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Fine roots biomass and morphology in a chronosequence of young *Pinus sylvestris* stands growing on a reclaimed lignite mine spoil heap

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Abstract. The morphology of fine roots (≤2 mm diameter) as well as fine and coarse root biomass was investigated in a chronosequence consisting of 6-, 9-, 11-, 15-, 17- and 20-year-old Scots pine (*Pinus sylvestris*) stands growing on a reclaimed lignite mine spoil heap. Core method of destructive root sampling was used to establish whether root morphology and biomass varied with stand age in the upper 20 cm of soil. Fine root biomass ranged from 0.78 to 3.11 Mg ha^{-1}, coarse root biomass ranged from 0.82 to 2.74 Mg ha^{-1}, whereas root necromass ranged from 1.03 Mg ha^{-1} to 2.87 Mg ha^{-1} in the chronosequence studied. Fine root diameter as well as length, projected area, and surface area expressed per unit area increased significantly with stand age. Moreover, our study revealed that when stand age increases, specific fine root biomass increases, whereas specific root length and area decreases. The results support our hypothesis that stand age has an effect on standing fine root biomass and morphology.

Additional key words: biomass allocation; belowground biomass; Scots pine; specific root length; specific root area; root tips density; mine dump; reclaimed post-industrial area.

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Introduction

Fine roots are physiologically the most active parts of the tree root system. Although fine root biomass is usually less than 5% of the total tree biomass (Vogt et al. 1996), they are considered as playing a key role in carbon and nutrient cycling and accumulation in the soil. It has been found in many studies that trees allocate a large proportion of photosynthate carbon to fine roots. For example, Janssens et al. (2002) estimated that 28–49% of gross primary production (GPP) is transferred to the root system in a Scots pine forest. Moreover, as reviewed by Simard et al. (2002), 10–50% of photosynthates produced by a tree are allocated to ECM fungi associated with its roots. Thus, fine roots are a strong sink of carbohydrates and their death and rapid turnover (decomposition) is responsible for transferring a large amount of carbon into the soil (Norby and Jackson 2000, Finér et al. 2007). Fine roots are a main component of soil organic matter and clearly influence soil microbial activity and decomposition processes,

considered as one of the main pathways through which carbon enters the soil, playing also a fundamental role in the development of soil when considered as a substrate.

Despite the important role of fine roots in stand dynamics, there are relatively few studies on how fine root biomass and morphology varies in relation to forest stand age (e.g. Vanninen et al. 1996, Helmisaari and Hallbäcken 1999, Makkonen and Helmisaari 2001, Claus and George 2005, Børja et al. 2008). It has been shown that the size of a root system depends on age (Vogt et al. 1987, Vanninen and Mäkelä 1999, Claus and George 2005, Fujimaki et al. 2007) and that the relative proportion of fine roots to total stand biomass decreases with increasing stand age (Ovington 1957, Helmisaari et al. 2002). For example, Bakker et al. (2008) investigated root biomass in a chronosequence of *Fagus sylvatica* consisting of 9-, 26-, 82- and 146-year-old stands; they revealed that standing fine root biomass was significantly higher in the younger stands than in the older stands. Decline in fine root biomass with age was also observed for coniferous forests, for example for *Pseudotsuga menziesii* (Vogt et al. 1987), *Pinus sylvestris* (Vanninen and Mäkelä 1999) and *Cryptomeria japonica* (Fujimaki et al. 2007), where fine root biomass generally increased to a peak at canopy closure and than gradually decreased in maturing stands. Finér et al. (2007) stated that the fine root biomass increases until canopy closure and thereafter it does not increase or in some cases even decreases. Similar results were obtained earlier by Vogt et al. (1987), Vanninen et al. (1996), Helmisaari et al. (2002), and Claus and George (2005). However, Fujimaki et al. (2007) found that fine root biomass of *Cryptomeria japonica* increased at an early stage of forest maturation, reaching its maximum value before canopy closure in 15-year-old stand and then declined with increasing stand age. Generally, fine root biomass increases rapidly after planting of saplings, peaks at an early stage of forest maturation and stabilizes or decreases when the stand reaches equilibrium at later stages of development. Vogt et al. (1987) suggested that changes in fine root biomass are related to above-ground biomass dynamics and changes of stand structure.

The literature on fine root morphology in relation to stand age is scarce. Attributes describing fine root morphology and fine root biomass may be assumed to indicate below-ground competitive ability of trees (Fitter 1987, Bauhus and Messier 1999a, Grams et al. 2002). Fine root morphology as well as vertical and horizontal biomass distribution are fundamental root system features playing a key role in the nutrient and water acquisition efficiency of trees, thus controlling the soil exploitation process. Alteration of these architectural traits is considered as tree adaptation to variability of main soil resources (Fitter 1987). Fine root morphology may change with stand age since the physiology and nutrient and water demands of trees change with their growth and development of the stand.

Alterations in root system architecture may occur without a distinct change in total root biomass (Hodge 2004, Børja et al. 2008). It was shown in many studies that morphological plasticity of fine roots may be considered as a mechanism by which plants respond to variation in soil water and nutrient availability and physical conditions (Lõhmus et al. 1989, Ostonen et al. 1999, Hodge 2004). Moreover, competition among individuals of the same species or among different plant species influences the process of root growth. While roots of forest trees vary widely in morphology and physiology, relatively little is known about what environmental factors govern this variation and consequently how this variation may be linked with plant functioning (Brunner and Godbold 2007). For example, specific root length (SRL) is often considered a measure of fine root ability to proliferate in the soil and thus related to their nutrient uptake; it was shown that high SRL allows rapid nutrient uptake per unit root mass (Eissenstat 1992, Børja et al. 2008). Moreover, other morphological features of fine roots, e.g., root surface area and root tip density are considered to reflect stand absorptive potential (Eissenstat et al. 2000, Craine 2006, Børja et al. 2008).

Our primary objective was to determine the age-related pattern of fine root development and estimate fine root biomass and morphology along a chronosequence of young Scots pine (*Pinus sylvestris* L.) stands since it is not evident in the literature whether fine root biomass and morphology are affected by stand age in the younger phases of stand development. The studied range of stand ages (6 to 20-year-old) is considered as the most dynamic period in stand development. We hypothesized that fine root biomass and morphological traits will vary with the age of the forest stands. To estimate changes in fine root biomass and morphology at various stages of forest development, stands of different age were studied at the same time providing valuable data on the influence of stand age on these key root features.

Material and methods

Study site

The study was conducted in six pure Scots pine (*Pinus sylvestris* L.) stands aged 6, 9, 11, 15, 17, and 20 years in Bełchatów Forest District, Poland (51°12' N, 19°25' E). The study plots were situated on Mount Kamieńsk, which is the largest (relative height ca. 180 m, ca. 400 m a.s.l., base surface 1500 ha) artificial overlayer spoil bank in Poland made as a result of

Bełchatów brown coal mining activity (Krzaklewski 2005, Jagodziński and Kałucka 2008).

Forest reclamation of the lignite mine spoil heap started in the mid-1980s. The most common tree species used for reforestation were *Betula pendula* (ca. 25% of the total area), *Pinus sylvestris* (20%), *Alnus* spp. (15%), *Robinia pseudoacacia* (12%), and *Quercus* spp., *Populus* spp., *Salix* spp., *Acer* spp., *Fraxinus* spp., and *Larix decidua*. The initial density of the Scots pine stands (monocultures) included in this study was ca. 12000 trees per hectare (initial spacing – 1.5 m × 0.6 m). Since the natural mortality of trees was high during the first stage of stand development, only light clearings and thinning was applied (except for the 6-year-old stand). The stands had limited understory vegetation.

The spoil heap is formed of approximately 1300 million m^3 of various Quaternary and Tertiary overburden sediments covering the coal seam, which were mixed, loosened and aerated. The oxidation of pyrite (FeS_2), the mineral typical for Tertiary substrates, results in severe acidification (pH <2.5). In cases where such materials had not been isolated inside the mine dump, but had been instead deposited near its surface, extensive amounts of lime (chalk of lake origin from the open pit) and alkaline ash from the nearby lignite-fired power plant were applied to neutralize the high acidity. The spoil substrates are mainly of slightly alkaline sandy-clayey character, low in organic matter and are very poor in nutrients. Top soil and humus which had been separated prior to the mining process as well as lignite and charcoal were also used for the spoil surface reclamation (Kowalik et al. 1999, Krzaklewski 2005, Pająk and Krzaklewski 2007).

The analyses of the dump surface material revealed that soil horizons have not yet formed under any of the stands examined. Thin litter horizon begins to form in places under the groups of trees which are ca10 years old; it is still not differentiated and does not exceed 1 cm depth even in the 20-year-old plantation. The pH (in H_2O) of the damp surface layers was rarely less than 8 (with $CaCO_3$ almost always present). The content of C_{org}, total N and P is very low, especially in the layers deeper than 10 cm (Świtoniak and Kałucka, *in preparation*).

According to long-term meteorological observations (1971–2000) from the closest meteorological station, mean annual temperature is 8.0°C, mean annual precipitation is 571 mm, and mean growing season length (calculated as the number of days with mean temperature =5°C) is 213 days (Concise Statistical Yearbook of Poland 2007).

Root collection data

In September 2006, we measured diameters at breast height and heights of trees in each stand. The research site area varied from 600 m^2 for the 6-year-old stand to 900–1000 m^2 for the remaining stands. Selected stand characteristics are presented in Table 1. The 6-year-old stand was rather open, with average tree cover not exceeding 30%, and dense understory vegetation consisting mainly of *Festuca rubra, Poa pratensis* and *Calamagrostis epigeios* (Sieradzki, Kałucka and Jagodziński, *in preparation*). The other stands had not been thinned intensively during their development, thus had more closed canopy (40–95% cover), relatively poor or hardly any herbaceous layer and, in the oldest ones, a well developed moss layer (l.c.).

Table 1. Characteristics of the studied Scots pine stands (means ± SE). One-way ANOVAs were performed separately for the stand density, tree diameters at breast height, height of trees and stand basal area. Same letters indicate a lack of statistically significant differences between analyzed stand traits according to Tukey's posteriori test ($p<0.05$)

Stand age (years)	Stand density (trees ha^{-1})	DBH (cm)	Height (m)	Basal Area (m^2 ha^{-1})
6	6127a	1.44e	1.41e	0.66d
	(58)	(0.04)	(0.02)	(0.15)
9	5744ab	2.78d	2.44d	4.03d
	(119)	(0.07)	(0.04)	(0.60)
11	5220bc	2.82d	2.57d	3.67d
	(120)	(0.06)	(0.03)	(0.15)
15	5237bc	5.76c	4.94c	14.83c
	(97)	(0.08)	(0.09)	(1.14)
17	4910c	6.71b	5.59b	18.91b
	(90)	(0.09)	(0.10)	(0.59)
20	4982c	8.29a	8.01a	29.36a
	(109)	(0.11)	(0.17)	(0.48)
ANOVA	F	*P*	F	*P*	F	*P*	F	*P*
P>F	21.823	0.0009	332.687	<0.0001	1612.44	<0.0001	323.728	<0.0001

Root biomass was estimated by soil core sampling. Twelve randomly selected cores per stand were taken in September 2006. The root corer used in the study was a cylindrical tube, 4.7 cm in diameter and 20 cm long with a sharp edge to cut fine roots (Arts MFg. & Supply, American Falls, Idaho, USA). Deeper soil layers were not examined as a vast body of studies show that fine roots proliferate mainly in nutrient-rich zones in the upper soil layer and are clearly concentrated in the horizons, where nutrient and moisture conditions are most favorable, i.e. in the organic horizon and the upper part of the mineral soil. Soil samples were placed in plastic bags and stored in a refrigerator (4°C) during root collection in the field, before being transported to the laboratory and stored at –3°C in a cooling chamber until sample preparation. Roots from different soil horizons were treated together.

In the laboratory, the roots were separated from soil by sieving over 2 mm sieves and then transferred to floating basins with water. From there they were collected manually with tweezers and sorted into the following classes: (1) fine roots (≤2 mm of diameter), (2) coarse roots (>2 mm of diameter) and (3) dead roots. Dead roots were separated based on vitality assessment using morphological criteria of root color of the central cylinder, elasticity of particular root segments and root structure (e.g., the degree of cohesion between the cortex and periderm) (Vogt and Persson 1991, Bauhus and Messier 1999a). The roots of plants other than Scots pine (i.e. herbaceous species) were not examined.

Selected live fine root traits were analyzed using the digital image analysis software WinRhizo V3.10 (version 2003a, b; Regent Instruments Inc., Quebek, Canada; http://www.regentinstruments.com) and Epson Perfection 3200 PHOTO transmitting light scanner (Epson; http://www.epson.com). The roots with a diameter greater than 2 mm were excluded from the morphological analysis. The fine roots were placed on a scanner in a transparent tray (15 cm × 10 cm), filled with deionised water to allow root spreading. The roots were scanned at 400 dpi resolution; the program calculated architectural traits for all the fine roots altogether and in 0.2 mm diameter sections. Previous tests by Bauhus and Messier (1999b) using the same technique showed negligible errors for fine root morphological measurements through root overlapping. From the digitized images obtained, the following fine root morphological parameters were determined:

– mean root diameter (mm),
– total root length (cm),
– total root volume (cm^3),
– number of root tips,
– total projected area (cm^2),
– total surface area (cm^2).

After morphological analysis, the dry biomass of roots was determined by drying them at 65°C for at least 48 hours in air-forced dryer (ULE 600; Memmert GmbH+Co.KG, Germany) until weight constancy was reached. Root samples were weighted with 0.0001 g accuracy (BP 210 S Sartorius, Göttingen, Germany;). The dry biomass as well as root morphological features were used to compute variable root parameters. The following variables were calculated:

– specific fine root length (m g^{-1} root),
– fine root tips density (tips m^{-1} root length),
– specific fine root tips density (tips g^{-1} roots),
– specific fine root surface area (cm^2 g^{-1} root), characterizing absorbing area of a mass unit and
– specific fine root mass (g cm^{-2} root).

As we divided fine roots into 10 diameter classes (0–0.20, 0.21–0.40, …, 1.81–2.00 mm), we also calculated the percentage of fine root length and root tips number in particular root diameter classes.

Statistical analysis

The biomass and morphological data were analyzed by one-way analysis of variance (ANOVA, P>F) to determine differences in means among stands. Data presented as percentage values were transformed before analysis of variance according to the C. I. Bliss equation. If critical differences were found, multiple comparisons were carried out based on Tukey's honestly significant difference (HSD) test for equal sample sizes at $p<0.05$; in all cases a null hypothesis was rejected at the 5% level of significance ($\alpha=0.05$). Statistical analyses were performed using JMP 8.0 (SAS Institute Inc., Cary, NC, USA; http://www.sas.com/). All the data shown in tables are mean values ± standard error (SE).

Results

Our study revealed statistically significant differences among stands differing in age in fine roots biomass (*P<0.0001*), coarse roots biomass (*P=0.03*) and total live roots biomass (*P<0.0001*) on stand area basis (m^2; Table 2). Fine root biomass ranged from 0.78 to 3.11 Mg ha^{-1}, whereas coarse root biomass ranged from 0.82 to 2.74 Mg ha^{-1}. Fine, coarse and total live roots biomass (y) significantly depend on stand age (x); the relationships are as follows: $y=13.6215x+15.0929$ ($r^2=0.74$, *P=0.03*), $y=11.2543x+3.9826$ ($r^2=0.74$, *P=0.02*) and $y=24.8757x+19.0756$ ($r^2=0.83$, *p=0.02*), respectively. Fine root biomass in the oldest stand is ca. 4 times higher than in the youngest one, whereas coarse root biomass and total live root biomass is over three-fold higher. Taking into account all the stands studied, fine roots biomass equals on average 56.3% of total Scots pine live roots biomass in the upper 20 cm of soil. Fine roots to total live roots

biomass ratio ranged from 48.9% in the 6-year-old stand to 78.7% in the 15-year-old stand; the ratio is not dependent on stand age (r^2=0.003, *p=0.92*).

Dead root biomass (necromass) expressed per unit area (m^2) differed statistically significantly among stands (*p=0.04*; Table 2). When stand age increases dead root biomass linearly increases (r^2=0.88, *p=0.01*) from 103 g m^{-2} in the youngest stand to 287 g m^{-2} soil in the oldest stand. Dead root biomass is almost three-fold higher in the 20-year-old stand in comparison with the 6-year-old stand. We found no statistically significant differences among stands in dead to total root biomass ratio (biomass and necromass in total; *p=0.14*). Taking into account all the stands studied, dead roots biomass amounts on average to 35.3% of total live roots biomass found in the upper 20 cm of soil. Moreover, we found no statistically significant influence of stand age on live-to-dead

Table 2. The biomass and morphological traits of roots (means ± SE) harvested in the studied Scots pine stands differing in age. One-way ANOVAs were performed separately for the root traits studied to show significance of differences among stands. Same letters indicate a lack of statistically significant differences between analyzed stands according to Tukey's posteriori test (p<0.05)

Root trait	Stand age (years)						F	*P*
	6	9	11	15	17	20		
Fine root biomass (g m^{-2} soil)	78.12d	176.70bc	144.44cd	262.40ab	180.69bc	310.68a	15.1706	<0.0001
	(14.39)	(20.23)	(14.75)	(25.89)	(17.24)	(28.19)		
Coarse root biomass (g m^{-2} soil)	81.55b	99.77ab	148.13ab	145.64ab	152.82ab	273.82a	2.5669	0.0345
	(27.51)	(24.46)	(48.38)	(61.54)	(56.50)	(41.27)		
Total live root biomass (g m^{-2} soil)	159.68c	276.46bc	292.57bc	408.04ab	333.52bc	584.49a	7.9267	<0.0001
	(34.53)	(39.73)	(47.11)	(67.00)	(61.81)	(58.78)		
Root necromass (g m^{-2} soil)	103.19b	154.07ab	142.03ab	165.19ab	232.85ab	286.97a	2.4264	0.0438
	(12.87)	(18.75)	(25.60)	(24.81)	(59.74)	(66.85)		
Total live and dead root biomass (g m^{-2} soil)	262.87c	430.53bc	434.60bc	573.23b	566.36b	871.46a	9.6586	<0.0001
	(40.85)	(48.64)	(66.62)	(78.68)	(75.89)	(82.67)		
Live to dead root ratio	1.65	2.04	2.51	2.93	2.64	2.22	0.7360	0.5952
	(0.32)	(0.34)	(0.42)	(0.54)	(0.83)	(0.56)		
Root necromass proportion in total root biomass (%)	42.94	37.80	32.07	30.49	40.87	29.47	1.7353	0.1381
	(4.14)	(4.33)	(3.12)	(3.72)	(6.44)	(5.76)		
Fine root diameter (mm)	0.3787b	0.4193ab	0.3923b	0.3968b	0.3983b	0.4765a	6.4697	<0.0001
	(0.0176)	(0.0103)	(0.0124)	(0.0099)	(0.0112)	(0.0193)		
Fine root length (m m^{-2} soil)	1558c	2829abc	2241bc	3700a	2913ab	3735a	7.5341	<0.0001
	(230)	(342)	(183)	(342)	(361)	(317)		
Fine root projected area (m^2 m^{-2} soil)	0.5818d	1.1781bc	0.8792cd	1.4560ab	1.1272bc	1.7115a	11.1393	<0.0001
	(0.0796)	(0.1441)	(0.0794)	(0.1285)	(0.1127)	(0.1471)		
Fine root surface area (m^2 m^{-2} soil)	1.8279d	3.7013bc	2.7620cd	4.5743ab	3.5411bc	5.3767a	11.1393	<0.0001
	(0.2501)	(0.4526)	(0.2495)	(0.4038)	(0.3540)	(0.4620)		
Fine root volume (cm^3 m^{-2} soil)	175.3c	388.0b	273.6bc	455.7ab	346.7bc	632.3a	13.0474	<0.0001
	(27.1)	(50.3)	(29.4)	(40.1)	(29.1)	(63.4)		
No. of fine root tips (th. m^{-2} soil)	506.4c	1037.0ab	720.7bc	1223.7a	988.0abc	1186.4ab	5.8273	0.0002
	(78.5)	(122.0)	(68.3)	(132.8)	(140.2)	(116.0)		
Fine root tips density (tips m^{-1} fine root length)	324ab	374a	320b	325ab	332ab	314b	3.1280	0.0133
	(15)	(14)	(13)	(10)	(12)	(10)		
Specific fine root tips density (tips g^{-1} fine roots)	7135a	5955ab	5127bc	4666bc	5315b	3890c	10.5252	<0.0001
	(550)	(245)	(348)	(245)	(404)	(271)		
Specific fine root mass (g cm^{-2} fine roots)	0.00407c	0.00484bc	0.00520ab	0.00572a	0.00516ab	0.00579a	11.9781	<0.0001
	(0.00028)	(0.00017)	(0.00014)	(0.00019)	(0.00015)	(0.00015)		
Specific fine root area (cm^2 g^{-1} fine roots)	260.10a	209.66b	193.79b	176.94b	195.57b	174.50b	11.5457	<0.0001
	(19.49)	(7.71)	(5.14)	(5.58)	(5.44)	(4.58)		
Specific fine root length (m g^{-1} fine roots)	22.35a	16.04b	15.96bc	14.33bc	15.79bc	12.25c	14.1715	<0.0001
	(1.70)	(0.73)	(0.83)	(0.62)	(0.70)	(0.57)		

root biomass ratio ($p=0.60$); on average, live-to-dead root biomass ratio amounted to 2.32 (±0.22).

Stand age significantly influenced total root biomass expressed per unit area ($p<0.0001$; Table 2). When stand age (x) increases, total root biomass (y) linearly increases ($y=36.8169x+44.5546$; $r^2=0.89$, $p=0.005$). It is ca. three times higher in the 20-year-old stand than in the 6-year-old stand.

The stands differed not only in respect of fine root biomass in the upper layer of soil but also in the fine root morphology. The comparison of the stands showed striking differences in roots structural indices. Fine root diameter, length, projected area, surface area and volume were significantly affected by stand age ($p<0.0001$; Table 2). When stand age increases, fine root length ($y=133.9903x+1087.5881$; $r^2=0.70$, $p=0.04$), projected area ($y=0.0642x+0.3213$; $r^2=0.71$, $p=0.04$), surface area ($y=0.2016x+1.0093$; $r^2=0.71$, $p=0.04$) and fine roots volume ($y=24.6279x+58.4324$; $r^2=0.68$, $p=0.04$) expressed per unit area increase linearly. There was no statistically significant relationship between stand age and mean diameter of fine roots ($r^2=0.44$, $p=0.15$). Taking into account all the stands studied, mean fine roots diameter is 0.41 mm.

Total fine roots length per 1 m^2 soil ranged from 1.6 km in the 6-year-old stand to 3.7 km in the 20-year-old stand (Table 2). Most of them (85.8% on average) are fine roots with diameter not exceeding 0.6 mm. Stand age significantly influences the percentage of fine root length in total fine root length in 0.2 mm diameter classes (Table 3). Statistically significant relationships between stand age and proportion of fine root length were found for two classes, i.e. for roots with diameters ranging from 0.01 to 0.20 mm and from 0.41 to 0.60 mm. While stand age increases, the proportion of the length of fine roots with diameter not exceeding 0.2 mm in total fine root length linearly decreases ($r^2=0.91$, $p=0.003$), whereas the proportion of the length of fine roots with diameters from 0.41 to 0.60 mm in total fine root length linearly increases ($r^2=0.72$, $p=0.03$). For the remaining fine root diameter classes no statistically significant relationships were found among stand age and proportion of the length of fine roots in total fine root length, although increasing trends could have been noticed.

Number of fine root tips per 1 m^2 differed significantly among stands differing in age ($p=0.0002$; Table 2). In the youngest stand, ca. 500 thousand of root tips were found per 1 m^2 of soil, whereas in the oldest one – ca. 1200 thousand. We found no statistically significant relationship between stand age and number of root tips per 1 m^2; an increasing linear tendency ($r^2=0.58$, $p=0.08$) was noticed. However, we found statistically significant influence of stand age on fine

Table 3. Percentage of fine root length (%) in particular root diameter classes. One-way ANOVAs were performed separately for the root trait studied to show significance of differences among stands. Same letters indicate a lack of statistically significant differences between analyzed stands according to Tukey's posteriori test ($p<0.05$)

Root diameter class (mm)	Age (years)						F	*P*
	6	9	11	15	17	20		
0.01–0.20	30.85a	26.79ab	28.77ab	24.39bc	23.43bc	19.58c	8.1069	<0.0001
	(1.81)	(1.65)	(1.36)	(1.21)	(1.77)	(1.08)		
0.21–0.40	41.48ab	41.19ab	41.06ab	45.61a	45.19a	40.66b	3.9184	0.0035
	(1.05)	(1.41)	(0.91)	(1.30)	(0.91)	(1.06)		
0.41–0.60	16.47b	16.98b	15.90b	17.53ab	18.66ab	21.42a	4.3062	0.0018
	(1.18)	(0.89)	(1.15)	(0.76)	(1.45)	(0.72)		
0.61–0.80	4.14b	4.61ab	5.06ab	4.14b	4.30b	5.88a	4.4685	0.0014
	(0.36)	(0.31)	(0.42)	(0.29)	(0.39)	(0.30)		
0.81–1.00	3.19b	4.20ab	3.80ab	3.22b	3.33b	5.06a	4.1682	0.0023
	(0.49)	(0.26)	(0.34)	(0.33)	(0.41)	(0.39)		
1.01–1.20	1.74b	3.02a	2.54ab	2.30ab	2.43ab	3.38a	2.8541	0.0212
	(0.43)	(0.42)	(0.28)	(0.24)	(0.27)	(0.37)		
1.21–1.40	0.49b	1.06a	0.88ab	0.87ab	0.84ab	1.26a	3.1462	0.0129
	(0.13)	(0.20)	(0.14)	(0.12)	(0.15)	(0.14)		
1.41–1.60	0.47	0.74	0.63	0.56	0.66	0.96	2.0415	0.0835
	(0.14)	(0.15)	(0.15)	(0.07)	(0.14)	(0.10)		
1.61–1.80	0.39	0.40	0.41	0.37	0.32	0.68	2.1940	0.0647
	(0.13)	(0.06)	(0.15)	(0.06)	(0.06)	(0.09)		
1.81–2.00	0.08b	0.14ab	0.12ab	0.13ab	0.07b	0.21a	2.6652	0.0292
	(0.04)	(0.02)	(0.04)	(0.02)	(0.02)	(0.03)		

Table 4. Percentage of fine root tips number (%) in particular root diameter classes. One-way ANOVAs were performed separately for the root trait studied to show significance of differences among stands. Same letters indicate a lack of statistically significant differences between analyzed stands according to Tukey's posteriori test ($p<0.05$)

Root diameter class (mm)	Age (years)						F	*P*
	6	9	11	15	17	20		
0.01–0.20	62.89a	54.03bc	57.09ab	54.48bc	53.43bc	47.43c	7.8882	<0.0001
	(2.42)	(1.86)	(1.67)	(1.70)	(1.84)	(1.67)		
0.21–0.40	29.65c	36.50ab	33.82bc	37.02ab	37.14ab	39.71a	7.0945	<0.0001
	(1.31)	(1.52)	(1.23)	(1.51)	(1.12)	(1.24)		
0.41–0.60	5.26b	6.37ab	6.27ab	6.03b	6.62ab	8.80a	4.1635	0.0023
	(1.03)	(0.41)	(0.61)	(0.44)	(0.63)	(0.51)		
0.61–0.80	1.00b	1.13ab	1.19ab	1.05b	1.29ab	1.67a	3.2408	0.0110
	(0.22)	(0.11)	(0.16)	(0.09)	(0.17)	(0.11)		
0.81–1.00	0.72b	1.03ab	0.82ab	0.71b	0.78ab	1.23a	3.2076	0.0116
	(0.21)	(0.06)	(0.09)	(0.05)	(0.11)	(0.12)		
1.01–1.20	0.25b	0.51a	0.45a	0.35ab	0.39ab	0.62a	2.7788	0.0241
	(0.12)	(0.05)	(0.08)	(0.05)	(0.04)	(0.09)		
1.21–1.40	0.03b	0.16a	0.12ab	0.15a	0.12a	0.22a	3.2766	0.0103
	(0.02)	(0.03)	(0.03)	(0.04)	(0.03)	(0.05)		
1.41–1.60	0.07	0.11	0.14	0.06	0.11	0.16	1.5793	0.1775
	(0.05)	(0.02)	(0.03)	(0.02)	(0.03)	(0.03)		
1.61–1.80	0.04	0.06	0.07	0.06	0.06	0.11	0.9008	0.4857
	(0.02)	(0.03)	(0.03)	(0.02)	(0.01)	(0.03)		
1.81–2.00	0.02	0.03	0.01	0.02	0.02	0.03	0.2819	0.9215
	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)		

root tips density and specific fine root tips density. When all the stands studied were considered, the average number of 331 root tips per 1 m of fine root length and 5273 root tips per 1 g of fine root dry mass were observed. Ca. 97% of total root tips number were found on fine roots with diameters not exceeding 0.6 mm; 54.5%, 35.9% and 6.7% of total root tips were observed on the roots with diameters ranging from 0.01 to 0.20 mm, 0.21 to 0.40 mm, and 0.41 to 0.60 mm, respectively. We found statistically significant differences among most of the stands in percentage of the total root tips number in particular fine root diameter classes (Table 4). For only three diameter classes (i.e. from 1.41 to 2.0 mm) no differences among stands in percentage of tips number were found.

Our data show statistically significant influence of stand age on specific fine root mass, specific fine root area and specific fine root length (*P<0.0001*; Table 2). Along with an increase of stand age specific fine root biomass increases ($y=0.0001042x+0.0037729$; $r^2=0.75$, *P=0.03*), whereas specific root area ($y=-4.9942088x+266.68501$; $r^2=0.70$, *P=0.04*) and specific root length ($y=-0.5426497x+23.174433$; $r^2=0.71$, *P=0.03*) decrease.

Discussion

Our data support the hypothesis that stand age affects standing root biomass in the upper 20 cm of soil in the young Scots pine stand chronosequence. In the present study fine root biomass increased from 78 g m^{-2} in the 6-year-old stand to 311 g m^{-2} in the 20-year-old stand, whereas coarse root biomass increased from 82 to 274 g m^{-2} in the age range examined. Taking into account all the stands studied the mean fine root biomass of 199 g m^{-2} is lower than the mean values of 230 g m^{-2} reported for boreal forests and 500 g m^{-2} reported for temperate coniferous forests (Jackson et al. 1997).

According to Helmisaari et al. (2002), who studied a chronosequence of Scots pine stands in eastern Finland, fine root biomass amounted to 220, 357 and 259 g m^{-2} in 15-, 35-, and 100-year-old stands, respectively; the results are only slightly higher than our data for 15- and 20-year-old stands. The above mentioned authors found that fine root biomass was the highest at canopy closure in the pole stage stand (35-year-old). Our fine root biomass results also are in the same range as those reported for Scots pine by Vanninen and Mäkelä (1999), where fine root biomass varied between 118 and 412 g m^{-2} in

23–178-year-old Scots pine stands. The cited authors reported that the fine root biomass was not correlated with stand age in a poor *Calluna* type site, whereas in a more fertile *Myrtillus* type site they found either no relationship or fine root biomass decreased when stand age increased. Our data are also comparable to the fine root biomass range of 130–330 g m^{-2} reported by Oleksyn et al. (1999) for 12-year-old Scots pine stands consisting of 19 populations growing in a provenance experiment site in Poland.

The differences in fine root biomass between the studies cited may result from many causes, including different environmental conditions (e.g. climate, site) and stand characteristics. Moreover, the literature data on fine root biomass display considerable divergences being in part due to the different methods and sampling depth used to assess the biomass data (Jackson et al. 1997, Dauer et al. 2009). For example, Finér et al. (2007) found that fine root biomass ranged from 138 to 725 g m^{-2} (377 g m^{-2} on average) for 12–131-year-old Scots pine stands growing in the temperate zone and from 26 to 467 g m^{-2} (229 g m^{-2} on average) for 15–220-year-old Scots pine stands growing in the boreal zone. Moreover, fine root biomass was significantly higher in the temperate zone than in the boreal zone when calculated by stand area basis, whereas when the fine root biomass was calculated on the basis of stocking, there were no differences between zones in the mean fine root biomass per tree. Additionally, no significant differences in the fine root biomasses between different fertility classes in pine stands were found. Similarly to our results, the fine root biomass of pine stands studied by Finér et al. (2007) increased with stand age in the temperate zone whereas the fine root biomass per tree increased with stand age in pine stands both in temperate and boreal zone.

Even though the stands examined in the present study grow in a relatively harsh environment (degraded soil with low nutrient concentration and water deficit) typical of dumping grounds, resulting in slow tree growth and relatively high mortality of trees during the first years of stand development, the canopies tend to close around the 10th year of stand growth (Grochulski, pers. comm.). Our data revealed that the stand fine root biomass linearly increases along the increasing stand age, and fine root biomass in the oldest stand is ca. 4 times higher than in the youngest one. We also calculated fine root biomass per tree by dividing stand values by stem number. Mean fine root biomass per tree increased from 127 g in the 6-year-old stand to 624 g in the 20-year-old stand, and followed the same trajectory as stand fine root biomass (Fig. 1). The trajectory of fine root biomass changes found in our study illustrates well the changes of stand structure and development over years. As shown, fine root biomass generally increased with stand age and reached maximum value in the oldest studied, 20-year-old stand. The decreases of fine root biomass of older stands in comparison with younger stands (e.g. 11-year-old vs. 9-year-old and 17-year-old vs. 15-year-old) may reflect higher intra-specific competition due to tree overcrowding (Litton et al. 2003, Jagodziński and Oleksyn 2009a, 2009b, 2009c). As previously shown, when stand age increases, tree density decreases whereas the mean tree dimensions considerably increases (Jagodziński and Kałucka 2008). However, it cannot be excluded that these root biomass drops may result from locally less favourable soil conditions.

The trajectory of changes of mean fine root biomass per tree over age revealed in our study is similar to that showed by Børja et al. (2008), who found for *Picea abies* chronosequence (10-, 30-, 60-, and 120-year-old stands) that stand fine root biomass showed a peak in a 30-year-old stand (with density 2.5 and 5 times higher than the 60- and 120-year-old stands, respectively) and then decreases, whereas when expressed per individual tree, the fine root biomass increased with tree age. The cited results show that although individual older trees have more fine root biomass than younger ones, the fine root biomass for the whole stand decreases with age because tree density decreases; this suggests that tree density is an important factor influencing fine root biomass of the stand (Litton et al. 2003, Børja et al. 2008, Jagodziński and Oleksyn 2009b).

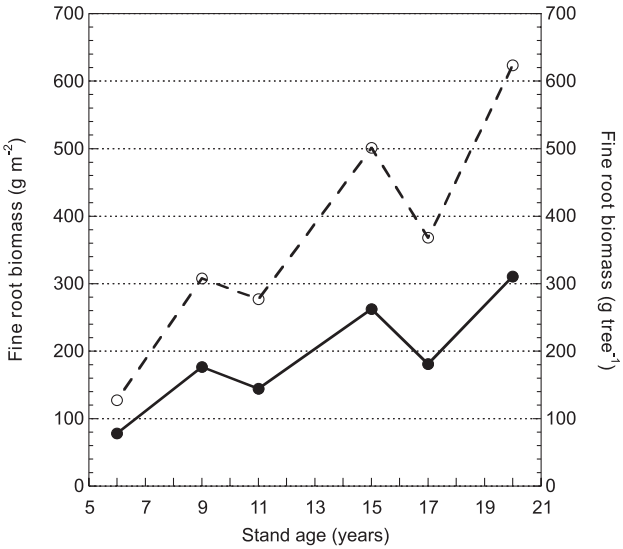

Fig. 1. Effect of stand age on fine root biomass (<2 mm) for each of the stands of Scots pine examined (solid line) compared with that for the average individual Scots pine tree (dashed line). The mean individual Scots pine tree fine root biomass was calculated by dividing the root biomass values for each stand per ha (from Table 2) by the number of trees in the stand per ha (Table 1)

We found that dead root biomass (necromass) differed significantly among stands differing in age, but the differences were significant only between the two outermost stands (6- and 20-year-old). When stand age increases dead root biomass linearly increases from 103 g m^{-2} in the youngest stand to 287 g m^{-2} of soil in the oldest stand. Our data revealed also no significant differences among stands in total live to dead root biomass ratio. For *Picea abies* chronosequence, Børja et al. (2008) found that stand age had significant effect on fine root biomass and the biomass/necromass ratio whereas it did not affect absolute values of necromass. In the cited study mean fine root biomass on the stand level was linearly correlated with age although variation was large in individual soil cores. In our study, the coefficients of variation (CV) were larger for coarse root biomass (mean CV = 107%) than fine root biomass (mean CV = 55%). Moreover, CV for fine root biomass was distinctly higher for the youngest stand (64%) in comparison with the older stands (mean CV = 35%). This suggests that richly branched network of Scots pine fine roots is more or less evenly distributed in the upper layer of the soil of forest stands studied, except the youngest stand. High fine root biomass variation between samples (cores) was also found by other authors, e.g. by Persson (1978) in 15–20 years old Scots pine stands. Taking into account all the stands growing on the lignite mine spoil heap examined, dead root biomass amounts on average to 35.3% of total root biomass found in the upper 20 cm of soil.

The stands studied differed not only in respect of fine root biomass in the upper layer of soil but also in the fine root morphology; our data revealed significant differences among stands in all the fine root morphological indices analyzed. When stand age increases, fine root length, projected area, surface area and volume expressed per unit area (m^2) increases linearly. In comparison with fine root biomass, their length and surface area are more important in explaining soil resource exploitation of trees. For example, specific root length (SRL) is often used as a measure of the ability of roots to proliferate in the soil and of space sequestration efficiency of competing trees. The stand absorptive potential may be also described by the analysis of root surface area and root tip density (Eissenstat 1992, Eissenstat et al. 2000). Exploitation efficiency of trees may increase with the rise of absorbing root surface area and root length per unit biomass (Bauhus and Messier 1999a, Leuschner et al. 2004). In our study specific fine root length decreased from 22.4 m g^{-1} in the youngest stand to 12.3 m g^{-1} in the oldest stand and specific fine root area decreased from 206.1 cm^2 g^{-1} to 174.5 cm^2 g^{-1}, respectively. Significantly higher specific root length and specific root surface area were found for the youngest stands in comparison with the remaining stands; for the 9-year-old stand and older stands both traits studied were fairly similar. Specific fine root tips density was also the highest for the youngest stands. According to Ostonen et al. (2007), specific root length is the highest for ectomycorrhizal (ECM) short roots (roots of mostly first and second order, tips regarded as first order), which are functionally responsible for nutrient and water uptake. Mycorrhizal activity of trees growing in the youngest stand seem to be very high resulting in efficient exploitation of nutrient and water resources.

Similarly to the chronosequence of Japanese cedar (Fujimaki et al. 2007), our study showed high variation in SRL among stands. Specific root length reflects biomass allocation to root elongation, thus its variation may be interpreted as the pattern of soil exploitation by fine roots. The highest SRL in the youngest stand, where trees were relatively small and roots were sparse despite high stand density, may indicate active soil penetration by fast growing roots. In aging stands, SRL seemed to decrease with an increase in fine root length per m^2 soil suggesting that fine root development may be related to density-dependent processes (Litton et al. 2003, Jagodziński and Oleksyn 2009b). Changes in specific root area are probably a way for plants to respond to changes in environmental conditions (Lõhmus et al. 1989). Ostoten et al. (1999) stated that root density and specific fine root area are connected with physiological activity of fine roots. When assuming that the nutrient and water acquisition changes proportionally to root length it may be expected that roots with higher SRL might be more efficient in nutrient and water uptake from the soil. However, it should be kept in mind that short root morphology (also specific root length and specific root area, root length and diameter) is primarily shaped by ECM fungus species (van der Heijden and Kuyper 2003, Ostonen et al. 2009), which indicates that the type of mycobiont and ECM fungal succession has an important influence on the functional properties of fine roots.

In our study, stand age significantly influenced total number of fine root tips, fine root tips density and specific fine root tips density. The specific fine root tips density diminished with increasing stand age and ranged from 7100 tips g^{-1} in the 6-year-old stand to 3900 tips g^{-1} in the 20-year-old stand. As the diameter of fine roots did not differ statistically except for the oldest stand and fine root tips density varied only very slightly, it seems that decreasing specific fine root tips density may result from increasing density of root tissue (cf. Ostonen et al. 2007). In mature stands of Scots pine in Finland, ECM short root tip frequency (no. per milligram of fine roots of diameter <1 mm) varied between 7 and 12 mg^{-1} (Helmisaari et al. 2009). ECM root tip number in that study was estimated at 687–2866 thousand m^{-2}, which is compara-

ble to our results. Ectomycorrhizal short root tips accounted for 28% of the biomass of fine roots with diameter <2 mm and 50% of the biomass of fine roots with diameter <1 mm (Helmisaari et al. 2007). According to Børja et al. (2008) stand age has no effect on root tip density for any root fraction with means of about 2 tips cm^{-1} root length. Fine root tips density examined in the present study equaled 314–374 m^{-1} root length and was lower than ECM tips density (ramification index) in naturally regenerating pine stands in post-arable land in NE Poland (490–510 and 710–920 m^{-1} depending on year; Kałucka 2009), comparable to the one found in Scots pine stands situated in a zone of low air pollution (270–380 m^{-1}) and higher than ECM root tips density in the stands suffering from industrial emissions in Poland (130–220 m^{-1}; Józefaciukowa et al. 1995). According to Meyer (1987) ECM ramification index is an indication of the fine root vitality.

In conclusion, fine root biomass and morphology changes, which occur during stand development within the most dynamic stage of stand growth, may be closely connected with increasing demands of trees for water and nutrient uptake. The plasticity of fine root biomass and morphology considered as a function of stand age may be a plant strategy leading to more efficient soil exploitation by roots.

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