of the protection zones of the water reservoirs, one of the main non-commercial functions is to guarantee the water quality (Barnes et al. 1998) by the transformation of the surface runoff to the subsurface flow. Considering the low root density in the soil profile, Norway spruce does not represent the ideal tree species for the increasing of the soil porosity. Nevertheless, the demands on the forest stands regarding the protection of the water sources quality (Gubka 2002) and the ability to form distinctively differentiated stands (Vencurik 2003, 2006) are the reasons for the dominance of Norway spruce in the 1st protection zone of the water reservoirs.

We assume that the changes of stem density cause the significant changes of the fine root fraction on stand as well as on individual tree level. Therefore, the tending interventions could significantly influence the porosity and the water-holding capacity of the soil in forest stand. Total fine roots biomass can be lower in the stand with lower stem density, but due to the lower competition of individuals, the root characteristics such as SRL, SSA and RDT can alter and thus the rooting density and soil porosity can be higher than in the stand with higher stem density. The goal of this study was to evaluate the quantity of fine root system as well as the selected morphological parameters of fine roots and their relation to the stand density of the Norway spruce stand with the water management function. In particular, we addressed following issues: (*i*) We assumed that the fine root bio- and necromass is increasing with the growing aboveground stand density, but the goal was to quantify the magnitude of this difference between two forest stands with significantly different stem density. (*ii*) We analysed if there were different patterns of fine root distribution in soil profile in the plots with different stem density. (*iii*) Another question was whether the decrease of total biomass, length, volume and surface of fine roots in the plot with lower stand density would be proportional to the decrease of stem density, i.e. whether the quantity of fine roots per individual tree would remain unchanged. (*iv*) We were interested how the root morphological characteristics (SRL, SSA and RDT)

Table 1. Meteorological data from weather station of water reservoir Klenovec

	Month												Year
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
Mean temperature (°C)													
1995–2010	–2.1	0.0	3.6	10.0	15.0	18.2	19.8	19.0	14.1	9.4	4.2	–1.3	9.2
2010	–2.6	–0.5	3.9	9.9	14.2	18.2	20.8	18.4	12.9	7.0	6.9	–0.5	9.1
Precipitation (mm)													
1995–2010	40.3	40.9	41.8	67.6	91.5	96.4	111.7	87.4	65.9	47.9	69.1	58.1	819
2010	84.5	70.3	23.9	93.7	262.6	119.9	139.4	100.3	166.0	33.0	174.5	139.9	1408

will react on the different stand density.

Materials and methods

Study area

The research was conducted in the stands of 1st protection zone of the water reservoir Klenovec (48°36'N, 19°52'E) in Central Slovakia. Investigated area is located in Slovenské Rudohorie Mts. at the elevation of 370 m a.s.l. The mean annual temperature reaches 9ºC and the mean annual precipitation 800–820 mm. Detailed characteristics of temperature and precipitation are reported in Table 1. The bedrock is formed by granodiorites and the most common soil types are dystric Cambisols.

Water reservoir Klenovec was built in the period 1968–1974. After its completion, the pure Norway spruce (*Picea abies* (L.) Karst.) stand was planted on its shores in a 100 m wide strip around the reservoir. In the whole stand no systematic tending has been applied since its establishment that resulted in its heterogenous density with a high mean stem number per hectare and a low static stability of individual trees in some parts of the stand. During the last decade (before the establishment of research plots), some damage of individual trees by snow occurred and caused the decrease of canopy cover in some parts of the stand. The samples for our study were taken from two permanent research plots with different stem density (plot with lower stem density–LD, plot with higher stem density–HD, Table 2). Both research plots were located on an eastern slope of 25%, in the distance of approx. 50 m from each other. The forest stands in surveyed plots were 35 years old, with a mono-layered structure and no plant understory. The so far last snow damage occurred in winter 2009/2010 and it affected also the LD-plot. Broken trees were removed from the plot in spring 2010, but as the damaged stems were distributed randomly, no distinct canopy gap was formed.

Fine root sampling and processing

Root biomass was estimated by soil coring in fall 2010. Five cores per stand were systematically taken from the humus layer and mineral soil with an 80 mm soil corer. In each research plot, a line transect was established. On the line transect, five points for the fine root sampling were marked, whereas the distance of subsequent points was 4 m. The intact humus and soil cores were divided into six layers by depth: humus, 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm and 30–40 cm. In this case, zero depth corresponds to the boundary between the humus layer and mineral soil. The soil samples were transported from the stand to the laboratory and stored frozen at –18°C until analysis. After thawing, the whole sample was sieved under water through mesh with 1 mm size. Fine roots with diameter less than 2 mm were manually picked out, washed twice and separated into dead and live fine roots according to the generally used criteria for

Table 2. Main dendrometric characteristics of investigated plots in the Norway spruce stands in 1st protection zone of the water reservoir Klenovec

	Stem density	Growing stock	Basal area	Crown projection area	Tree diameter*	Tree height*	Tree crown length*	Tree crown volume*
	(N ha^{-1})	(m^3 ha^{-1})	(m^2 ha^{-1})	(m^2 ha^{-1})	(cm)	(m)	(m)	(m^3)
HD-plot	1,133	526	44.9	6,990	21.4 ± 6.8	23.3 ± 3.5	9.7 ± 2.7	25.7 ± 17.7
LD-plot	500	328	27.8	5,995	26.5 ± 4.5	25.0 ± 2.7	11.1 ± 2.4	51.1 ± 35.9

*mean ± SD

identification of live and dead roots and their parts (Göbl 1995, Hertel and Leuschner 2006).

Live tree roots were spread on a water-filled, transparent plastic tray and scanned with a transmitting light scanner at 1000dpi. The images were analysed with WinRhizo Reg 2009. The result of the image processing is the data about total length, mean diameter, total surface area, volume and root tips number of the entire root system or its analysed part. The another part is the distribution of these parameters according to the diameter classes. The class range was set to 0.5 mm. The classified and measured roots were dried at 70°C for 3 days and weighted to determine the value of dry bio- and necromass. The following variables were calculated from the WinRhizo outputs: specific root length (SRL) in m g^{-1}, specific root surface area (SSA) in cm^2 g^{-1} and root tissue density (RTD) in g cm^{-3}.

The relation between the cumulative fine root fraction (*y*) and the soil depth (*d*) was approximated by the exponential function $y = 1 - \beta^d$ (Gale and Grigal 1987). Parameter β could reach the values from 0 to 1, whereas the higher its value, the deeper the fine roots occur.

Because fine root biomass, length, volume and root tips number for a whole stand, as presented in our study, may differ greatly from that of an individual tree, we calculated these characteristics per tree by dividing stand values by tree number.

Results

Total weight of fine roots in the soil layer 0–40 cm reaches 178.5 g m^{-2} in the plot with lower stand density (LD-plot). From this amount, living roots represent 161.3 g m^{-2} (90.4%) and dead roots 17.2 g m^{-2} (9.6%). In the plot with higher stand density (HD-plot), the total weight is 263.1 g m^{-2}; living roots constitute 220.5 g m^{-2} (83.8%) and dead roots 42.6 g m^{-2} (16.2%). Regarding the vertical distribution in the soil profile (Fig. 1a), fine roots are concentrated into the uppermost mineral soil layers. The litter (Ol- and Of-horizons) is very thin (max. 30 mm), with a very heterogenous rooting density in both investigated stands. The Ol- and Of-horizons are in average only 10 mm thick (min. 0 mm, max. 15 mm) in the LD-plot and no fine roots are present there. In the HD-plot, the total thickness of these layers varies from 10 to 30 mm (17 mm in average) and the fine root concentration amounts from 0.011 to 0.137 g m^{-2}. The proportion of dead roots differs according to soil layer and its highest value was found in both research plots in the depth 30–40 cm (Fig. 2).

The changes of cumulative root fraction by soil depth were analysed using the model by Gale and Grigal (1987). The cumulative proportion of the fine root biomass in the layer 0–10 cm reaches 67% in the LD-plot and 78% in the HD-plot. The fine root biomass of the uppermost soil layer in the HD-plot is nearly two times higher than in the LD-plot and it is the main reason for the different values of total biomass (Fig. 3).

Despite the high difference in the living root weight, total length of fine roots calculated per 1 m^2 (root length density) in the entire studied soil profile do not differ significantly between the surveyed stands. In the 40 cm deep profile, the fine root length per 1 m^2 is 2.781 m in the HD-plot and 2.724 m in the LD-plot. The fine root density, expressed as the living root length per the 10 mm thick layer is variable, but its decrease with the increasing soil depth is visible (Fig. 1b). In both plots, the correlation between the fine root density and the soil depth was confirmed as weak (r^2=0.49 in the HD-plot, r^2=0.42 in the LD-plot), but the value of standardized regression coefficient (beta) is significantly different from zero in both cases (Table 3).

The volume of living fine roots in the entire soil profile reaches 389.7 cm^3 per 1 m^2 in the HD-plot, however, it increases up to 504.8 cm^3 per 1 m^2 in the LD-plot. To the increased volume contribute above all the roots in layers from 5 to 30 cm, where the root volume is distributed more uniformly than in the case of root weight and length (Fig. 1c).

As well as the root volume, the number of root tips is higher in the LD-plot (1.132×10^6 root tips per 1 m^2) than in the HD-plot (1.042×10^6 root tips per 1 m^2). In the HD-plot, the decline of root tips number with increasing soil depth is observable, while in the LD-plot the distribution of root tips number is more uniform (Fig. 1d). The distribution of total length, surface, volume and root tips number of living fine roots according to diameter classes is different in investigated plots (Table 4). The observed differences were confirmed as highly significant according to the results of multiple analysis of variance. For all analysed variables, the proportions of the first diameter class are higher in the HD-plot, but the following three diameter classes up to 1 mm have a higher proportion in the LD-plot.

Various distributions of fine roots in the diameter classes are reflected also in the various values of morphological parameters as specific root length (SRL), specific surface area (SSA) and root tissue density (RTD) (Table 5). The values of specific root length show an increase with increasing soil depth in the HD-plot. In the LD-plot, the change of this basic morphological parameter with increasing soil depth is less and its maximum values are lower. In the RTD values, no visible trend (increase or decrease with the changing soil depth) was observed in any of surveyed plots. Distribution of mean values of SSA in particular

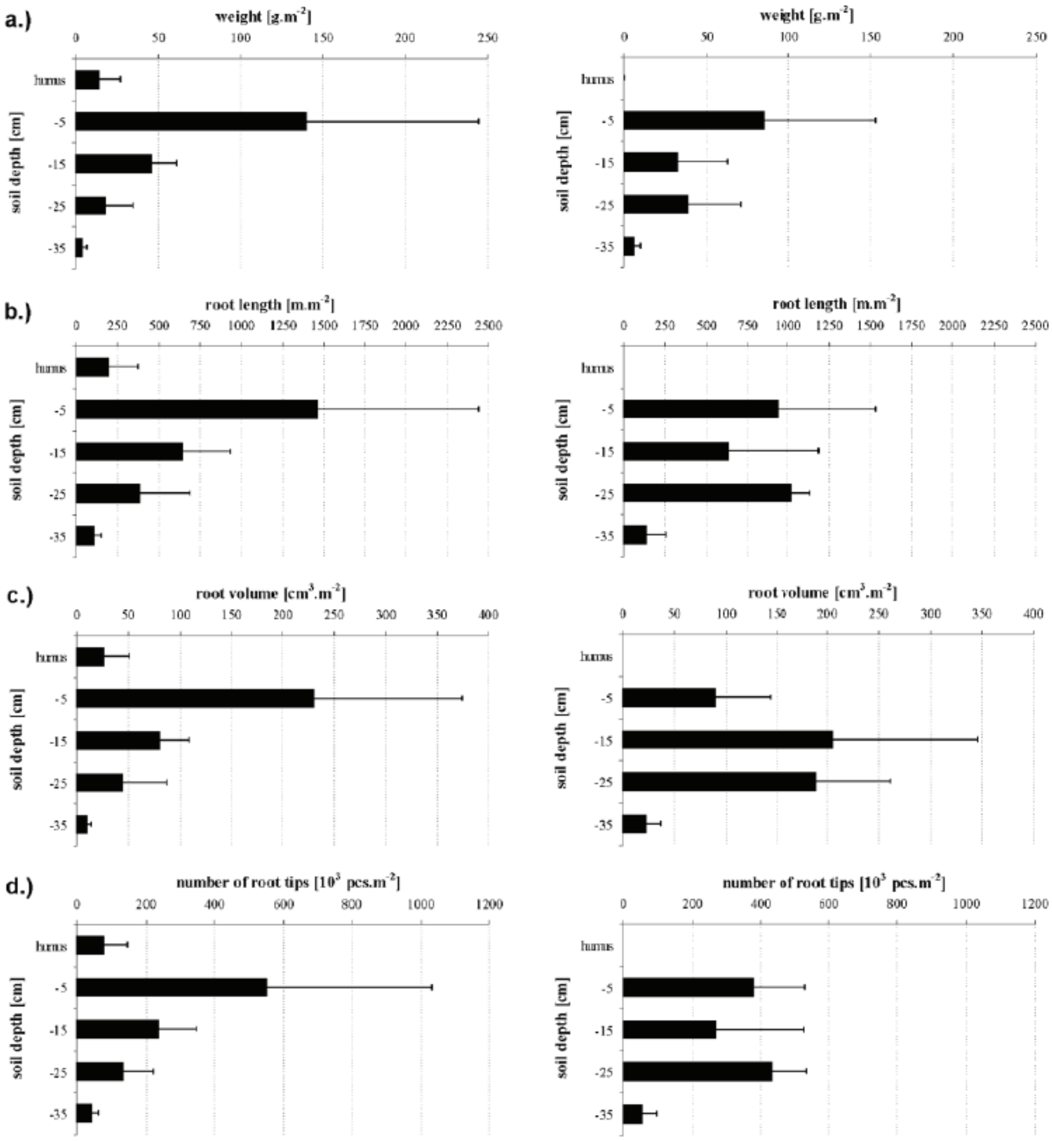

Fig. 1. Vertical distribution of fine root characteristics in the soil profile – weight of living fine roots (*a*), length of living fine roots (*b)*, volume of living fine roots (*c*), number of root tips (*d*). Left column refers to HD-plot, right column to LD-plot, the error bars represent the standard deviation.

soil layers is similar to those of previous parameters.

The most distinctive differences between the studied plots regarding the distribution of all morphological parameters according to the diameter classes are between the first two diameter classes. Although the diameter class 0.26–0.50 mm dominates within the finest roots in both plots, its proportion is different. Much higher differences were found in the diameter class 0–0.25 mm, where the higher proportions were confirmed in the HD-plot. The differences in the distributions according to diameter classes were highly significant for all analysed variables (Table 4).

The values of fine root parameters for an individual tree (Table 6) showed clearly, that the root mass, length, surface, volume and root tips number per individual tree are higher in the LD-plot. Fine root mass in the LD-plot is 1.56 times higher than in the HD-plot and it represents the parameter with the lowest difference between the investigated plots. Number of root tips in the LD-plot exceeds that of the HD-plot by the factor of 2.46. Despite the fact, that the root diameter class 0–0.25 mm, where most of the root tips are concentrated, has a higher share on root length in the HD-plot, the root tip frequency in the LD-plot (4.15 root tips per cm length) is higher than in the HD-plot (3.75 root tips per cm length). However, this difference was not confirmed as significant. The parameter with the highest difference between the

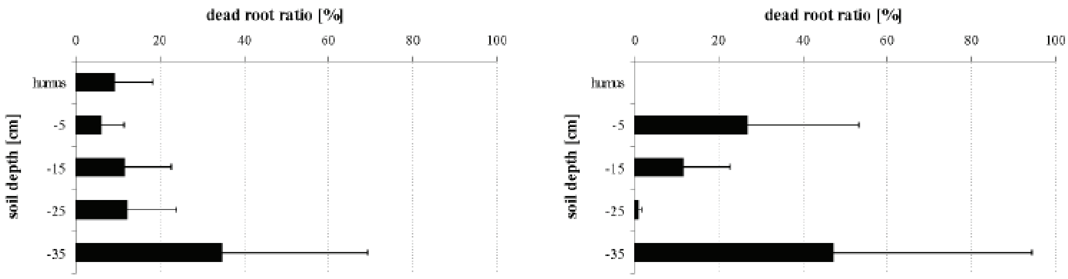

Fig. 2. Vertical distribution of dead root ratio in the soil profile. Left image refers to HD-plot, right image to LD-plot, the error bars represent the standard deviation.

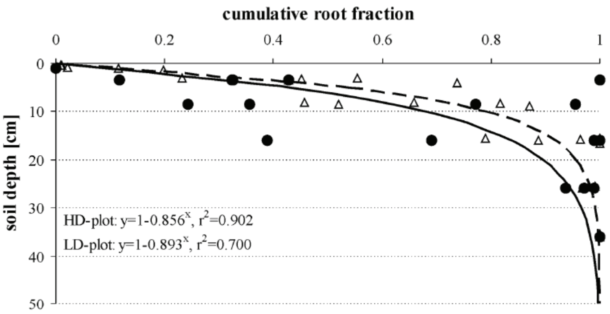

Fig. 3. Relation between the cumulative proportion of fine roots and the soil depth (HD-plot – white triangles and dashed line, LD-plot – black dots and solid line).

Table 3. Basic parameters of linear regression between the fine root density in particular investigated soil layers and the soil depth

	a	b	Beta
HD-plot	140.2	–3.830	–0.489*
LD-plot	103.8	–1.928	–0.427*

analysed plots is the root volume per individual tree, which is 3.2 times higher in the LD-plot than in the HD-plot. Regarding the relationship between crown volume and fine root biomass, we found 69.8 g of fine roots per 1 m^3 of crown volume in the LD-plot and 90.4 g per 1 m^3 in the HD-plot.

Discussion

The comparison of two research plots with different stand density showed significant differences in the quantity of living and dead fine roots, in their distribution in soil profile and in morphological parameters as well as in quantitative characteristics of fine roots calculated per individual tree. As expected, the biomass, necromass, total length, volume and surface of fine roots were higher in the HD-plot than in the LD-plot. On the other hand, these parameters calculated per individual tree had higher values in the LD-plot.

Fine root biomass of trees expressed as the weight of fine roots per the area unit of forest ecosystem can be surprisingly high. Jackson et al. (1996) compiled a review on the values of fine root biomass for terrestrial ecosystems. They report the values up to 5 kg of fine roots per 1 m^2 in the tropical rainforests, while the other forest and shrub ecosystems reach the fine root biomass with comparable values only rarely. The values of fine root biomass are significantly less in the Norway spruce commercial forests and they range from 34 g m^{-2} (Kocourek and Bystřičan 1989) to 550 g m^{-2} (Sandhage-Hoffmann and Zech 1993). In their thorough review concerning fine roots biomasses of European beech, Scots pine and Norway spruce, Finér et al. (2007) report that the mean living fine root biomass of spruce reached 297 ± 143 g m^{-2} and the necromass 190 ± 95 g m^{-2}. Differences in fine root biomass estimates among studies may be a result of several factors including local site conditions and sampling depth, tree species composition, age and stand basal area. In the stand comparable with our research object (30 year old Norway spruce stand on glaciofluvial acidic sandy soils) found Børja et al. (2008) similar value of the total fine root mass 398 g m^{-2}. Schmidt (2002) mentions the values of fine root biomass of Norway spruce from 437 to 759 g m^{-2} according to the soil depth. Our results lie close to this range and reach on average 692 g m^{-3} (HD-plot) or 332 g m^{-3} (LD-plot), respectively, whereby the fine root mass declines with the increasing soil depth. Fine roots are always concentrated in the soil layers with

Table 4. Proportions (in per cent) of fine root diameter classes according to separate quantitative parameters

Parameter	Plot	Root diameter class in mm					Wilks λ
		0–0.25	0.26–0.50	0.51–0.75	0.76–1.00	1.00–2.00	
Length	HD-plot	34.4	45.2	11.7	4.1	4.6	0.550^{***}
	LD-plot	20.4	50.3	18.5	6.9	3.9	
Surface	HD-plot	17.1	42.4	18.3	8.8	13.4	0.530^{***}
	LD-plot	9.1	43.2	25.3	12.2	10.2	
Volume	HD-plot	6.9	31.5	21.8	13.8	26.0	0.543^{***}
	LD-plot	3.5	31.9	28.1	17.1	19.4	
Number of root tips	HD-plot	73.5	23.5	2.4	0.6	0.0	0.437^{***}
	LD-plot	55.2	38.6	5.1	1.1	0.0	

Table 5. Fine root morphological characteristics (mean ± SD) in investigated plots

		HD-plot	LD-plot	p-level
SRL	($m\ g^{-1}$)	15.90 ± 6.02	14.3 ± 5.12	0.611 (NS)
RTD	($g\ cm^{-3}$)	0.539 ± 0.090	0.405 ± 0.098	0.001*
SSA	($cm^2\ g^{-1}$)	188.1 ± 47.9	214.8 ± 59.1	0.116 (NS)

the highest nutrient supply (Kutschera and Lichtenegger 2002).

Low values of dead fine roots ratio on total fine root mass that were confirmed in both research plots are not typical for Norway spruce stands. We assume the reason was the combination of favourable moisture regime in mineral soil layers during 2010 and of accelerated fine roots growth in the parts, where the impact of competition was reduced after the removal of individual broken stems in spring 2010. Favourable moisture and temperature conditions in the soil helped to accelerate the decomposition of root systems, that remained after the stems removed in spring 2010.

Hertel (1999) considers the presence of available nitrogen to be the most important factor that influences the stratification of fine roots. Jackson et al. (1996) compared in their work root data across biomes for various plant functional groups and used a model of vertical root distribution based on the asymptotic equation presented by Gale and Grigal (1987). The average rooting distribution for all trees across all relevant biomes was shaped by $\beta = 0.970$ with 60% roots in the top 30 cm and 78% in the top 50 cm. For the conifer forests of temperate zone they report the value $\beta = 0.976$ and 52% of the total root biomass in the top 30 cm. Although the fine root distribution is affected by different factors than the distribution of coarse roots, the presented model is appropriate for the description of the relation between the fine root biomass and the soil depth as well. In our study, the parameters of Gale-Grigal's model (Fig. 3) as well as the values of all quantitative characteristics confirmed the significant influence of stand density on the fine root distribution in the soil profile. The shape of the function describing the fine root distribution is directly related to the fine root density in the uppermost soil layer (0–10 cm). The stand density in the LD-plot is so low, that the present trees are not able to effectively occupy the soil layer with the highest nutrients supply. On the other hand, the model of fine root distribution lets assume a deeper rooting and a better static stability of the trees in the LD-plot.

In our study, stand density had no effect on root length density for a whole stand. On the other hand, a higher total fine root volume and higher number of root tips was confirmed in the LD-plot. These disproportions resulted in significantly different fine root morphology. The results of Finér et al. (2011) indicate that environmental factors or forest stand can not explain a significant amount of the variation in the total fine root biomass, whereas the mean basal area of the forest stand can explain 49% of the total fine root biomass and 79% of the fine root biomass of trees at the tree level.

The higher fine root biomass per 1 m^3 of tree crown volume in the HD-plot can be also considered as the reaction on the higher competition in the aboveground space. We assume, that this is a similar phenomenon as the increase of root to shoot mass ratio of the seedlings growing under suboptimal conditions (Köstler et al. 1968), or the increasing fine root proportion of the total belowground as well as total stand biomass along a latitudinal gradient (Ostonen et

Table 6. Values of fine root parameters calculated per individual tree

	Biomass (g)	Length (m)	Surface (m^2)	Volume (m^3)	Number of root tips
HD-plot	2,322	24,546	32.13	0.0034	9.201×10^6
LD-plot	3,569	54,496	63.61	0.0109	22.610×10^6

al. 2007a).

Trees could not only respond to the presence of competitors by changes in fine root biomass and its spatial distribution, but also with modification of fine root morphological traits such a specific root length, root tissue density, specific surface area and root tips abundance. Fine root morphological adaptation is a secondary strategy that further helps to improve mineral nutrition of tree at low fertility sites (Ostonen et al. 2007a). The effect of site conditions on fine root morphology is exactly in case of Norway spruce one of the most evident. Differences in fine root morphology are the response to the differences of the environment, where the fine roots are growing. As the soil conditions in our study were homogenous, the differences in morphological parameters likely concern the intraspecific competition and subsequent worsening of growth conditions. Konôpka et al. (2007) found that drought can significantly reduce root tips frequency and increase RTD. RTD can be considered a characteristic of root functional status, because it is closely associated with physiological activity (Ostonen et al. 2007a). A high tissue mass density is generally associated with species characteristic of stressed environments (Ryser 2006). A reduction in nutrient availability has been shown to lead to an increased root mass density within a species (Ryser and Lambers 1995). Ostonen et al. (2007b) found in their study, mean root density varied from 310 to 540 g cm^{-3}, what is comparable with our results. These authors confirmed that RTD of short roots tends to decrease with increased site fertility. Moreover, RTD varied between different parts of the root system and among the root tips. Young, unsuberized parts of growing roots are relatively low in dry matter. Root tissue density increases as the fine root become suberized. In our investigation, total number of root tips is higher in the LD-plot than in the HD-plot and this have an impact on lower value of total RTD in the LD-plot. Better conditions for the fine root forming and growth in the LD-plot are confirmed also by a higher mean diameter of fine roots, that amounts to 0.499 mm in the LD-plot and 0.420 mm in the HD-plot.

SRL in the entire soil profile has a higher mean value in the HD-plot, though the values in both plots lie in the SRL range for Norway spruce reported by more authors (Ostonen et al. 2007a, Borken et al. 2007, Børja et al. 2008). Direct reason of the higher SRL in the HD-plot is the higher proportion of root length as well as the higher total root length in the first diameter class (Table 4). Due to their dominantly primary structure (Hishi 2007), these roots have the lowest values of RTD, i.e. they contribute to the total weight and mean RTD of fine roots at least. According to Eissenstat and Yanai (1997), the root length is assumed to be proportional to resource acquisition (benefit) and the root mass to be proportional to construction and maintenance (cost). Besides the RTD, the values of SRL are affected also by the values of root diameters (D). Ostonen et al. (2007b) showed in their survey, that the variation of RTD was higher than the variation of D, but D contributes to SRL by its squared value, which means the impact of root diameter is more essential for SRL. This explains, why in our study despite the higher value of RTD in the HD-plot, the lower value of D resulted in higher SRL.

Important factor that impacts SRL is the drought stress. According to Ostonen et al. (2007b), drought is a composite stress affecting, in the first place, the functioning of thinner roots. In their summary, SRL decreased, but not significantly, by 11% as a result of soil dehydration. On the other hand, fertilisation reduced SRL significantly by 13%, but there was a significant difference in SRL responses between different fertilisation types. The reduction of SRL was significant in case of fertilisation with inorganic nitrogen, whereas the use of organic nitrogen showed only nonsignificant differences. In our study, the LD-plot had a thinner litter layer and no fine roots were found in any sample from this layer. Concerning the monthly precipitation rates and monthly mean temperatures (Table 1), we assume that the root systems were not exposed to any noticeable drought stress in 2010. Nevertheless, we can not exclude intensive, spatially and temporally limited dehydration of very thin litter layer in the LD-plot during the end of fine roots growing period (October 2010). On the other hand, we assume that the reason of lower SRL value in the LD-plot is the more intensive fine roots decomposition due to the favourable temperature and moisture regime of the soil and therefore the more intensive release of nutrients (above all of nitrogen) into the soil.

Reduction of stand density causes also the changes in the competition between individual trees. Fujii and Kasuya (2008) showed that small *Pinus densiflora* trees suffering from strong competition exhibited lower fine root biomass and higher SRL and root tips frequency (number of root tips per cm length). Similarly, in our case the value of SRL is higher in the HD-plot, although the root tips frequency has higher values in the LD-plot.

SRL is not affected only by one of mentioned factors and the fine root systems are more likely influenced by the synergy of soil conditions improvement and reduction of intraspecific competition in Norway spruce stand.

This study shows, that the quantitative traits and the morphological variability of Norway spruce fine roots are related to the stand density. Total fine root biomass increases with the stand density; however, in the Norway spruce stands with lower density (approx. less than 500 trees per hectare in the age of 40 years) a more intensive fine root growth of individual trees is observable. This suggests, that after the decrease of stem density due to a natural disturbance or a deliberate human intervention (thinning), the stand requires certain time until the trees are able to occupy by their roots the soil space liberated by the removing of their competitors.

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