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Fine root biomass and morphology in an age-sequence of post-agricultural *Pinus sylvestris* L. stands

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Abstract: The purpose of this study was to examine how stand age affects fine root biomass and morphology in different stages of first generation Scots pine forest development in post-agricultural fields. Stands of different ages (6-, 10-, 16-, 28-, and 47-yr-old) were studied at the same time to provide data on biometrical fine root features, i.e. biomass, length, surface area, volume, number of tips, root tip density, specific root tip density, specific root area, specific root length and fine root tissue density. Soil cores from the upper 20 cm of soil were used for the study. The results of the study show that fine root characteristics did significantly differ among stands of different age. Fine root biomass ranged from 0.9 Mg ha^{-1} (6-yr-old stand) to 2.3 Mg ha^{-1} (47-yr-old stand), whereas coarse root biomass ranged from 0.2 Mg ha^{-1} to 3.2 Mg ha^{-1}, respectively. Fine root biomass in the older stands (10–47-yr-old) remains constant and is ca. 4 times higher than in the youngest stand (6-yrs-old). This shows that the fine root biomass of Scots pine in the upper soil horizons reached a constant biomass at a younger stand age than found in previously published papers, although at the same stage of stand development, i.e. canopy closure. Fine root length, surface area and volume expressed on per stand area basis were significantly different among stands; the highest values were found in the 10-yr-old stand, during the time of canopy closure. This means that stand age (i.e. age of trees in pure even-aged monocultures) is not a major factor influencing the fine root dynamics, instead stage of development and other stand and habitat characteristics may play an important role. Moreover, we found significant linear relationships among stand age and fine root length, surface area and number of fine root tips expressed on a per tree basis. Our study showed that stand age affects both fine root biomass and morphology in Scots pine forests when growing on post-agricultural fields. The differences revealed in our study indicate high plasticity of Scots pine fine roots in response to stand changes over age.

Additional key words: Scots pine; basal area; root biomass; specific fine root length; specific fine root tip density; specific fine root area; fine root tissue density.

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Introduction

Fine roots play a key role in regulation of biogeochemical cycles in forest ecosystems, especially of macro- and microelement accumulation in the soil. They are also of major importance for meeting tree requirements for water and nutrients via continuous exploitation of new soil volumes and symbiotic associations with mycorrhizal fungi. Results of many studies have shown that fine root biomass depends on a wide range of both abiotic and biotic factors, such as soil properties (texture, chemistry, moisture, nutrient availability), climatic conditions (annual temperature, precipitation, geographical location and elevation), and stand characteristics (tree species, stand age, stand density, basal area, and intra- and interspecific competition between plants) (Leuschner et al. 2004; Majdi et al. 2005; Dauer et al. 2009; Jagodziński and Oleksyn 2009a, 2009b, 2009c; Farfał 2010; Jagodziński and Kałucka 2010; Yuan and Chen 2010; Finér et al. 2011). Moreover, studies have also shown that the factors mentioned above control, at least partly, the timing and duration of tree root growth and decomposition (Norby and Jackson 2000; Hobbie et al. 2010; Goebel et al. 2011). Fine root biomass as well as production, turnover rates and nutrient content depend strongly on both climatic and site variables, as concluded by Yuan and Chen (2010) based on a large dataset for boreal forest ecosystems.

Although the functions of fine roots in forest ecosystems are well known, the existing knowledge of the fine root dynamics is much more deficient in comparison with that of aboveground parts of trees (Yuan and Chen 2010). The majority of investigations have focused on the aboveground biomass and stand structure changes with stand age, whereas there are fewer studies of how stand age affects patterns of fine root biomass development and even more rarely – fine root morphology (Vanninen et al. 1996; Helmisaari and Hallbäcken 1999; Makkonen and Helmisaari 2001; Claus and George 2005; Børja et al. 2008; Jagodziński and Kałucka 2008, 2010). The studies concerning changes of fine root biomass in sequences of tree stands differing in age show more or less similar patterns. The biomass can be significantly higher in younger stands than in older stands as was revealed for *Fagus sylvatica* chronosequences by Bakker et al. (2008; 9-, 26- versus 82-, and 146-year-old stands) and Claus and George (2005; 15-, 30 versus 62-, and 111-year-old stands). Similar patterns in fine root biomass were also shown for *Pseudotsuga menziesii*, *Pinus sylvestris*, and *Cryptomeria japonica*, where fine root biomass increased to a peak at canopy closure and progressively decreased in maturing stands (Vogt et al. 1987; Vanninen and Mäkelä 1999; Fujimaki et al. 2007). In a *Picea abies* chronosequence, Claus and George (2005) found that stand age had a significant effect on standing fine root biomass with the highest values observed in the youngest stands. The reverse pattern was reported by Persson (1983) who compared *Pinus sylvestris* stands that were 20 and 120 years old and found that fine root biomass was higher in the older stand. On the other hand, according to the meta analysis by Yuan and Chen (2010) based on a large dataset of root studies in boreal forests, fine root biomass in Scots pine stands increased until the age of ca. 100 years and then remained constant or decreased thereafter. Vogt et al. (1987) suggested that changes of fine root biomass in ageing stands were related to above-ground biomass dynamics and changes of stand structure, thus with the trajectory of stand development. The changes of fine root biomass may be a result of biomass accumulation in developing stands in the soil organic horizons. Grier et al. (1981) and Yuan and Chen (2010) stated that as a stand ages, increased amounts of root detritus and other organic material enrich the soil in nutrients, and that nutrient input makes the upper soil horizons more conducive to further root growth and development.

Knowledge of stand age-related changes of fine root morphology is more scarce than that about fine root biomass. Root systems show a high degree of plasticity in their growth and development as a response to many ecological variables, e.g. site fertility (Helmisaari et al. 2007; Ostonen et al. 2007), stand developmental stage (Vogt et al. 1983; Vanninen et al. 1996; Vaninen and Mäkelä 1999; Helmisaari et al. 2002), and interactions among trees in mixed stands (Schmid and Kazda 2001; Schmid 2002; Curt and Prévosto 2003; Bolte and Villanueva 2006). Morphological adaptations of fine roots to environmental conditions enable trees to grow even in harsh soil habitats (Ostonen et al. 2006, 2007; Jagodziński and Kałucka 2010). Fine root biomass and fine root morphology examined together may show the competitive ability of trees below ground.

The objective of this study was to examine how stand age affects fine root biomass and morphology in an age-sequence of first generation Scots pine stands growing on post agricultural fields. We hypothesized that root biomass and morphology would vary between stands of different ages. This expectation is partly based on the results of our previous study (Jagodziński and Kałucka 2010), conducted in an age sequence of six pure Scots pine stands (6–20 yrs old) growing on a reclaimed lignite mine spoil heap (situated in close vicinity to the sites studied in the present research), that has shown that with stand ageing fine root biomass and morphology changes considerably. For example fine root length and surface area expressed per stand unit area in-

creased significantly with stand age. Moreover, the cited study revealed that when stand age increased, specific fine root biomass increased, whereas specific root length and area decreased. Because the previously studied stands were growing on highly degraded habitats (mine activity), it can be assumed that the observed changes in fine root biomass and morphology over stand age might result from the specificity of the analyzed habitats. Thus, we situated a similar set of study plots on post-agricultural forests growing on less degraded sites (previous agricultural activity). To estimate changes in fine root biomass and morphology in different stages of stand development, Scots pine stands varying in age but growing on similar habitats were simultaneously studied.

Material and methods

Study site

The study was conducted at the Bełchatów Forest District, situated in Bełchatów Plain, in Central Poland, at an altitude of ca. 200 m above sea level. Scots pine (*Pinus sylvestris* L.) stands were 6, 10, 16, 28, and 47 years old, each age represented by two replicate plots (500 m^2 each for the youngest stand, and 1000 m^2 for each of the remaining stands). All of the stands were planted as first generation stands on post-agricultural sites on sandy soils (podzol with ploughed horizon according to FAO World Soil Classification; Table 1). The initial density of the monocultural stands was ca. 12000 trees per hectare (initial spacing – 1.5 m × 0.6 m). The stands can be classified as

Table 1. Soil features in the post-agricultural Scots pine stands examined (podzol with ploughed horizon according to FAO World Soil Classification)

Stand age (years)	Soil horizon	Soil depth (cm)	Soil water content (% vol.)	Bulk density (g cm^{-3})	Silt d 0.05–0.002 mm (%)	pH in water	pH in KCl	$Carbon_{org}$ (%)	Nitrogen (%)	C/N
6	Ap	0–30	14.5	1.49	10	6.3	5.7	1.02	0.077	13
	Cg	30–90	10.8	1.54	5	6.3	5.3	–	–	–
10	Ol	1–0	–	–	–	5.0	4.5	54.10	1.090	50
	Ap	0–15	7.7	1.44	8	4.9	4.2	0.84	0.056	15
	Bv	15–50	7.1	1.45	4	5.1	4.6	0.21	0.016	13
10	Ol	1–0	–	–	–	5.1	4.8	54.30	1.590	34
	Ap	0–13	8.5	1.45	5	4.8	4.5	1.37	0.100	14
	Bv	13–45	5.0	1.57	3	4.8	4.6	0.10	0.010	10
16	Ol	1–0	–	–	–	5.3	4.7	51.80	1.440	36
	Ap	0–23	14.3	1.39	10	5.9	5.2	1.65	0.125	13
	C	23–60	5.7	1.64	8	5.9	4.8	–	–	–
16	Ol	1–0	–	–	–	5.3	4.8	54.60	1.250	44
	Ap	0–36	9.6	1.48	9	6.1	5.3	1.31	0.085	15
	Bv	36–55	4.9	1.61	2	5.5	4.7	0.08	0.007	11
28	Ol	2–1.5	–	–	–	4.5	4.1	55.80	0.964	58
	Of	1.5–0	–	–	–	4.1	3.3	44.20	1.430	31
	Ap	0–20	10.0	1.41	9	4.5	3.8	1.00	0.052	19
	Bv	20–45	7.7	1.46	5	4.8	4.5	0.21	0.015	14
28	Ol	1.5–1.0	–	–	–	4.5	4.1	56.20	0.920	61
	Of	1.0–0	–	–	–	4.9	4.1	35.00	1.130	31
	Ap	0–20	8.4	1.40	11	4.7	4.3	0.52	0.026	20
	Bv	20–70	7.9	1.51	11	4.7	4.5	0.17	0.010	17
47	Ol	5.0–4.5	–	–	–	4.4	3.8	57.00	0.829	69
	Of(h)	4.5–0	–	–	–	3.9	3.1	52.70	1.210	44
	Ap	0–10	5.8	1.55	1	4.7	4.1	0.53	0.022	24
	Bv	10–30	5.8	1.58	2	4.9	4.7	0.14	0.010	14
47	Ol	3.0–2.5	–	–	–	4.3	3.7	56.00	0.802	70
	Of(h)	2.5–0	–	–	–	3.9	3.1	48.90	1.410	35
	Ap	0–15	9.0	1.44	5	4.9	4.4	0.85	0.033	26
	Bv	15–50	7.2	1.43	4	4.7	4.5	0.15	0.010	15

mesophilous fresh pine forest with occasional presence of birch (*Betula pendula* Roth), oak (*Quercus robur* L., *Q. rubra* L.) and larch (*Larix decidua* Mill.; in younger stands only).

Long-term meteorological observations (1971–2000) from the closest meteorological station (65 km, Łódź), showed that the mean annual temperature of the study site 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 2005, we measured diameters at breast height and heights of trees in all the plots examined. Selected stand characteristics are presented in Table 2.

Root biomass was estimated by soil core sampling. Twelve randomly selected cores per plot were collected in September 2005 (24 samples per stand age). A cylindrical tube 4.7 cm in diameter and 20 cm long with a sharp edge to cut roots was used as the soil corer (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 with roots were placed in plastic bags and stored in a refrigerator (4°C) during sample collection in the field. After being transported to the laboratory they were stored in a cooling chamber (–3°C) until sample preparation. Roots from different soil horizons were not separated.

In the laboratory, the roots were manually sorted 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 three classes: (1) fine roots (≤2 mm diameter), (2) coarse roots (>2 mm diameter) and (3) dead roots. Dead roots of Scots pine were separated form live roots based on vitality assessment using morphological criteria such as: elasticity of particular root segments, root structure (e.g. the degree of cohesion between the cortex and periderm) and root color of the central cylinder (Vogt and Persson 1991; Bauhus and Messier 1999a). The dead root biomass was omitted in the further analysis due to considerable contamination of the roots by sand particles. The roots of plants other than Scots pine (i.e. herbaceous species) were not examined.

Fine root morphology was assessed using the digital image analysis software WinRhizo V3.10 (version 2003a,b; Regent Instruments Inc., Quebek, Canada;

Table 2. Characteristics of the Scots pine stands varying in age (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)	Location	Stand density (trees ha^{-1})		DBH (cm)		Height (m)		Basal Area (m^2 ha^{-1})	
6	51°18'00"N, 19°23'50"E	12700 (700)	A	1.43 (0.13)	D	1.59 (0.16)	E	1.79 (0.44)	C
10	51°18'14"N, 19°25'38"E; 51°14'06"N, 19°27'10"E	3890 (150)	BC	6.48 (0.07)	C	4.35 (0.02)	D	13.92 (0.21)	BC
16	51°12'53"N, 19°22'39"E; 51°13'03"N, 19°22'44"E	5155 (225)	B	7.01 (0.40)	C	7.09 (0.21)	C	22.07 (1.23)	AB
28	51°11'06"N, 19°23'34"E; 51°14'59"N, 19°26'26"E	1914 (453)	CD	13.35 (0.78)	B	13.77 (0.18)	B	27.47 (3.20)	A
47	51°16'35"N, 19°26'22"E; 51°11'04"N, 19°23'43"E	1092 (68)	D	18.00 (0.50)	A	16.35 (0.14)	A	29.14 (3.40)	A
ANOVA P>F		F	P	F	P	F	P	F	P
		138.0	<0.0001	202.0	<0.0001	1582.3	<0.0001	26.9	0.0014

http://regentinstruments.com) and an 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 in grey scale at 400 dpi resolution with a filter of 1 mm^2; the program calculated architectural traits for all the fine roots altogether and in 0.2 mm diameter sections. The tests by Bauhus and Messier (1999b) using the same technique showed negligible errors in fine root morphological measurements due to the root overlapping. The digitized root images allowed determination of the following fine root morphological parameters:

- mean root diameter (mm),
- total root length (m m^{-2} of soil),
- total root surface area (m^2 m^{-2} of soil),
- total root volume (cm^3 m^{-2} of soil),
- number of root tips (no. m^{-2} of soil).

Because the number of root tips measured by WinRhizo may be overestimated as the program counts cut roots as tips also, we counted tips and cut roots for three samples of fine roots for each stand under the microscope to calibrate the results obtained by WhinRhizo.

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 constant weight. Root samples were weighed with 0.0001 g accuracy (BP 210 S Sartorius, Göttingen, Germany; http://sartorius.dataweigh.com). Dry root biomass as well as root morphological features were used to calculate the following root parameters:

- fine root tip density (tips m^{-1} root length),
- specific fine root tip density (tips g^{-1} roots),
- specific fine root surface area (cm^2 g^{-1} roots),
- specific fine root length (m g^{-1} roots),
- fine root tissue density (g cm^{-3} fine roots).

Fine root biomass, length, surface area and tips number were also calculated at the tree level by dividing the parameters at the stand level (Table 3) by the stand density shown in Table 2.

When the fine roots (≤2 mm diameter) were scanned and analyzed by the WinRhizo technique, the programe divided the fine roots into 10 diameter classes (0–0.20, 0.21–0.40, …, 1.81–2.00 mm). We used these data to calculate the percentage of fine root length and root tip number in particular root diameter classes among fine roots.

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 differing in age. Data presented as percentage values were transformed before analysis of variance according to the C. I. Bliss equation. If significant differences were found, multiple comparisons were carried out based on Tukey's test (HSD) for equal sample sizes at $p<0.05$; in all cases a null hypothesis was rejected at the 5% level of significance ($\alpha=0.05$). The data were also analyzed using regression analysis for examining relationships between stand age and root biomass and particular morphological features (both expressed on a stand area basis and tree basis). Statistical tests and analyses were performed using JMP 8.0 software (SAS Institute Inc., Cary, NC, USA; http://www.sas.com). All the data shown in tables are mean values ± standard error (SE).

Results

Root biomass

Our study revealed statistically significant differences among stands differing in age of fine root biomass ($p<0.0001$), coarse root biomass ($p=0.0009$) and total live root biomass ($p<0.0001$) on a stand area basis (m^{-2}; Table 3). Fine root biomass in the upper 20 cm of soil ranged in the stand chronosequence studied from 0.91 to 2.33 Mg ha^{-1}, coarse root biomass ranged from 0.23 to 3.15 Mg ha^{-1}, and total live root biomass ranged from 1.14 to 5.48 Mg ha^{-1}. Fine root biomass in the older stands (10–47 yrs old) remained constant; the mean value for these stands was ca. 4 times higher than in the youngest one (6-year-old). Mean coarse and total live root biomass expressed on stand area basis (m^2) increased linearly with stand age (Fig. 1). In comparison with the youngest stand, the coarse root biomass in the oldest stand (47-year-old) was ca. 13 times higher, and the total live root biomass was almost five-fold higher. Taking into account all the stands studied, fine root biomass equaled, on average, 63% of total Scots pine live root biomass in the upper 20 cm of soil. The biomass proportion of fine roots to total live roots (fine and coarse) ranged from 80% in the 6-year-old stand to 43% in the 47-year-old stand and linearly diminished over stand age (Fig. 1).

Fine root morphology

The stands differed not only with respect to fine root biomass but also in fine root morphology in the upper layer of soil. Comparison among the stands showed striking differences in root structural indices. There were statistically significant differences among stands in mean fine root diameter (all roots with diameter ≤2 mm pooled together) – the thinnest fine roots were found in 6-year-old stands (mean value: 0.55 mm), whereas the thickest ones were in the 47-year-old stands (0.66 mm); the mean fine root di-

Table 3. The biomass and morphological traits of roots (≤2 mm diameter; means ± SE) harvested in the 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		10		16		28		47			
Fine root biomass (g m^{-2} soil)	91.20 (11.19)	B	245.72 (16.92)	A	186.09 (21.46)	A	255.83 (31.29)	A	233.15 (16.61)	A	9.43	<0.0001
Coarse root biomass (g m^{-2} soil)	23.29 (13.52)	B	87.50 (29.53)	B	93.94 (27.50)	B	213.30 (52.36)	AB	314.70 (73.13)	B	5.24	0.0009
Total live root biomass (g m^{-2} soil)	114.49 (16.44)	C	333.22 (34.33)	BC	280.03 (44.77)	BC	469.13 (49.41)	AB	547.85 (77.92)	A	7.89	<0.0001
Fine root diameter (mm)	0.55 (0.02)	C	0.57 (0.02)	BC	0.65 (0.02)	AB	0.64 (0.02)	ABC	0.66 (0.02)	A	6.12	0.0002
Fine root length (m m^{-2} soil)	1265 (141)	C	3625 (292)	A	1716 (256)	BC	2531 (277)	B	2016 (110)	BC	15.83	<0.0001
Fine root surface area (m^2 m^{-2} soil)	2.20 (0.27)	C	6.38 (0.52)	A	3.40 (0.44)	BC	5.08 (0.58)	AB	4.10 (0.24)	B	12.86	<0.0001
Fine root volume (cm^3 m^{-2} soil)	310.0 (44.2)	C	913.2 (84.6)	A	544.7 (63.7)	BC	819.4 (103.9)	AB	675.7 (45.4)	AB	9.15	<0.0001
No. of fine root tips ($\times 10^3$ m^{-2} soil)	382.5 (48.8)	B	913.3 (83.8)	A	312.3 (49.4)	B	444.4 (51.7)	B	334.2 (18.9)	B	20.57	<0.0001
Fine root tip density (tips m^{-1} fine root length)	294 (11)	A	248 (9)	B	181 (5)	C	175 (5)	C	166 (4)	C	44.27	<0.0001
Specific fine root tip density (tips g^{-1} fine roots)	4371 (434)	A	3788 (313)	A	1642 (132)	B	1805 (124)	B	1572 (117)	B	24.55	<0.0001
Specific fine root area (cm^2 g^{-1} fine roots)	248.69 (15.87)	AB	258.21 (8.95)	A	181.34 (9.73)	C	204.25 (10.24)	BC	185.55 (8.70)	C	12.72	<0.0001
Specific fine root length (m g^{-1} fine roots)	14.81 (1.30)	A	14.99 (0.87)	A	9.01 (0.59)	B	10.35 (0.72)	B	9.33 (0.58)	B	12.97	<0.0001
Fine root tissue density (g cm^{-3} fine roots)	0.31 (0.02)	AB	0.28 (0.01)	B	0.35 (0.02)	A	0.31 (0.01)	AB	0.35 (0.01)	A	5.24	0.0009

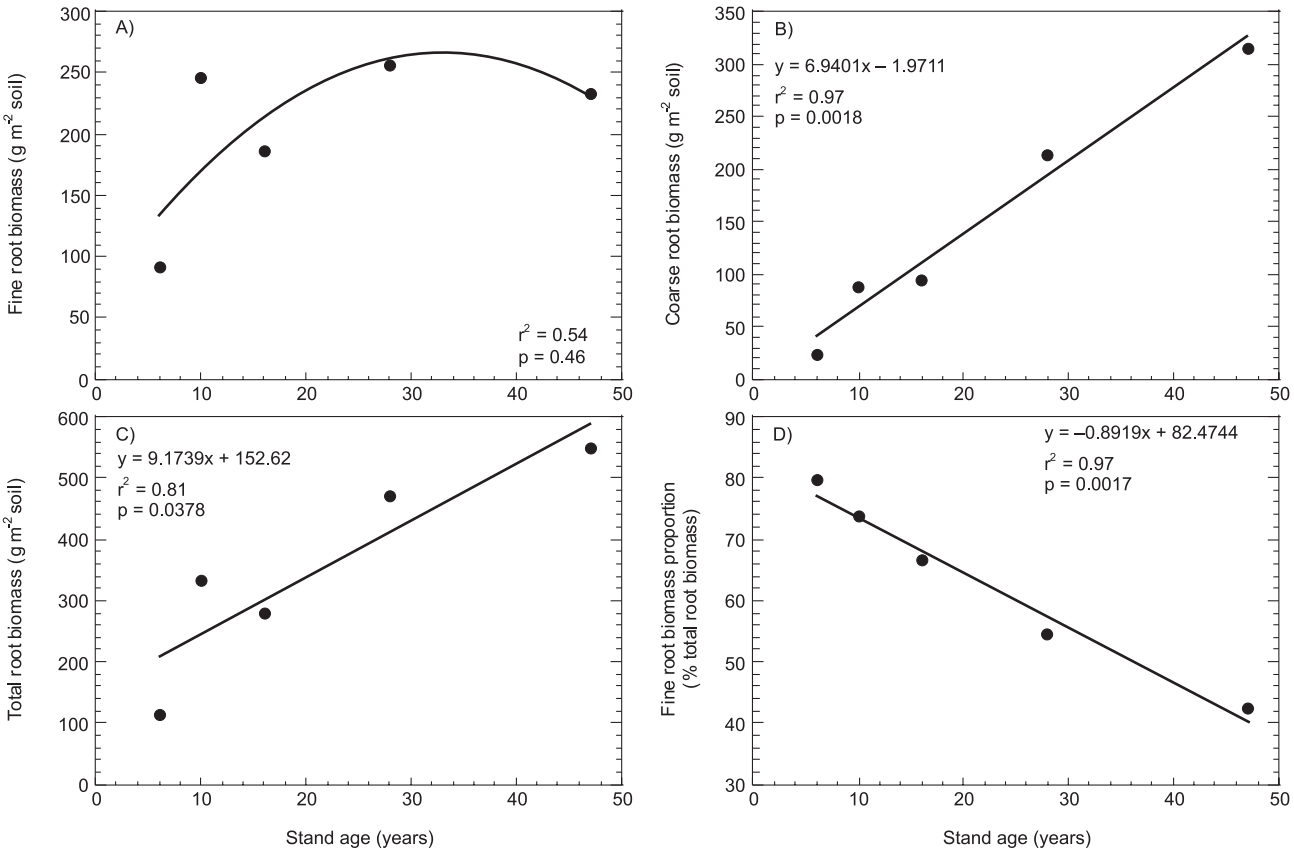

Fig. 1. Effect of stand age on fine (A), coarse (B) and total root biomass (C; g m^{-2} soil) and fine root biomass proportion in total root biomass (D; %)

ameter in the oldest stand was 20% higher than in the youngest one. Fine root length, surface area and volume expressed on a per stand area basis (m^2) were significantly different among stands (*p<0.0001*; Table 3). The highest mean values of fine root length, surface area and volume were found in 10-year-old stands.

Total fine root length per 1 m^2 of soil ranged from 1.3 km in the 6-year-old stand to 2.0 km in the 47-year-old stand; however, as mentioned above, the highest fine root length was found in 10-year-old stand (Table 3). Taking into account ten 0.2 mm diameter classes of fine roots, we found that most of them (67% on average) were fine roots with diameter not exceeding 0.6 mm, whereas fine roots with diameter less than 1 mm amounted on average to 86% of total fine root length in the stands studied. The percentage of fine root length in 0.2 mm diameter classes differed significantly among stands (Table 4). For example, the thinnest roots (≤0.2 mm diameter) were the most frequent in the 10 year old stand (36.6% of total length of fine roots), less frequent and on more or less a constant level in the older stands (16–47-yrs-old; ca. 24% of total length of fine roots) and the least frequent in the youngest stand (12.4% of total length of fine roots).

The number of fine root tips per 1 m^2 of soil differed significantly among stands of different age (*p<0.0001*; Table 3). The highest number of fine root tips was found in the 10 year old stand (913000 tips m^{-2} soil) and this value was significantly different than the values obtained for the remaining stands (mean value: 368000 tips m^{-2} soil). Taking into account fine root tips in 0.2 mm diameter classes, we found that 88% of all root tips were found on fine roots with diameters not exceeding 0.6 mm; 49%, 25% and 15% of 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 (Table 5). We noticed statistically significant differences among stands in percentages of root tips in all fine root diameter classes (Table 5).

Our data revealed statistically significant differences among stands studied in fine root tip density (Table 3). When all the stands were considered, the average number of 213 root tips per 1 m of fine roots was observed. Fine root tip density diminished when stand age increased from 294 tips m^{-1} fine root length (the youngest stand) to 166 tips m^{-1} fine root length (the oldest stand). Moreover, the stands studied differed significantly in specific fine root tip density, specific fine root area and specific fine root length (Table 3). For example, the highest values of specific fine root tip density was found in the younger stands (6 and 10 years old) and the mean specific fine root tip density for both of these stands (4080 tips g^{-1} fine

Table 4. Percentage of fine root length (≤2 mm diameter; %) 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)	Percentage of fine root length (%)										F	P
	6-yr-old stand		10-yr-old stand		16-yr-old stand		28-yr-old stand		47-yr-old stand			
0.01–0.20	12.4 (1.0)	C	33.6 (2.0)	A	24.8 (1.9)	B	24.2 (1.2)	B	22.9 (1.0)	B	22.34	<0.0001
0.21–0.40	37.3 (2.5)	A	20.0 (1.9)	B	13.8 (0.7)	C	15.6 (0.7)	BC	12.3 (0.5)	C	35.68	<0.0001
0.41–0.60	26.4 (0.9)	A	20.1 (0.8)	B	23.8 (0.9)	A	25.6 (0.7)	A	24.2 (0.5)	A	12.53	<0.0001
0.61–0.80	7.7 (0.7)	B	10.0 (0.7)	B	16.2 (0.9)	A	15.8 (0.8)	A	17.7 (0.5)	A	37.27	<0.0001
0.81–1.00	6.4 (0.8)	A	3.9 (0.3)	C	4.6 (0.3)	ABC	4.3 (0.4)	BC	5.2 (0.2)	AB	6.37	0.0002
1.01–1.20	4.6 (0.5)	C	7.1 (0.6)	B	10.9 (0.8)	A	8.9 (0.7)	AB	11.6 (0.7)	A	19.04	<0.0001
1.21–1.40	1.9 (0.2)		2.2 (0.2)		2.7 (0.3)		2.6 (0.2)		2.6 (0.2)		2.22	0.0747
1.41–1.60	1.6 (0.2)	A	1.0 (0.1)	B	0.9 (0.1)	B	0.9 (0.1)	B	1.1 (0.1)	AB	3.57	0.0100
1.61–1.80	1.2 (0.2)		1.3 (0.1)		1.5 (0.2)		1.4 (0.2)		1.5 (0.2)		0.65	0.6285
1.81–2.00	0.4 (0.1)		0.9 (0.1)		0.9 (0.1)		0.8 (0.1)		0.8 (0.1)		3.31	0.0147

Table 5. Percentage of fine root tips (≤2 mm diameter; %) 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)	Percentage of fine root tips (%)										F	P
	6-yr-old stand		10-yr-old stand		16-yr-old stand		28-yr-old stand		47-yr-old stand			
0.01–0.20	33.1 (2.2)	C	59.4 (2.2)	A	51.5 (2.1)	AB	47.9 (1.6)	B	52.0 (1.2)	B	22.10	<0.0001
0.21–0.40	46.0 (1.2)	A	22.7 (2.1)	B	19.3 (0.5)	BC	21.4 (1.0)	BC	16.1 (0.5)	C	49.52	<0.0001
0.41–0.60	13.6 (1.1)	A	10.5 (0.6)	B	15.6 (1.0)	A	17.0 (0.5)	A	15.8 (0.5)	A	14.82	<0.0001
0.61–0.80	2.4 (0.3)	B	3.7 (0.4)	B	7.0 (0.6)	A	7.4 (0.4)	A	8.5 (0.4)	A	40.00	<0.0001
0.81–1.00	2.1 (0.3)	A	1.0 (0.1)	C	1.2 (0.2)	BC	1.4 (0.1)	ABC	1.7 (0.2)	AB	7.36	<0.0001
1.01–1.20	1.6 (0.2)	B	1.8 (0.2)	B	3.4 (0.5)	A	3.4 (0.3)	A	4.0 (0.3)	A	15.12	<0.0001
1.21–1.40	0.4 (0.1)	B	0.5 (0.1)	B	0.9 (0.2)	AB	0.8 (0.1)	AB	1.0 (0.1)	A	4.62	0.0021
1.41–1.60	0.4 (0.1)	A	0.2 (0.0)	B	0.3 (0.1)	AB	0.2 (0.1)	AB	0.3 (0.1)	AB	4.10	0.0046
1.61–1.80	0.2 (0.1)	A	0.2 (0.0)	A	0.5 (0.1)	A	0.4 (0.1)	A	0.4 (0.1)	A	2.96	0.0249
1.81–2.00	0.1 (0.0)	B	0.1 (0.0)	AB	0.3 (0.1)	A	0.2 (0.1)	AB	0.3 (0.1)	AB	3.20	0.0175

roots) was ca. 2.4-fold higher than the mean specific fine root tip density calculated for the three older stands (1673 tips g^{-1} fine roots). Moreover, we found statistically significant relationships between fine root tip density and specific fine root tip density and stand basal area. When stand basal area increases, both of these indices linearly decrease (Fig. 2).

We also calculated biomass, length, surface area and volume of fine roots per tree by dividing the fine root indices per stand (Table 3) by stem number per ha (stand density; Table 2). None of the fine root traits listed above was significantly dependent on stand age when expressed on a stand area basis. However, when these values were expressed per tree, there were statistically significant linear relationships between stand age and fine root biomass, length, surface area and volume (Fig. 3); when stand age increased all the root indices expressed on a per tree basis increased. For example, mean fine root biomass per tree increased from 72 g in the 6-year-old stand to 2135 g in the 47-year-old stand, fine root length per tree increased from 996 m to 18458 m, fine root surface area per tree increased from 1.7 m^2 to 37.6 m^2, and fine root volume per tree increased from 244 cm^3 to 6187 cm^3, respectively.

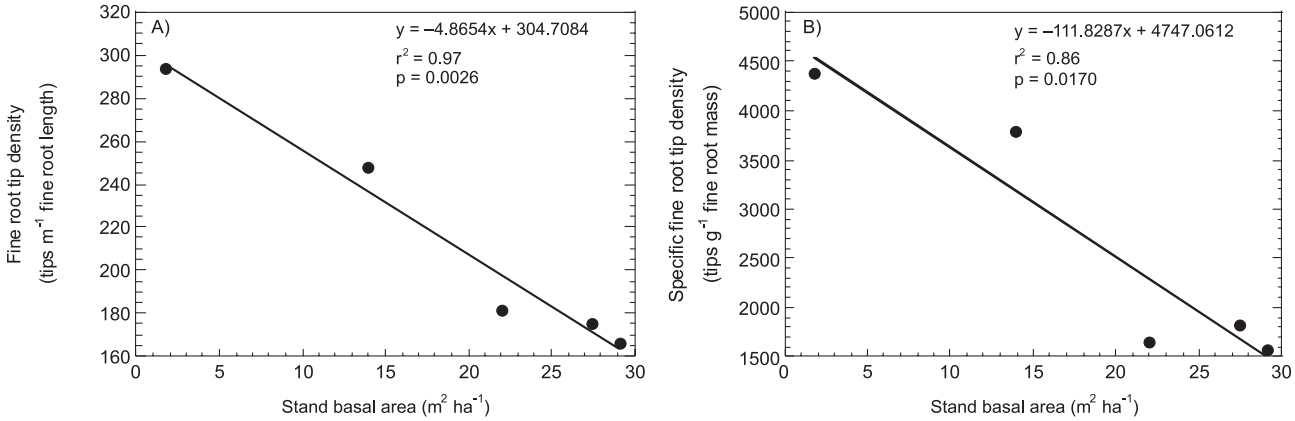

Fig. 2. Effect of stand basal area (m^2 ha^{-1}) on fine root tip density (A) and specific fine root tip density (B)

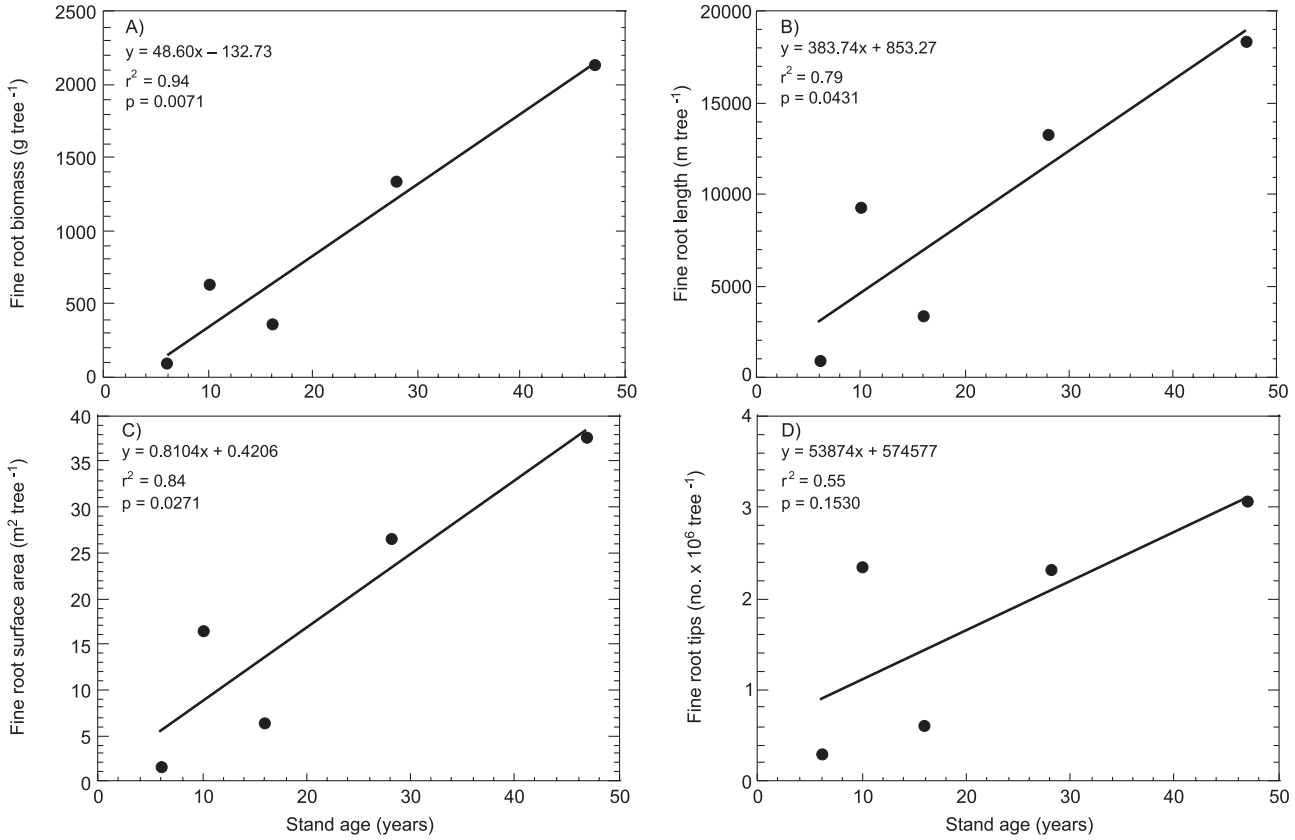

Fig. 3. Effect of stand age on fine root (≤2 mm diameter) biomass (A), length (B), surface area (C), and root tips (D) for the average individual Scots pine tree in each stand. The mean individual Scots pine tree fine root indices were calculated by dividing the particular root features values for each stand per ha (shown in Table 3) by the number of trees in the stand per ha (shown in Table 2)

Discussion

The results of the study show that fine root characteristics of Scots pine differed significantly among stands of different age. The highest increase of fine root biomass per stand area over the age range studied occurred between the 6 and 10 year old stands (from 0.91 to 2.46 Mg ha^{-1}) and fine root biomass appeared to remain at a steady level in four older stands (10–47 years old), meaning no further increase in fine root biomass in the upper 20 cm of soil (mean value: 2.30 Mg ha^{-1}). This clearly showed that the biomass of Scots pine fine roots in the upper soil reached a constant biomass much earlier during stand age than found in previously published papers, although at the same stage of stand development (at the time of canopy closure).

For example Helmisaari at al. (2002), who examined a chronosequence of *Pinus sylvestris* stands in Fin-

land, revealed a peak in fine root biomass at the age of 35 years, coinciding with the canopy closure and thus concluded that the time of canopy closure is clearly related to maximum fine root biomass. Similar results were shown by Claus and George (2005) for *Fagus sylvatica*, *Quercus cerris* and *Picea abies* chronosequences; they found that fine root biomass reached maximum values in ca. 25-year-old stands and later on fine root biomass started to decline, reaching a steady-state in mature stands. According to Peichl and Arain (2006), who investigated a *Pinus strobus* chronosequence consisting of 2-, 15-, 30-, and 65-year-old stands, fine root biomass (<2 mm in diameter) peaked in the 30-year-old stand and it was also related to the degree of canopy closure. The coincidence of maximum fine root biomass with reaching the stage of closed canopy in developing stands was also shown for *Pinus ponderosa* (Law et al. 2003). Our study reveals the same pattern although the fine root biomass peak was observed in much younger stands; the stage of canopy closure in the first-generation post-agricultural stands examined was reached at the age of 8–9 years. This may indicate that stand age (i.e. age of trees in an even-aged monoculture) is not a prime factor influencing fine root dynamics. As pointed out by Vogt et al. (1987), and more recently by, e.g., Finér et al. (2007), fine root biomass may be associated rather with above-ground stand development and stand structure as well as changing habitat features.

The results obtained in our study show a steady-state of fine root biomass after canopy closure, in 10–47 years old stands. The literature data concerning fine root biomass changes after canopy closure are not ambiguous. In our study, fine root biomass in older stands was estimated at the level of ca. 2.30 Mg ha^{-1}, which is a slightly lower value than that of 2.97 Mg ha^{-1} characterizing the European Scots pine forests (Finér et al. 2007). Claus and George (2005) showed a decline in fine root biomass with age in the sequence of four *Fagus sylvatica* stands where total fine root biomass for 0–30 cm (plus the organic layers) was 5.3–6.4 Mg ha^{-1} for the 15- and 30-year-old stands and fell to 2.4 Mg ha^{-1} and 3.3 Mg ha^{-1} for the 62- and 111-year-old stands, respectively. Similar patterns were found for coniferous forests (Vogt et al. 1987; Vanninen and Mäkelä 1999; Fujimaki et al. 2007) and deciduous forests (Idol et al. 2000), where fine root biomass also increased to a peak at canopy closure, after which it gradually declined in maturing stands. In a *Cryptomeria japonica* plantation chronosequence (4 to 88 years old), fine root biomass increased from year 4 to 15 and then decreased from year 15 to 88, but the difference between 15 and 88 year old plantations were not statistically significant (Tateno et al. 2009). However, as has been mentioned earlier, a steady-state or a kind of leveling off in fine root biomass in mature stands was also observed (Claus and George 2005; Yuan and Chen 2010). The changes of fine root biomass may also be a result of biomass accumulation in organic soil horizons in developing stands. As shown in our study, the organic horizon in the younger stands (e.g. 6, 10 and 16 years old) consists of one sublayer (Ol), which is relatively thin (1 cm depth) and is characterized by an accumulation of mainly needles and twigs which are unaltered (Table 1). In the older stands (28 and 47 years old) the organic layer is thicker (up to 5 cm depth) and consists of two sublayers (Ol and Of or OF(h)). The Of and Oh sublayers are characterized by an accumulation of at least partly decomposed organic matter. As a stand ages, increased amounts of root detritus and other decomposed organic material enrich the soil in nutrients, and that nutrient input makes the upper part of soil more suitable for further root growth and development.

We hypothesized that stands differing in age may differ not only in fine root biomass but also in root morphology. In support we found statistically significant differences among stands in all the fine root morphological indices analysed. Among many fine root morphological traits (e.g. surface area, volume, specific root length, specific root area, specific fine root tip density), specific root length (SRL) is considered the best fine root trait that characterizes the economic aspects of root systems developmental trajectories. Roots with high SRL are believed to be less expensive to produce by the plant and increasing SRL is considered one of the possible fine root morphological features leading to an increase of the volume of soil exploited per unit biomass invested in fine roots (Withington et al. 2006; Ostonen et al. 2007). The fine roots collected from the younger stands (6- and 10-year old) generally had greater specific root length (SRL) and specific fine root area, smaller mean fine root diameter and more root tips per unit root length, biomass and stand area than in the older stands (16-, 28-, and 47-year-old). The changes in fine root biomass and SRL with stand development are well documented (Claus and George 2005; Fujimaki et al. 2007; Ostonen et al. 2007; Børja et al. 2008). They are thought to result from changes in the nutrient requirements of tree communities (Bond-Lamberty et al. 2006). Low SRL may indicate a slow rate of fine root proliferation in the soil and difficulties in the acquisition of water and nutrients relative to the cost of resources used for the construction and maintenance of a root system (Eissenstat 1991, 1992; Eissenstat and Yanai 1997). Moreover, higher SRL permits plants to increase the exploration of soil volume in the younger phases of stand development, which was clearly shown for the 6- and 10-year-old stands studied. SRL also appears to be the best indicator of differences in potential growth rate (Comas and Eissenstat

2004). Also, it is an important morphological parameter that reflects the benefit of absorptive capability relative to the cost of root maintenance (Hishi 2007). According to Ostonen et al. (2007) the ranges of mean SRL of Scots pine for variable fine root categories derived from different studies are as follows: ECM roots – from 24.7 to 51.5 m g^{-1}, <1 mm fine roots – 20 m g^{-1}, and <2 mm fine roots – from 6.5 to 15 m g^{-1}. The range 9.33 to 14.99 m g^{-1} obtained for the ≤2 mm fine roots in our study is concurrent with these results. Specific root length and mean fine root diameter have proven to be efficient for characterizing the soil exploitation strategy of tree species (Finér et al. 1997; Bauhus and Messier 1999a). However, the diameter of ECM root tips depends strongly on the diversity of ECM symbiotic fungi, which vary considerably in different site conditions (Helmisaari et al. 2009). The proportion of fungal mantle in ECM root volume is a highly variable factor and was estimated to range from 17–28% in *Picea abies* (Ostonen and Lõhmus 2003). Similarly, the proportion of fungal tissue in root biomass of *Pinus sylvestris* seedlings ranged from 12 to 22% (Hobbie and Colpaert 2003). The study by Ostonen et al. (2009) showed that ECM fungus species are the primary influence on ECM short-root size, including specific root length and specific root area.

Our previous study in a chronosequence of young *Pinus sylvestris* stands (from 6 to 20 years old) growing on a reclaimed lignite mine spoil heap, situated in the vicinity of the age-sequence of post-agricultural Scots pine stands studied here, has shown that stand age clearly influence both fine root biomass and morphology (Jagodziński and Kałucka 2010); we found that fine root biomass as well as length, surface area and volume expressed per unit soil area increased significantly within the age-range studied. Moreover, the cited study has demonstrated that when stand age increases, specific fine root biomass increases, while specific root length and area decreases. Mean fine root biomass in the stands representing similar age ranges, e.g. 6-, 9-, 11-, 15- and 17-years-old stands growing on lignite mine spoil heap and 6-, 10- and 16-years-old stands growing on post-agricultural sites, equals 168.5 g m^{-2} and 174.3 g m^{-2} in the upper 20 cm of soil, respectively. The mean values of number of fine root tips per 1 m^2 of soil area (895163 vs. 536048 tips m^{-2}), fine root tip density (335 vs. 241 tips m^{-1} fine root length), specific fine root tip density (5640 vs. 3267 tips g^{-1} fine root mass) and specific fine root length (16.9 vs. 12.9 m g^{-1} fine root mass) were clearly higher for stands growing on the lignite mine spoil heap than for the post-agricultural stands examined. The higher values of all the indices mentioned above in stands growing on highly disturbed soils on the lignite mine spoil heap indicate higher belowground competition in these stands in comparison with post-agricultural stands. On the other hand, it also indicates the high fine root plasticity of Scots pine. However, the trajectories of changes of the fine root parameters mentioned above were similar for both sites. For example, in post-agricultural stands, the specific fine root tip density diminished with increasing stand age from ca. 4400 tips g^{-1} in the 6-year-old stand to ca. 1600 tips g^{-1} in the 47-year-old stand. Similarly, in stands growing on lignite mine spoil heap, the index diminished from 7100 tips g^{-1} in the 6-year-old stand to 3900 tips g^{-1} in the 20-year-old stand (Jagodziński and Kałucka 2010). This suggests that these patterns might be a general pattern, at least for pine plantations growing in human-disturbed habitats.

In conclusion, our analyses showed that stand age likely affected both fine root biomass and morphology in Scots pine forests when growing on post-agricultural fields. We showed that the biomass of Scots pine fine roots of the upper soil reaches a constant biomass at a younger stand age than found in previously published papers, although at the same stage of stand development, so that age of trees in an even-aged monoculture is not a prime factor influencing the fine root dynamics – instead other stand and habitat characteristics may play an important role. The stand development does progress with age, but a given developmental stage could be reached at different ages in different stands growing under various conditions. These differences shown in our study indicate high plasticity of Scots pine fine roots in response to stand changes with age. To maximize water and nutrient uptake from the upper part of soil for supporting highly dynamic growth of individual trees during the first stages of stand development, trees allocate relatively high proportions of net primary production to fine roots and modify fine root morphology. The potential of fine roots in the stands exploiting the soil supplies or an effort to compensate for nutrient deficiencies in rather poor sandy soils seems to be relatively high.

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