Plant Soil (2014) 381:225–234
DOI 10.1007/s11104-014-2114-9

REGULAR ARTICLE

Relation of fine root distribution to soil C in a *Cunninghamia lanceolata* plantation in subtropical China

Yingchun Liao · M. Luke McCormack · Houbao Fan · Huimin Wang · Jianping Wu · Jie Tu · Wenfei Liu · Dali Guo

Received: 4 November 2013 / Accepted: 7 April 2014 / Published online: 30 April 2014

Abstract
Background and aims Growth and distribution of fine roots closely depend on soil resource availability and affect soil C distribution in return. Understanding of relationships between fine root distribution and soil C can help to predict the contribution of fine root turnover to soil C accumulation.
Methods A study was conducted in a subtropical *Cunninghamia lanceolata* plantation to assess the fine root mass density (FRMD), fine root C density (FRCD) of different fine root groups as well as their relations with soil C.
Results The FRMD and FRCD of short-lived roots, dead roots and herb roots peaked in the 0–10 cm soil layer and decreased with soil depth, while FRMD, FRCD of long-lived roots peaked in the 10–20 cm soil layer. Soil C was positively related to FRMD and FRCD of total fine roots (across all three soil layers), dead roots (0–10 cm) and herb roots (10–20 cm) as well as FRCD of short-lived roots (20–40 cm) ($P < 0.05$).
Conclusions Soil C was mainly affected by herb roots in upper soil layers and by woody plant roots in deeper soil layers.

Responsible Editor: Katja Klumpp.

Y. Liao · M. L. McCormack · H. Wang (✉) · D. Guo
Qianyanzhou Ecological Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences,
A11, Datun Road, Chaoyang District,
Beijing 100101, China
e-mail: wanghm@igsnrr.ac.cn

Y. Liao
e-mail: liaoyingc@163.com

M. L. McCormack
e-mail: mltmcc@gmail.com

D. Guo
e-mail: guodl@igsnrr.ac.cn

Y. Liao · H. Fan · J. Wu · J. Tu · W. Liu
Institute of Ecology & Environmental Science, Nanchang Institute of Technology,
Nanchang 330099, China

H. Fan
e-mail: hbfan@nit.edu.cn

J. Wu
e-mail: jpwu@nit.edu.cn

J. Tu
e-mail: tujie8058@163.com

W. Liu
e-mail: liuwf729@126.com

Y. Liao
University of Chinese Academy of Sciences,
Beijing 100039, China

Keywords Fine roots · Soil C · Soil N · Fine root mass density · Fine root C density

Introduction

Fine roots play important roles in the biogeochemical cycles of terrestrial ecosystems (Davis et al. 2004; Norby and Jackson 2000; Yuan et al. 2012) and make up a large fraction of annual net primary production (Gower et al. 1996; Finér et al. 2007). Fine roots constitute the most dynamic portion of the tree root system and are believed to contribute significantly to carbon and nutrient turnover (Asaye and Zewdie 2013). With the rapid turnover and decomposition rate of fine roots, they provide ~30 to 80 % of the total organic carbon into soil (Steele et al. 1997; Brown 2002; Ruess et al. 2003; Howard et al. 2004) and are increasingly recognized as a key parameter for the accurate assessment of ecosystem carbon budgets (Guo et al. 2008). Therefore, knowledge of fine roots is essential for a detailed understanding of their role as C stores and sources of soil litter input in terrestrial ecosystems (Makita et al. 2011).

Previous studies have viewed fine roots ≤2 mm in diameter as homogenous units. But recent findings indicate that substantial variability exists within roots ≤2 mm with respect to their form and function (Pregitzer et al. 1998, 2002; Wells and Eissenstat 2001). Root branching structure is a fundamental characteristic of form that can be intimately linked to functions that control fine root C allocation and fates (Fitter 2002), Guo et al. (2004) reported that fine root N and lignin concentrations decreased, while total non-structural carbohydrate (TNC) and cellulose concentrations increased with increasing root order. The metabolic activity of fine roots is higher for lower-order and smaller diameter roots (Pregitzer et al. 1998, 2002; Guo et al. 2004, 2008; Makita et al. 2009). Recently, a few studies have reported evidence for conceiving woody plant root systems as composed of a two-tier system of root types (non-woody short-lived vs woody long-lived) (Riley et al. 2009; Gaudinski et al. 2010; Xia et al. 2010). Thus, to better understand belowground C cycling, we must evaluate the biomass and functions of fine roots of different order.

Soil environmental factors in natural ecosystems may be heterogeneous even on a small scale (Jackson and Caldwell 1993; Ryel et al. 1996; Šmilauerová and Šmilauer 2002) and roots frequently grow in these heterogeneous environments that also include interactions from neighboring plants and physical impediments in the rhizosphere (Fang et al. 2013). This soil heterogeneity affects fine root distribution which may affect soil C content in return. Also, changes in fine root dynamics could be a major link between plant responses to long-term changes in soil organic matter and ecosystem C balance (Norby and Jackson 2000). Many studies have evaluated fine root biomass in forests for various species, sites, stand ages, and geographic regions (Jackson et al. 1997; Finér et al. 2007; Noguchi et al. 2007), but little is known about soil heterogeneity or its relationship with fine root distribution in the same stand.

To assess the contribution of plant fine roots to the accumulation of soil C, a study was conducted in a 28-year-old *Cunninghamia lanceolata* plantation. Our objective was to investigate patterns of fine root distribution for different fine root groups and their relation to soil C. Specifically, we determined the distribution of fine root mass density (mass of fine roots per unit soil volume, FRMD), fine root C density (C concentration of fine roots per unit soil volume, FRCD) in the *C. lanceolata* plantation. In addition, the distribution of soil C was also measured to determine its possible relationship with root parameters. We hypothesized that if roots are the dominant source of soil C input and contribute to soil C stabilization, the distribution of soil C should follow the same pattern as that of roots. In this study, we tested the hypothesis that the distribution of total fine roots was positively related to soil C concentrations.

Materials and methods

Site description

The study was conducted at Qianyanzhou Ecological Research Station (26°44′N, 115°4′E), Chinese Academy of Sciences (CAS). The station is situated in the northern part of the mid-subtropical zone and is characterized by highly weathered red earth hills. The average elevation is approximately 100 m. Mean annual precipitation is 1,489 mm, of which ~65 % falls between April and September (monthly averaged from 1983 to 2010). The annual mean temperature is 17.8 °C.

This study was conducted in a *C. lanceolata* plantation which covers about 4,000 m^2 at the Qianyanzhou station. All the trees in the study site were planted in

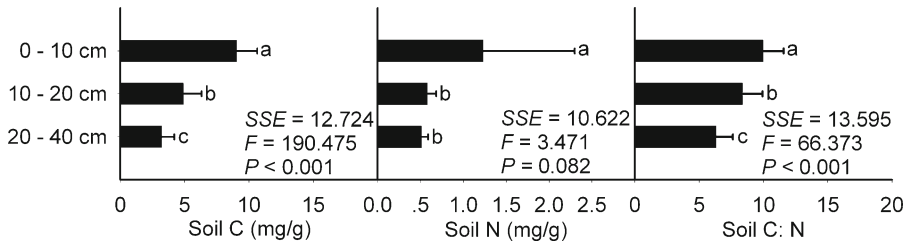

Fig. 1 Vertical distribution of soil C (mg/g), soil N (mg/g) and soil C: N in different soil layers of 0–10, 10–20 and 20–40 cm (The error bars represent ± 1SD of the mean; different letters indicate significant differences at $P < 0.05$; the results of the GLM for soil C, soil N and soil C: N are shown in the lower right corners)

1983 with a density of 2,425 plants per ha. The slope of the study site is 7–10° in the sampling area. There were some understory shrubs and grasses such as *Dicranopteris linearis*, *Syzygium grijsii*, *Dicranopteris linearis*, *Toxicodendron succedaneum*, *Herba Lophateri*, *Radix Rosae Cymosae*, *Lygodium conforme* and *Vitex negundogrowing* in the study area and the vegetation coverage rate reached 60 %. The average diameter at breast height (DBH) for *C. lanceolata* was 15.04 cm.

Root sampling

To ensure accurate characterization of patterns across the whole stand, samples were collected in five 20 m× 20 m plots which together equaled half of the total plantation area. In each plot, eight 20 cm×20 cm soil blocks were dug at random. The layers of each soil block were collected for 0–10, 10–20 and 20–40 cm, respectively. Soil and roots were separated during initial sampling and processed independently (120 soil samples). Roots were immediately placed into sealed polyethylene bags on ice in a cooler and then transported to the laboratory and stored in a freezer at −40 °C to ensure minimal damage to the live tissue and change in ion concentrations (Clemensson-Lindell and Persson 1992).

For processing in the lab, the roots were thawed, cleaned and immediately sorted. Live roots and dead roots were distinguished using several criteria: resilience, brittleness, color of bark and xylem (Vogt and Persson 1991). The *C. lanceolata* roots were classified by root branch orders (1–5 with root tips as first order roots) and root samples were separated into non-woody short-lived roots (short-lived roots, 1–3 order roots), woody long-lived roots (long-lived roots, 4–5 order roots), coarse roots (> 5 order roots, as only 3 soil blocks included coarse roots, we omitted the data in this analysis), live herb roots (herb roots) and dead roots (without classification by species or root groups of herb roots and dead roots). So there were 600 fine root samples for measuring biomass.

After separating the roots from the soil of each layer, the soil was air-dried and sieved with 0.15 mm mesh sieves. The biomass of each fine root groups was obtained after oven-drying at 80 °C to constant weight. Then the fine root samples were ground to pass a sieve

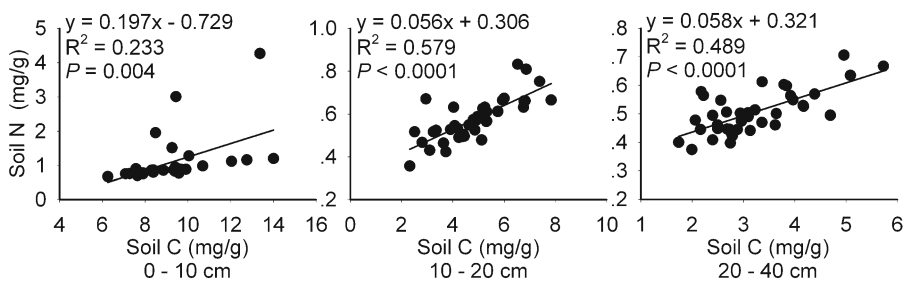

Fig. 2 Relationships between soil C (mg/g) and soil N (mg/g) in different soil layers of 0–10, 10–20 and 20–40 cm. Note the differences in vertical axis and horizontal axis scales

Table 1 Mean C (mg root C/g of soil) of roots in different soil layers and root groups. values are mean ± 1SD. There was a significant effect of root group (P <0.01) and different letters indicate significant differences at P <0.05. There was no significant effect of soil layer (P >0.05). For the other statistical tests, see Table 4

Depth (cm)	Short-lived roots		Long-lived roots		Herb roots		Dead roots	
0–10	450.7±41.3	A	478.8±18.8	A	427.3±20.6	AB	406.9±29.9	B
10–20	454.3±1.8	AB	468.1±10.6	A	446.9±20.0	B	420.2±11.6	C
20–40	442.6±9.8	AB	467.2±14.1	A	452.2±20.0	AB	404.6±44.1	B

of 1 mm in mesh size and stored prior to analysis. In some cases there was insufficient root sample material for C and N analysis. Here, some root samples of the same root group and soil layer were combined across soil blocks within a given plot (3 replicas × 3 soil layers × 5 root groups × 5 plots = 225 root samples for C and N analysis). Soil C and N, root C and N concentrations were analyzed through combustion (Elementar vario MAX, Germany).

The fine root mass densities (FRMD) (mg/cm^3) were obtained by dividing the fine root mass by the soil block volume at depth increments of 0–10, 10–20 and 20–40 cm, respectively. Fine root C densities (FRCD) were calculated by multiplying FRMD and C concentrations.

Statistical methods

Means of soil C and soil N, root C and root N, FRMD and FRCD in each root group and soil layer were calculated by averaging the means for the plots (n=5) and were compared by one-way ANOVA. Additionally, means of soil C and soil N, root C and root N, FRMD and FRCD were subjected to general linear model (GLM) with root group and soil layer as fixed factors, plot as random factor to assess their influences on FRCD and FRMD. Linear regression was used to test for possible relationships between FRMD and FRCD with soil C. Statistical tests were considered significant at $P \leq 0.05$. All analyses were carried out using SPSS 16.0 and SigmaPlot 10.0 statistical software.

Results

Soil C, N and C: N ratio

Soil C and N were highly heterogeneous among locations and different soil depths. Soil C and N concentrations were highest in the most upper soil layer (0–10 cm) and decreased with increasing soil depth (Fig. 1). The soil C concentration was 9.1 mg/g in the 0–10 cm soil layer and decreased rapidly in the 10–20 (4.9 mg/g) and 20–40 cm (3.2 mg/g) soil layers (P <0.01). The soil N concentrations also decreased sharply from the 0 to 10 cm soil layer to the 10–20 cm soil layer (P <0.01), but changed little between the 10–20 and 20–40 cm soil layers. The soil N concentration at the 0–10 cm was 0.9 mg/g and decreased to 0.6 mg/g at the 10–20 cm and 0.5 mg/g at the 20–40 cm. Soil C: N ratios decreased the same pattern as soil C and decreased from 9.95 (0–10 cm) to 8.36 (10–20 cm) and 6.31 (20–40 cm) (Fig. 1). Soil C and N were highly correlated with each other across the three soil layers (Fig. 2) (P <0.01) though there were several extreme points with high soil

Table 2 Mean N (mg root N/g of soil) of roots in different soil layers and root groups. values are mean ± 1SD. There was a significant effect of root group (P <0.01) and different letters indicate significant differences at P <0.05. There was no significant effect of soil layer (P >0.05). For the other statistical tests, see Table 4

Depth (cm)	Short-lived roots		Long-lived roots		Herb roots		Dead roots	
0–10	10.1±2.3	A	7.2±2.0	B	10.2±1.6	A	8.5±1.9	A
10–20	7.9±1.5	B	6.7±1.9	B	10.2±1.4	A	7.5±0.8	B
20–40	7.9±1.9	AB	6.5±1.5	B	9.5±1.0	A	6.5±1.9	B

Table 3 Mean C: N ratio of roots in different soil layers and root groups. Values are mean ± 1SD. Different letters indicate significant differences at $P < 0.05$, the lowercase letters for depth and capital letters for root groups. For the other statistical tests, see Table 4

Depth (cm)	Short-lived roots			Long-lived roots			Herb roots			Dead roots		
0–10	48.7±16.2	a	B	71.6±19.5	a	A	45.0±13.8	a	B	47.9±8.6	b	B
10–20	58.8±11.3	a	AB	75.1±20.6	a	A	44.4±7.0	a	B	56.8±6.6	ab	AB
20–40	58.3±13.9	a	A	75.5±16.2	a	A	50.4±8.5	a	B	65.0±14.1	a	A

C and soil N concentrations in the 0–10 cm soil layer. This may have been the result of some points including recently decomposed foliage or roots. However, the overall results and interpretation were not affected by these extreme points.

Root C, N and C: N ratio

Root C and N concentrations were not significantly different between the three soil layers (Tables 1 and 2) but differed among the different root groups. The C concentration of long-lived roots was the highest while the C concentration of dead roots was the lowest. The N concentration of herb roots was the highest in the three soil layers. The N concentration of long-lived roots was lower than any other root groups in the three soil layers. Our results coincided with previous studies (Xia et al. 2010) that the mean N concentration of non-woody roots is higher than woody roots.

The C: N ratio of roots can be used to indicate the type of material and ease of decomposition. Hard woody materials with high C: N ratios are more resilient than soft leafy materials with low C: N ratios (Bot and Benites 2005). In this study, the C: N ratio of each root group varied little between each soil layer except in dead roots ($P < 0.05$). The mean C: N of dead roots increased 18.6 % in the 10–20 cm soil layer and 35.7 % in the 20–40 cm soil layer compared with the 0–10 cm soil layer (Table 3). One possible explanation might be that the roots constituting the dead roots pool changed from mostly dead herb roots in the 0–10 cm soil layer to mostly dead *C. lanceolata* roots (dead short-lived, long-lived and possible coarse roots) in the 20–40 cm soil layer.

FRMD and FRCD distribution

The FRMD and FRCD of all fine root groups (short-lived roots, long-lived roots, herb roots and dead roots) were distributed mostly in the 0–10 and 10–20 cm soil layers (Tables 5, 6 and 7) and the distribution patterns of FRMD and FRCD were similar. The distribution of FRMD and FRCD for herb roots were distributed mostly in the 0–10 cm soil layer and decreased sharply in the 10–20 and 20–40 cm soil layers. The FRMD of total fine roots decreased by 17.6 % and 59.1 % in the 10–20 and 20–40 cm soil layers, respectively, while the FRCD of total fine roots decreased by11.4 % and 60.0 % in the 10–20 and 20–40 cm soil layers compared with the 0–10 cm soil layer.

The relationship between soil C and fine roots distribution

Fine roots provide the primary input of organic carbon into soil (Leuschner and Hertel 2003). So linear regression

Table 4 Results of ANOVA testing the effects of soil layer and root group on root C, root N and root C: N

Source of variation	Dependent variables								
	Root C			Root N			Root C : N		
	SSE	*F*	*P*	*SSE*	*F*	*P*	*SSE*	*F*	*P*
Soil layer	68.733	0.296	0.758	0.122	3.940	0.111	620.752	2.362	0.212
Root group	26.893	26.332	<0.001	0.250	6.244	<0.05	945.745	12.489	<0.05
Soil layer × root group	135.143	0.383	0.877	0.296	0.679	0.670	1939.029	0.635	0.701

Table 5 Mean FRMD (mg/cm^3) in different soil layers and root groups. Values are mean ± 1SD. Different letters indicate significant differences at P <0.05, the lowercase letters for depth and capital letters for root group. For the other statistical tests, see Table 7

Depth (cm)	Short-lived roots			Long-lived roots			Herb roots			Dead roots			Total fine roots		
0–10	0.34±0.21	a	B	0.51±0.43	a	B	0.38±0.39	a	B	0.43±0.59	a	B	1.76±0.96	a	A
10–20	0.29±0.23	ab	BC	0.59±0.44	a	B	0.12±0.14	b	C	0.41±0.41	a	BC	1.45±0.93	b	A
20–40	0.24±0.21	b	B	0.28±0.26	b	B	0.05±0.05	b	C	0.14±0.10	b	BC	0.72±0.48	c	A

analyses of soil C concentration and root distribution can help us appreciate the contribution of fine roots to soil C.

Overall, soil C values were positively correlated with FRMD and FRCD. Soil C had strong spatial correlations with the FRMD and FRCD of total fine roots in the three soil layers (Fig. 3 and 4). The FRMD and FRCD of dead roots were significantly related to soil C concentration in the 0–10 cm soil layer. In the 10–20 cm soil layer, herb roots seemed to contribute a lot to soil C and had significant correlation with soil C concentration. As the FRMD and FRCD of herb roots decreased sharply with soil depth the roots of *C. lanceolata* became the main contributors to total fine root biomass and thus to soil C. Accordingly, the FRCD of short-lived roots from *C. lanceolata* were significantly correlated with soil C concentration in the 20–40 cm soil layer (P <0.05) .

Discussion

Several recent studies have implicated fine roots and fine root associated C as the main contributors to soil C (Rasse et al. 2005; Clemmensen et al. 2013). In this study we measured the distribution of soil C and fine roots across a *C. lanceolata* plantation and within three soil depth increments. Our results indicated that the distribution of soil C was closely associated with the distribution of fine roots (FRMD and FRCD), supporting their role as an important component of soil C cycling. Furthermore, we found that the relationship between different groups of fine roots (short-lived vs. long-lived fine roots; herbs vs. *C. lanceolata*) and soil C changed at different soil depths indicating that the importance of each fine root group to soil C pools also changes with depth.

There is general agreement across previous studies that over 60 % of soil organic carbon is usually found in the top 0.3 m of soil (Olupot et al. 2010). In these shallow soil depths, fine root turnover constitutes an important addition of humus into the soil and is important for soil carbon accumulation (Bot and Benites 2005). Nitrogen is also an important factor which influences soil C accumulation. Knops and Tilman (2000) showed that the rate of carbon accumulation was controlled by the rate of nitrogen accumulation. In this study, soil C and soil N concentrations were highest in 0–10 cm soil layer and decreased with soil depth. Despite high spatial heterogeneity in both soil C and soil N, the two variables were consistently and positively correlated across the study area further indicating a strong coupling between the two (Fig. 2).

Rasse et al. (2005) reported that soil C is mostly composed of root C and that this trend increases with soil depth. In this study, fine roots of each group were distributed predominately in 0–10 cm and 10–20 cm soil layers (Tables 5 and 6). The percentage of the FRMD and FRCD of total fine roots in the 0–20 cm soil layer was more than 70 % of that across the 40 cm soil profile.

Table 6 Mean FRCD (mg/cm^3) in different soil layers and root groups. Values are mean ± 1SD. Different letters indicate significant differences at P <0.05, the lowercase letters for depth and capital letters for root group. For the other statistical tests, see Table 7

Depth (cm)	Short-lived roots			Long-lived roots			Herb roots			Dead roots			Total fine roots		
0–10	0.15±0.10	a	B	0.26±0.21	a	B	0.16±0.17	a	B	0.14±0.12	a	B	0.70±0.32	a	A
10–20	0.13±0.10	ab	BC	0.28±0.21	a	B	0.05±0.06	b	C	0.17±0.18	a	BC	0.62±0.41	a	A
20–40	0.10±0.08	b	B	0.10±0.10	b	B	0.02±0.02	b	C	0.06±0.04	b	BC	0.28±0.18	b	A

Table 7 Results of ANOVA testing the effects of soil layer and root group on FRMD and FRCD

Source of variation	Dependent variables					
	FRMD			FRCD		
	SSE	*F*	*P*	*SSE*	*F*	*P*
Soil layer	2.676	19.775	0.001	0.405	28.833	0.001
Root group	11.909	23.745	<0.001	1.800	28.660	<0.001
Soil layer × root group	5.010	7.873	<0.001	0.680	12.726	<0.001

This is consistent with the results of previous researches conducted in other forest ecosystem (Burke and Raynal 1994; Hendrick and Pregitzer 1996; Steele et al. 1997; López et al. 2001; Chen et al. 2006; Zhou and Shangguan 2007).

As predicted by our hypothesis, fine root distribution (FRMD and FRCD) of total fine roots followed the same pattern as soil C (Figs. 3 and 4). Soil C concentration was positively correlated with both FRMD and FRCD of total fine roots in all soil layers (P <0.05). However, the relationships differed among the different groups of fine roots in the different soil layers. The FRMD and FRCD of herb roots and dead roots had high correlation coefficients with soil C concentration in the 0–10 and 10–20 cm soil layers while the FRCD of *C. lanceolata* short-lived roots had high correlation coefficients with soil C in the 20–40 cm soil layers. This may be because herb roots had higher turnover rate than tree fine roots (Li et al. 2001) and contributed more to soil C than *C. lanceolata* in the upper soil layers. With the increases in soil depth, the FRMD and FRCD of herb roots decreased and the FRMD and FRCD of *C. lanceolata* roots accounted for a greater proportion of total fine roots.

In conclusion, soil C was closely related to the biomass of fine roots. Importantly, different groups of fine

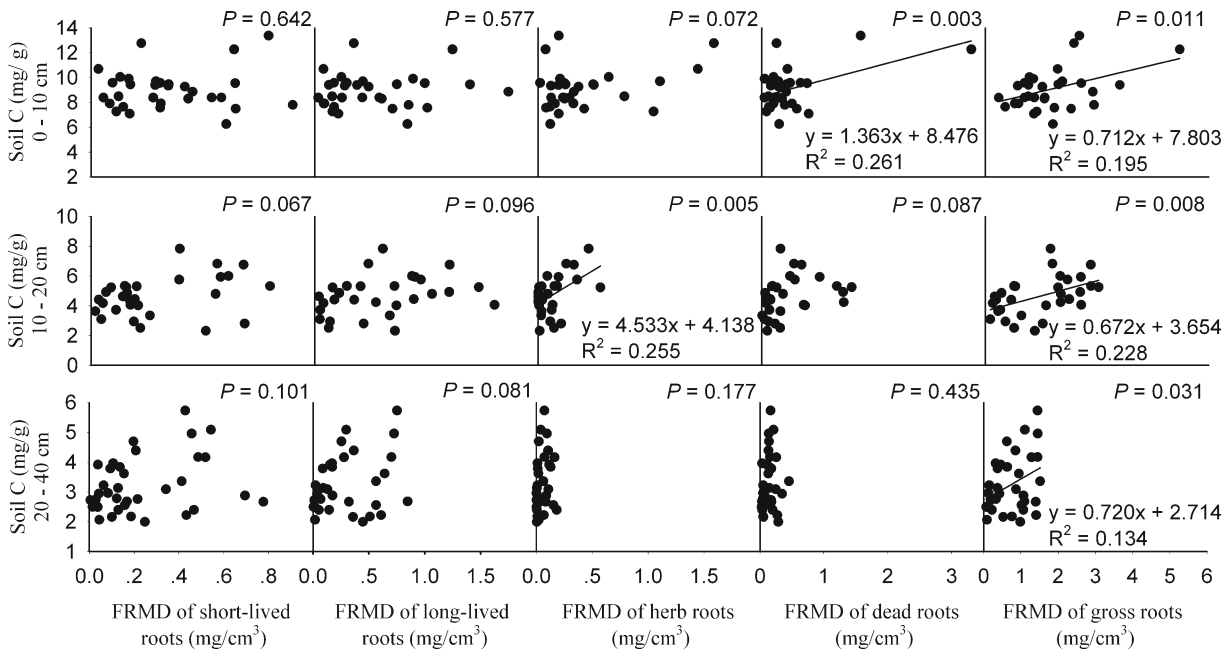

Fig. 3 Linear regressions of soil C and FRCD in different soil layers. Note the differences in vertical axis and horizontal axis scales

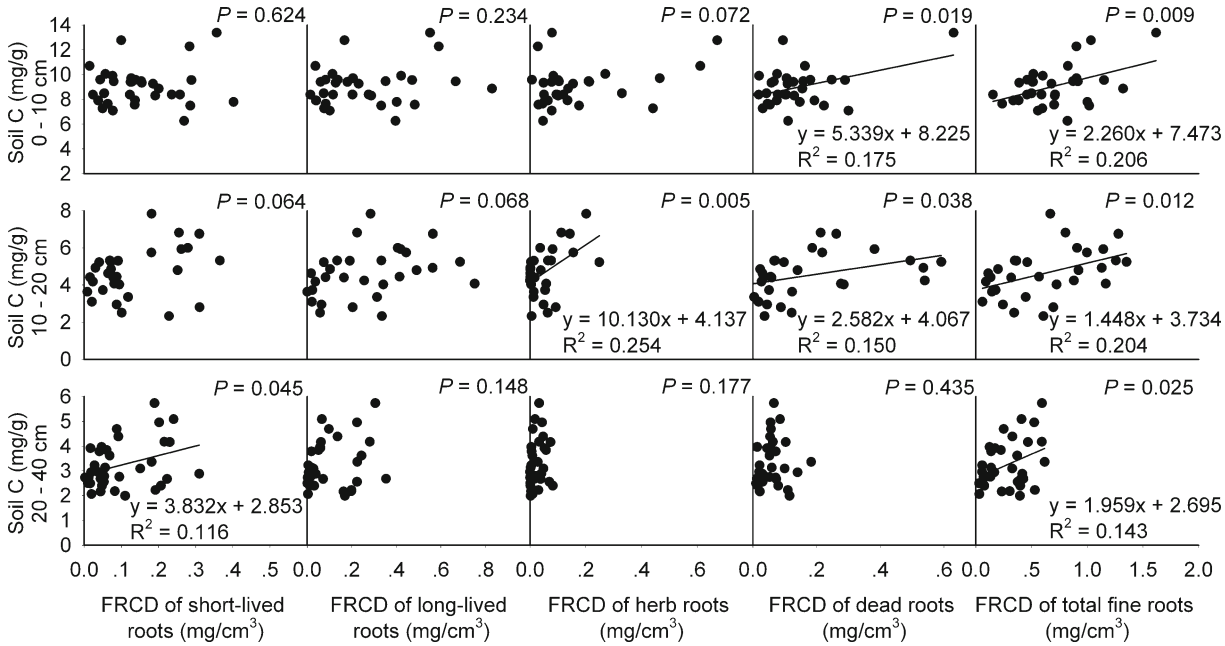

Fig. 4 Linear regressions of soil C and FRMD in different soil layers. Note the differences in vertical axis and horizontal axis scales

roots affect soil C differently throughout the soil profile. Soil resources and fine roots are closely correlated as resources influence fine root growth and the turnover of fine roots then affects soil C and resource availability (Lemenih and Itanna 2004; Domènech et al. 2006). The results of this study provide support for the hopothesis that roots play a key role in the accumulation and persistence of soil C, especially in deep soil layers. A potential limitation of this study is that we sampled during one single time period. Future studies should aim to confirm the robustness of these findings across multiple seasons. Additionally, conducting similar studies in different locations and with additional species can help determine whether these patterns are consistent across a range of biotic and abiotic factors and at multiple spatial scales. Still, the overall patterns revealed here support an emerging paradigm that fine roots and root associated C largely determine soil C dynamics in terrestrial ecosystems.

Acknowledgments This study was financially supported by the National Key Basic Research Program of China (2012CB416903), the National Natural Science Foundation of China (31210103920; 31200406; 31260172).

References

Asaye Z, Zewdie S (2013) Fine root dynamics and soil carbon accretion under thinned and un-thinned *Cupressus lusitanica* stands in, Southern Ethiopia. Plant Soil 366:261–271

Bot A, Benites J (2005) Natural factors influencing the amount of organic matter. In: The importance of soil organic matter: Key to drought-resistant soil and sustained food and production. Food and agriculture organization of the united nations, Rome, pp 11–14

Brown S (2002) Measuring carbon in forests: current status and future challenges. Environ Pollut 116:363–372

Burke MK, Raynal DJ (1994) Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162:135–146

Chen YH, Han YZ, Wang QC, Wang ZQ (2006) Seasonal dynamics of fine root biomass, root length density, specific root

length, and soil resource availability in a *Larix gmelini* plantation. Front Biol 3:310–317

Clemensson-Lindell A, Persson H (1992) Effects of freezing on rhizosphere and root nutrient content using two soil sampling methods. Plant Soil 139:39–45

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD (2013) Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339:1615–1618

Davis JP, Haines B, Coleman D, Hendrick R (2004) Fine root dynamics along an elevational gradient in the southern Appalachian Mountains, USA. Forest Ecol Manag 187:19–34

Domènech R, Vilà M, Gesti J, Serrasolses I (2006) Neighbourhood association of Cortaderia selloana invasion, soil properties and plant community structure in Mediterranean coastal grasslands. Acta Oecol 29(2):171–177

Fang S, Clark RT, Zheng Y, Iyer-Pascuzzi AS, Weitz JS, Kochian LV, Edelsbrunner H, Liao H, Benfey PN (2013) Genotypic recognition and spatial responses by rice roots. Proc Natl Acad Sci 110:2670–2675

Finér L, Helmisaari HS, Lõhmus K, Majdi H, Brunner I, Børja I, Eldhuset E, Godbold D, Grebenc T, Konôpka B, Kraigher H, Möttönen MR, Ohashi M, Oleksyn J, Ostonen I, Uri V, Vanguelova E (2007) Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.). Plant Biosys 141:394–405

Fitter AH (2002) Characteristics and functions of root systems. In: Waisel Y, Eshel E, Kafkafi U (eds) Plant roots, the hidden half, 3rd edn. Dekker, New York, pp 15–32

Gaudinski JB, Torn MS, Riley WJ, Dawson TE, Joslin JD, Majdi H (2010) Measuring and modeling the spectrum of fine-root turnover times in three forests using isotopes, minirhizotrons, and the Radix model. Global Biogeochem Cycles 24, GB3029

Gower ST, Pongracic S, Landsberg JJ (1996) A global trend in belowground carbon allocation: can we use the relationship at smaller scales? Ecology 77:1750–1755

Guo DL, Mitchell RJ, Hendricks JJ (2004) Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140:450–457

Guo D, Mitchell RJ, Withington JM, Fan PP, Hendricks JJ (2008) Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates. J Ecol 96:737–745

Hendrick RL, Pregitzer KS (1996) Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. Ecology 84:167–176

Howard EA, Gower ST, Foley JA, Kurcharik CJ (2004) Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Global Change Biol 10:1267–1284

Jackson RB, Caldwell MM (1993) Geostatistical patterns of soil heterogeneity around individual perennial plants. Ecology 81:683–692

Jackson RB, Mooney HA, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci U S A 94:7362–7366

Knops JMH, Tilman D (2000) Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. Ecology 81(1):88–98

Lemenih M, Itanna F (2004) Soil carbon stocks and turnovers in various vegetation types and arable lands along an elevation gradient in southern Ethiopia. Geoderma 123:177–188

Leuschner C, Hertel D (2003) Fine root biomass of temperate forests in relation to soil acidity and fertility, climate, age and species. Progr Bot 64:405–438

Li PZ, Fan SH, Wang LH, Xu SM (2001) Productivity and turnover of fine roots in poplar tree and grass roots. Chin J Appl Ecology 12(6):829–832 (in Chinese)

López B, Sabaté S, Gracia CA (2001) Vertical distribution of fine root density, length density, area index and mean diameter in a Quercus ilex forest. Tree Physiol 21:555–560

Makita N, Hirano Y, Dannoura M, Kominami Y, Mizoguchi T, Ishii H, Kanazawa Y (2009) Fine root morphological traits determine variation in root respiration of *Quercus serrata*. Tree Physiol 29:579–585

Makita N, Hirano Y, Mizoguchi T, Kominami Y, Dannoura M, Ishii H, Finér L, Kanazawa Y (2011) Very fine roots respond to soil depth: biomass allocation, morphology, and physiology in a broad-leaved temperate forest. Ecol Res 26:95–104

Noguchi K, Konopka B, Satomura T, Kaneko S, Takahashi M (2007) Biomass and production of fine roots in Japanese forests. J For Res 12:83–95

Norby RJ, Jackson RB (2000) Root dynamics and global change: seeking an ecosystem perspective. New Phytol 147:3–12

Olupot G, Daniel H, Lockwood P, McHenry M, McLeod M (2010) (2010) Root contributions to long-term storage of soil organic carbon: theories, mechanisms and gaps. In: Proceedings of the 19th World Congress of Soil Science: Soil Solutions for a Changing World. Brisbane, Australia, pp 112–115

Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR (1998) Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol 18:665–670

Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine North American trees. Ecol Monogr 72:293–309

Rasse DP, Rumpel C, Dignac MF (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilization. Plant Soil 269:341–356

Riley WJ, Gaudinski JB, Torn MS, Dawson TE, Joslin JD, Majdi H (2009) Fine-root mortality rates in a temperate forest: estimates using radiocarbon data and numerical modeling. New Phytol 184:387–398

Ruess RW, Hendrick RL, Burton AJ, Pregitzer KS, Sveinbjornssön B, Allen MF, Maurer GE (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol Monogr 73(4):643–662

Ryel RJ, Caldwell MM, Manwaring JH (1996) Temporal dynamics of soil spatial heterogeneity in sagebrush–wheatgrass steppe during a growing season. Plant Soil 184:299–309

Šmilauerová M, Šmilauer P (2002) Morphological responses of plant roots to heterogeneity of soil resources. New Phytol 154:703–712

Steele SJ, Gower ST, Vogel JG, Morman JM (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba. Canada Tree Physiol 17:577–587

Vogt KA, Persson H (1991) Measuring growth and development of roots. In: Lassoie JP, Hinckley TM (eds) Techniques and Approaches in Forest Tree Ecophysiology. CRC Press, Boca Raton, pp 477–501

Wells CE, Eissenstat DM (2001) Marked differences in survivorship among apple roots of different diameters. Ecology 82: 882–892

Xia MX, Guo DL, Pregitzer KS (2010) Ephemeral root modules in *Fraxinus mandshurica*. New Phytol 188:1065–1074

Yuan ZY, Chen HYH (2012) A global analysis of fine root production as affected by soil nitrogen and phosphorus. P Roy Soc B: Biol Sci 279(1743):3796–3802

Zhou Z, Shangguan Z (2007) Vertical distribution of fine roots in relation to soil factors in *Pinus tabulaeformis* Carr. Forest of the Loess Plateau of China. Plant Soil 291:119–129