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RESEARCH ARTICLE

Seasonal dynamics of fine root biomass, root length density, specific root length, and soil resource availability in a *Larix gmelinii* plantation

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Abstract Fine root turnover is a major pathway for carbon and nutrient cycling in terrestrial ecosystems and is most likely sensitive to many global change factors. Despite the importance of fine root turnover in plant C allocation and nutrient cycling dynamics and the tremendous research efforts in the past, our understanding of it remains limited. This is because the dynamics processes associated with soil resources availability are still poorly understood. Soil moisture, temperature, and available nitrogen are the most important soil characteristics that impact fine root growth and mortality at both the individual root branch and at the ecosystem level. In temperate forest ecosystems, seasonal changes of soil resource availability will alter the pattern of carbon allocation to belowground. Therefore, fine root biomass, root length density (RLD) and specific root length (SRL) vary during the growing season. Studying seasonal changes of fine root biomass, RLD, and SRL associated with soil resource availability will help us understand the mechanistic controls of carbon to fine root longevity and turnover. The objective of this study was to understand whether seasonal variations of fine root biomass, RLD and SRL were associated with soil resource availability, such as moisture, temperature, and nitrogen, and to understand how these soil components impact fine root dynamics in *Larix gmelinii* plantation. We used a soil coring method to obtain fine root samples (≤2 mm in diameter) every month from May to October in 2002 from a 17-year-old *L. gmelinii* plantation in Maoershan Experiment Station, Northeast Forestry University, China. Seventy-two soil cores (inside diameter 60 mm; depth intervals: 0–10 cm, 10–20 cm, 20–30 cm) were sampled randomly from three replicates 25 m×30 m plots to estimate fine root biomass (live and dead), and calculate RLD and SRL. Soil moisture, temperature, and nitrogen (ammonia and nitrates) at three depth intervals were also analyzed in these plots. Results showed that the average standing fine root biomass (live and dead) was 189.1 $g \cdot m^{-2} \cdot a^{-1}$, 50% (95.4 $g \cdot m^{-2} \cdot a^{-1}$) in the surface soil layer (0–10 cm), 33% (61.5 $g \cdot m^{-2} \cdot a^{-1}$), 17% (32.2 $g \cdot m^{-2} \cdot a^{-1}$) in the middle (10–20 cm) and deep layer (20–30cm), respectively. Live and dead fine root biomass was the highest from May to July and in September, but lower in August and October. The live fine root biomass decreased and dead biomass increased during the growing season. Mean RLD (7,411.56 $m \cdot m^{-3} \cdot a^{-1}$) and SRL (10.83 $m \cdot g^{-1} \cdot a^{-1}$) in the surface layer were higher than RLD (1 474.68 $m \cdot m^{-3} \cdot a^{-1}$) and SRL (8.56 $m \cdot g^{-1} \cdot a^{-1}$) in the deep soil layer. RLD and SRL in May were the highest (10 621.45 $m \cdot m^{-3}$ and 14.83$m \cdot g^{-1}$) compared with those in the other months, and RLD was the lowest in September (2 198.20 $m \cdot m^{-3}$) and SRL in October (3.77 $m \cdot g^{-1}$). Seasonal dynamics of fine root biomass, RLD, and SRL showed a close relationship with changes in soil moisture, temperature, and nitrogen availability. To a lesser extent, the temperature could be determined by regression analysis. Fine roots in the upper soil layer have a function of absorbing moisture and nutrients, while the main function of deeper soil may be moisture uptake rather than nutrient acquisition. Therefore, carbon allocation to roots in the upper soil layer and deeper soil layer was different. Multiple regression analysis showed that variation in soil resource availability could explain 71–73% of the seasonal variation of RLD and SRL and 58% of the variation in fine root biomass. These results suggested a greater metabolic activity of fine roots living in soil with higher resource availability, which resulted in an increased allocation of carbohydrate to these roots, but a lower allocation of carbohydrate to those in soil with lower resource availability.

Keywords *Larix gmelinii*, fine root biomass, root length density, specific root length, soil resource availability, seasonal dynamics

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1 Introduction

Root biomass is the carbon allocated to the root system in a forest ecosystem. Coarse root biomass changes slightly during the growing season, but fine root (⩽2 mm in diameter) biomass changes markedly because of their continuous growth and mortality (i.e., turnover) (Fahey and Hughes, 1994; Vogt et al., 1996; Li et al., 1998; Wen et al., 1999). Therefore, the dynamics of fine root biomass may exhibit the pattern of carbon allocation to belowground (Bloomfield et al., 1996; Gill and Jackson, 2000). It is a strategy for trees to keep a quantity of fine root biomass in order to uptake enough nutrients and water from soil (Hendrick and Pregitzer, 1992). However, this capability is not only regulated by total C assimilated from tree canopy (Shipley and Meziane, 2002; Körner, 2003) but also influenced by soil resource availability (e.g., soil moisture, temperature, and nutrients) (Gower et al., 1992; Bloomfield et al., 1996; Domisch et al., 2002). Previous studies reported that C allocation to belowground increased with the increase in soil resource availability, and these C investments accelerated fine root growth and biomass accumulation for absorbing nutrients and water from soil (Steele et al., 1997; Burton et al., 2000; Gaudinski et al., 2001; King et al., 2002). Since soil resource availability changes markedly with the seasonal rhythm (Pregizer et al., 2002), the fine root biomass also displays fluctuations in temporal variations (Vogt et al., 1996; Zhang, 2001). Therefore, the study of the relationship between soil resource availability and fine root biomass will help us in understanding the mechanism of C allocation to fine roots and fine root turnover in the forest ecosystem (Pregizer et al., 2002; Lauenroth and Gill, 2003).

Soil resource availability not only changes seasonally, but also varies with soil depths (Canadell et al., 1996). However, this variation may alter the structure and function of fine roots in soil in different seasons or in the same season (Pregitzer et al., 2000; Hutchings and John, 2003). Two sensitive indexes, i.e., root length density (RLD) and specific root length (SRL), the former indicates the status of soil resource availability, the latter reflects the fine root physiological function, are used in studying fine root dynamics with soil resource availability in spatial and temporal variations. However, most studies in past only focused on the changes of fine root biomass (López et al., 2001), such as comparing the average fine root biomass in poor or rich soil condition (Fahey and Hughes, 1994; Vogt et al., 1996), the RLD and SRL were ignored. *Larix gmelinii* is a dominant tree in temperate forest ecosystem in Northeastern China and a key plantation species. It is also a sensitive species to soil resource availability. The objective of this study was to examine whether seasonal variations of fine root biomass, RLD, and SRL were associated with soil resource availability, such as soil moisture, temperature, and nitrogen, and to understand how these soil factors impact fine root dynamics in different seasons and soil depths in a *L. gmelinii* plantation.

2 Materials and methods

2.1 Study area

This work was conducted at Maoershan experimental station (127°30′–127°34′E, 45°21′–45°25′N) in Northeast Forestry University, Heilongjiang Province, China. The study area has a continental temperate monsoon climate with a mean temperature for January, July, and annually of −19.6°C, 20.9°C, and 2.8°C, respectively. The length of the growing season ranges from 120 to 140 days. The mean annual precipitation is 723 mm, and 477 mm in June, July, and August. The accumulated temperature more than and equal to 10°C amounts to 25°C. The sample plots are located at a southwest-facing slope (approximately 13°). Their elevations range from 450 to 500 m above sea level. Plantation of *L. gmelinii* was established in 1986 by planting two-year-old seedlings using a 1.5 m×2.0 m planting grid. At the year of sampling, the average height and diameter at breast height of the trees were 10.3 m and 9.1 cm, respectively. Prior to the root sampling in May 2002, three 25 m×30 m plots were randomly placed in the plantation.

2.2 Methods

2.2.1 Root sampling

From May to October in 2002, 24 samples were collected at random with soil sequential cores (60 mm in inner diameter) during the growing season. Every soil core was sampled at three depth intervals (0–10 cm, 10–20 cm, and 20–30 cm) and a total of 72 samples were excavated at each plot for every sampling time. Core samples were sealed in plastic bags, numbered, and placed in a cooler with ice and transported to the station for root processing. At the station, core samples were washed with flowing water using a size 40 screen mesh (0.42 mm in diameter) and root samples were placed in a cooler with ice. After bringing the root samples back to the lab, the roots were sorted into three classes base on the diameter size, i.e., ⩽2 mm, 2–5 mm, and >5 mm (Smith et al., 1999). The dead root and living root were classified based on the characteristics of figuration, color, and flexibility (Wang et al., 1995; Huang et al., 1999).

2.2.2 Estimation of root biomass, root length density, and specific root length

Every month, about 2/3 live roots (⩽2 mm in diameter) of each soil core was dried for 48 hours under 65°C to constant and weighed with electronic scales (0.001 g). Meanwhile, another 1/3 roots were placed on the glass board with a graph paper to measure root length (0.1 mm). Then, they were dried for the calculation of SRL. The total dry mass of each soil core was determined by two parts described above. RLD was calculated base on the total root length within the core volume. Dead roots and other living roots (>2 mm in diameter) were immediately dried and weighed after they were sorted in the lab. Average fine root biomass ($g \cdot m^{-2}$), SRL ($m \cdot g^{-1}$), and RLD ($m \cdot m^{-3}$) per unit area with each soil depth were calculated for 24 samples. Mean values of three soil depths represented the monthly average values per unit area.

2.2.3 *Soil nitrogen, temperature, and moisture*

Twenty-four soil samples (each was about 80 g) in each soil depth were carefully collected using size 20 screen mesh (0.84 mm) from soil cores excavated every month and immediately stored in a refrigerator. NO_3^-–N and NH_4^+–N contents were analyzed in the lab. A sample (20 g) of mixed fresh soil was extracted by using 100 mL of 2 M KCL, shaken for 1 hour, and determined using automated colorimetry (Type-722, China). Another 20-g fresh sub sample was measured for nitrate using a distillation and colorimetric method. In this study the NO_3^-–N and NH_4^+–N contents were the mean value of 24 soil cores, and the total nitrogen availability was determined by adding the NO_3^-–N and NH_4^+–N contents. Soil moisture content was measured during the analysis of soil nitrogen content. Temperature data came from the Maoershan Ecosystem Experimental Station.

2.3 Statistical analysis

Data for the fine roots were analyzed by using ANOVA to determine the differences of fine root biomass, RLD, and SRL in different seasons and soil depths. Regression was used to identify the relationship between fine root biomass, RLD, SRL, and soil moisture content, soil temperature as well as available soil nitrogen. Furthermore, stepwise regression was also used to examine the integrative effects of soil moisture content, soil temperature, and available soil nitrogen on fine root dynamics.

3 Results

3.1 Seasonal patterns of fine root biomass

Fine root (≤2 mm in diameter) biomass of *L. gmelinii* in different soil depths and seasons showed significant differences (Fig. 1). Annual mean biomass (lived and dead) was 189.1 $g \cdot m^{-2} \cdot a^{-1}$ within the soil depth range of 0–30 cm. However, 50% (95.4 $g \cdot m^{-2} \cdot a^{-1}$) of the total biomass were obtained in the topsoil (0–10 cm), 33% (61.5 $g \cdot m^{-2} \cdot a^{-1}$), and 17% (33.2 $g \cdot m^{-2} \cdot a^{-1}$) in the sub-soil (10–20cm), and deep soil (20–30 cm), respectively. Schenk and Jackson (2002) suggested that the pattern of fine root biomass decreased with the descending soil depth, which was consistent with the decrease in soil resource availability. Total fine root biomass (live and dead) was higher in May–July and September ranging from 194.6 to 214.4$g \cdot m^{-2} \cdot a^{-1}$, and lower in August and October, 155.9 $g \cdot m^{-2} \cdot a^{-1}$ and 157.1 $g \cdot m^{-2} \cdot a^{-1}$, respectively (Fig. 1a). In contrast to fine root biomass within the soil depth range of 0–20 cm that had a similar pattern in seasonal variation, fine root biomass in deep soil (20–30 cm) gradually decreased during the growing season. Despite the total fine root biomass displayed seasonal variations, no significant difference was found among months ($P > 0.05$).

When total roots of *L. gmelinii* were sorted into live roots and dead roots, both estimations exhibited inverse seasonal trends (Fig. 1b and c). In May and June, the living fine root biomass obtained the highest values (177.8 $g \cdot m^{-2}$ and 170.1 $g \cdot m^{-2}$) and the dead fine root biomass were reduced to the lowest values (36.6 $g \cdot m^{-2}$ and 32.5 $g \cdot m^{-2}$). In contrast, the living fine root biomass decreased throughout the rest of the growing season and reached the lowest in September and October (an average of 87.1 $g \cdot m^{-2}$). Yet, dead fine root biomass increased and reached the highest (average 88.1 $g \cdot m^{-2}$), suggesting fine root production and turnover were simultaneous (Hendrick and Pregitzer, 1993; Bloomfield et al., 1996). The differences of lived and dead fine root biomass among seasons were statistically significant ($P<0.05$).

3.2 Seasonal patterns of RLD and SRL

The variations of RLD and SRL of *L. gmelinii* were associated with soil resource availability (Burke et al., 1991; Eissenstat, 1991; Burton et al., 2000). Annual estimations showed that the RLD and SRL in topsoil were the highest (7 411.56 $m \cdot m^{-3}$, 10.83 $m \cdot g^{-1}$) among the three soil depth intervals; the lowest (1 478.68 $m \cdot m^{-3}$, 8.56 $m \cdot g^{-1}$) in deep soil. Higher RLD and SRL in topsoil suggested that fine roots were widely distributed and thinner in diameter size in this soil layer and might increase the efficiency of the uptake of nutrients and water by the roots. However, lower RLD and SRL in deep soil might reflect a small root distribution and thicker in diameter size (Smit et al., 1999), which indicated that the main function of roots in this layer was the uptake of moisture (Burton et al., 2000). In addition, RLD and SRL varied with seasons (Fig. 2 and 3). When trees started to grow in Spring, roots had a strong ability to absorb the nutrients and water from the soil. Then, RLD and SRL reached their peak (10 621.5$m \cdot m^{-3}$ and 14.83$m \cdot g^{-1}$) during this period and gradually decreased throughout the rest of the growing season. Both of them were the lowest (2 198.20 $m \cdot m^{-3}$ and 3.77$m \cdot g^{-1}$) in September. The monthly RLD had a significant difference ($P<0.05$) among the three soil depth intervals in the growing season. However, SRL had a significant difference ($P<0.05$) only between May and June, and no significant difference was found for July, August, and October ($P>0.05$).

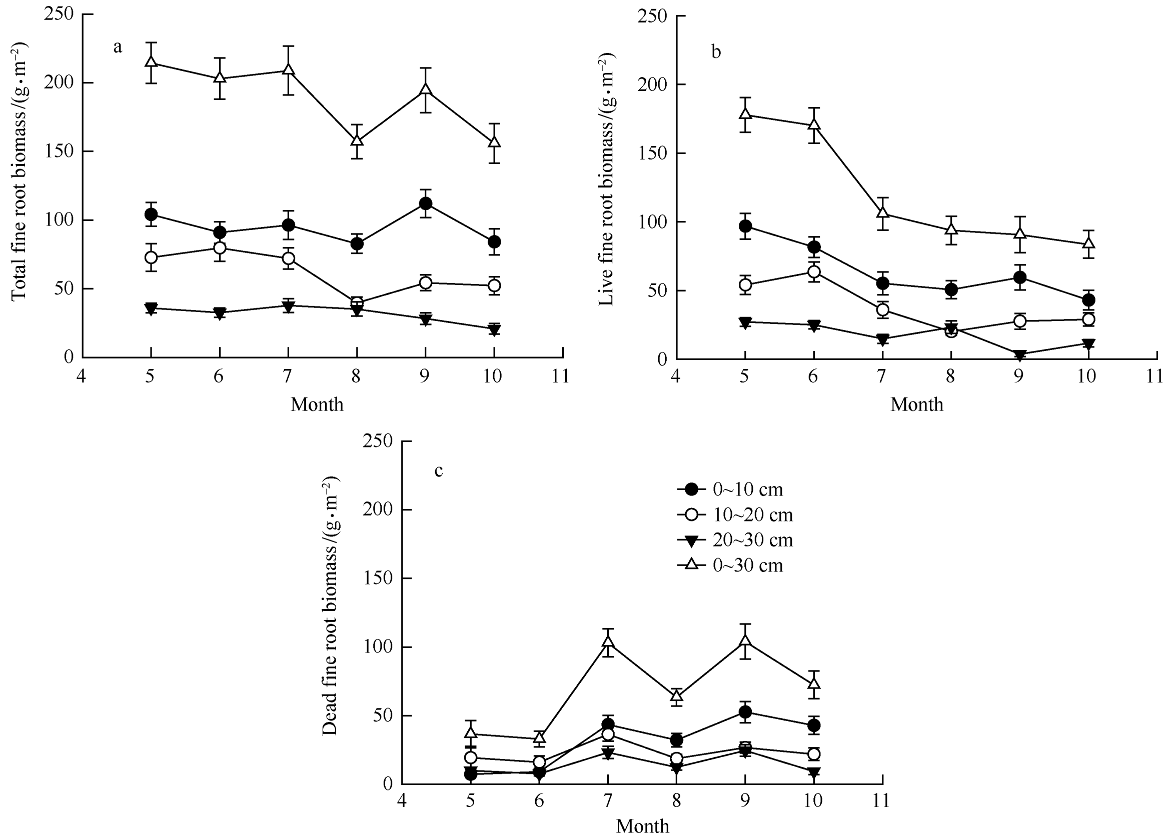

Fig. 1 Dynamics of total (a), live (b) and dead (c) fine root (≤2mm in diameter) biomass of *L. gmelinii* plantation in different soil depths and months

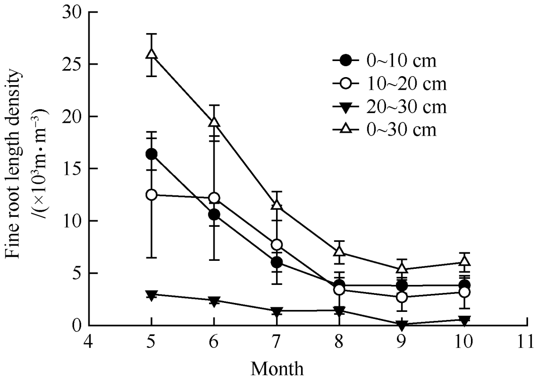

Fig. 2 Dynamics of fine root (≤2mm in diameter) length density (RLD) of *L. gmelinii* plantation in different soil depth intervals and months.

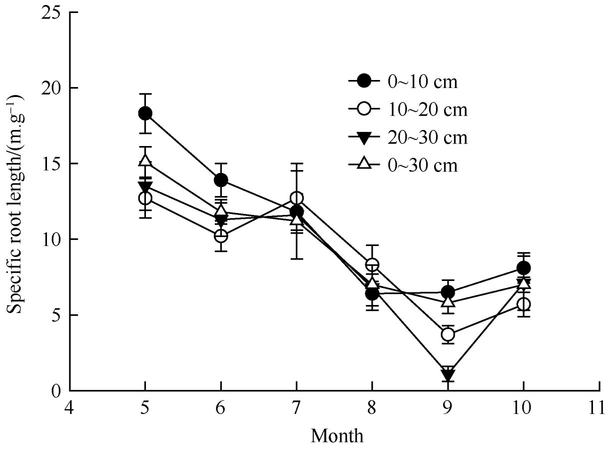

Fig. 3 Dynamics of specific root (≤2mm in diameter) length (SRL) of *L. gmelinii* plantation in different soil depth intervals and months.

3.3 Relationship between fine roots and soil resources availability

Soil moisture, temperature, and available nitrogen in temperate forest presented markedly seasonal patterns and directly influenced the dynamics of fine roots (Usman et al., 1999; Pregitzer et al., 2000). Simple regression analysis on correlations indicated that different correlations indeed existed between fine root parameters (biomass, RLD, and SRL) and soil factors (moisture, temperature, and available nitrogen) in *L. gmelinii* (Table 1). Soil temperature, overall, had weak relationships with fine root parameters. Soil moisture in depth range of 0–30 cm had a higher negative correlation ($r = -0.78$) with the dead fine root biomass, and a lower positive correlation ($r = 0.33$) with the live fine root biomass. The live fine root biomass in soil depth range of 0–20 cm increased with the increase in soil moisture (r = 0.31–0.35), but the biomass for the dead fine roots was on the contrary ($r = -0.69 - -0.70$). In deep soil (20–30 cm), the live fine root biomass decreased ($r = -0.81$, $P < 0.05$) and the dead fine root biomass increased ($r = 0.61$) with the increase in soil moisture (Table 1). Correlations of RLD and SRL decreased from topsoil to sub soil layer (r = 0.50–0.39 and r = 0.98–0.42) when soil moisture was reduced from 69% to 50%, and higher significant negative correlations of RLD and SRL were found in deep soil (Table 1, $r = -0.90$ and $r = -0.90$, $P < 0.05$). These correlations suggested that higher soil moisture availability might increase fine root density and reduce fine root diameter in topsoil, conversely, it might decrease fine root density and thicken fine root diameter in deep soil.

Total available nitrogen (NO_3^-–N and NH_4^+–N) in *L. gmelinii* plots was 16.8 $mg \cdot kg^{-1}$ (0–10 cm), 11.8 $mg \cdot kg^{-1}$ (10–20cm), and 7.9 $mg \cdot kg^{-1}$ (20–30 cm), respectively. In contrast to soil moisture, fine root biomass (total: r=−0.85, P<0.05; live: r=−0.39) and RLD (r=−0.20) in topsoil decreased, which was consistent with the increase in soil nitrogen availability. However, the dead fine root biomass ($r = 0.08$) and SRL (r=0.04) were uninfluenced (Table 1). In unfertile soil depth of 10–20 cm, fine root biomass (total: r=0.78, live: r=0.91, P<0.05), RLD (r=0.74) and SRL (r=0.23) increased as the soil nitrogen availability also increased. These correlations indicated that the pattern of carbon allocation to fine roots not only varied with soil nitrogen availability, but also revealed the discrepancy in the capability for nutrient acquisition from soil by roots (Gower et al., 1992; Nadelhoffer, 2000). In addition, the effects of the two types of nitrogen (NO_3^-–N and NH_4^+–N) on fine root biomass, RLD, and SRL in the soil depth range of 0–20 cm were consistent with that of total nitrogen (Table 1), but had stronger influence than ammonia or nitrate. Considering the mean nutrient value of three soil depths, impact of nitrate on fine root growth was greater than ammonia. Unfortunately, these relationships in topsoil were not found in deep soil, but it might suggest the strategy divergences of root function between topsoil and deep soil.

Fine root dynamics was affected by integration of soil moisture, temperature, and nutrients (Pregitzer et al., 2000). The kind of impact could be found in different soil depths. Stepwise regression on the basis of soil moisture, temperature, and available nitrogen revealed that the integration of the three factors had greater effect on total fine root biomass, RLD, and SRL (Table 1). Variations (71%–73%) of total fine root biomass, RLD, and SRL could be explained by these three factors and as well as 58% variation of living fine roots. The seasonal dynamics (58%–73% variations) of fine roots of *L. gmelinii* was mainly caused by seasonal soil resource availability.

Table 1 Correlation coefficients of fine root (≤2 mm in diameter) biomass, root length density (RLD) and specific root length (SRL) with soil moisture, temperature, NH_4^+, and NO_3^- in larch plantation

Soil depth /cm	Correlation coefficients r						
	r_W	r_T	r_{NH_4}	r_{NO_3}	$r_{NH_4\text{-}NO_3}$	r^2_{W+T}	r^2_{W+T+N}
			Total fine root biomass				
0–10	−0.37	0.001	0.36	0.33	−0.85*	0.40	0.79
11–20	0.01	0.03	0.48	0.52	0.78	0.04	0.61
21–30	−0.44	0.47	0.67	0.07	−0.59	0.89*	0.82*
0–30	−0.44	0.16	0.20	0.61	0.21	0.16	0.71
			Live fine root biomass				
0–10	0.31	0.04	−0.19	0.13	−0.39	0.11	0.54
11–20	0.35	−0.16	0.56	0.62	0.91*	0.10	0.88*
21–30	−0.81*	0.07	−0.13	0.06	0.07	0.79	0.79
0–30	0.33	0.08	0.04	0.61	0.57	0.11	0.58
			Dead fine root biomass				
0–10	−0.69	0.10	0.01	0.08	0.08	0.56	0.67
11–20	−0.70	0.31	0.24	0.29	−0.41	0.51	0.62
21–30	0.61	0.50	0.43	0.01	−0.43	0.43	0.46
0–30	−0.78	0.24	0.23	0.31	−0.60	0.61	0.38
			Root length density (RLD)				
0–10	0.50	0.05	0.10	0.07	−0.20	0.25	0.52
11–20	0.39	0.05	0.36	0.59	0.74	0.15	0.68
21–30	−0.90*	−0.20	0.18	0.30	0.10	0.89*	0.92*
0–30	0.36	−0.14	0.02	0.6	0.49	0.13	0.73
			Specific root length (SRL)				
0–10	0.98*	0.01	0.01	0.01	0.04	0.96*	0.98*
11–20	0.42	−0.21	0.09	0.20	0.23	0.28	0.33
21–30	−0.90*	−0.15	0.09	0.01	0.08	0.92*	0.96*
0–30	0.30	0.05	0.03	0.55	0.43	0.10	0.73

Note: r_W, r_T, r_{NH_4}, r_{NO_3}, and $r_{NH_4\text{-}NO_3}$ are correlation coefficients of fine root biomass, RLD and SRL with soil moisture, soil temperature, ammonia, nitrates, and total nitrogen availability respectively; r^2_{W+T} is multiple correlation coefficient of fine root biomass, RLD, SRL with two soil resources (moisture and soil temperature) availability; r^2_{W+T+N} is multiple correlation coefficient of fine root biomass, RLD, and SRL with three soil resources (moisture, soil temperature, and total nitrogen) availability.

*: P<0.05.

4 Discussions

Phenology of fine root growth and mortality in temperate forest exhibited seasonal pattern because of climate factors (Fahey et al., 1994; Pregitzer et al., 2000). Our study showed that fine root biomass, RLD, and SRL of *L. gmelinii* clearly revealed their seasonal variations (Figs. 1, 2 and 3). When leaves started to sprout and grow in May, it was necessary for roots to absorb enough nutrients and water in order to meet the demand of new foliage and branch developments (Canadell et al., 1996; Hendrick and Pregitzer, 1996). In this period, despite the soil beginning to thaw and moisture was relatively higher (50% in average), soil temperature (9.4°C on the average), and available nitrogen (13.9 $\mathrm{mg \cdot g^{-1}}$ in the depth range of 0–20cm) was relatively low, which compelled roots to keep higher biomass to sustain aboveground growth requirements. Therefore, the highest fine root biomass (177.8 $\mathrm{g \cdot m^{-2}}$), RLD (1 0621.45 $\mathrm{m \cdot m^{-3}}$) and SRL (14.83 $\mathrm{m \cdot g^{-1}}$) in Spring were reasonable to increase efficiencies on nutrient and water absorption by roots from soil (Eissenstat and Yanai, 1997).

Previous studies reported that fine roots in temperate deciduous forest grew earlier than leaves (Eissenstat and Van Rees, 1994; Hendrick and Pregitzer, 1996; Pregitzer et al., 2000), and their growth was needed to supply enough carbohydrates to them. Before foliage development in May, the carbon that roots consumed in physiological metabolism mainly came from the carbon pool stored in the roots from last year, but the main carbohydrates after the leaves spread were new carbohydrates assimilated by new leaves (Pregitzer, 2003). Unfortunately, fine roots depleted old carbohydrates stored in roots rapidly, and further, new carbohydrate was limitedly supplied to them, leading to some fine roots to senesce and die gradually subsequently in time (Aderson et al., 2003).

In contrast to May, living fine root biomass of *L. gmelinii* decreased by 40% (105.9 $\mathrm{g \cdot m^{-2}}$, Fig. 1b), dead fine root biomass increased by 181% (103.1 $\mathrm{g \cdot m^{-2}}$, Fig. 1c), RLD was lower by 53% (5 036.64 $\mathrm{m \cdot m^{-3}}$, Fig. 2) and SRL was reduced by 19% (12.03 $\mathrm{m \cdot g^{-1}}$, Fig. 3) in July, respectively. But the moisture (45% on average), soil temperature (18.9°C on average), and available nitrogen (an average of 15.7 $\mathrm{mg \cdot g^{-1}}$ in a depth range of 0–20 cm) were sufficient for root growth in this period. Pregitzer (2003) believed that the patterns of carbon allocation to aboveground and belowground had been changed in summer, and more carbohydrates were allocated to the stem and branches rather than to the roots even if soil resource availability was favorable for fine roots to absorb nutrients and water from soil. Our current study showed that the reduction of living fine roots (Fig. 1b and c) and RLD (Fig. 2) was consistent with the increase in fine root mortality. On the other hand, higher soil resource availability in the summer period often produced new roots with lower SRL (Espeleta and Donovan, 2002; Majdi, 2001). Perhaps it is a strategy for a tree to sustain the dynamic balance between the absorption of nutrients and water and the carbon consumption.

In autumn, the aboveground part of *L. gmelinii* stopped growing at the end of August. The canopy gradually senesced in September, and the demand of nutrients and water for aboveground or belowground decreased. After defoliation, a lot of photosynthate, such as starch, was stored in roots for maintaining root respiration before dormancy and growth of new fine roots by next spring. The continuous reduction of living fine root biomass (Fig. 1c), RLD (Fig. 2), and SRL (Fig. 3) was ascribed to the mortality of fine roots, the increase in root tissue density, and/or lignifications.

Dynamics of fine root biomass, RLD, and SRL of *L. gmelinii* in three soil depth intervals with different seasons clearly exhibit that the variations are consistent with seasonal changes of soil resource availability (Table 1). The structure and function of fine roots vary with soil depths and seasons (Nepstad et al., 1994; Schulze et al., 1996). Both variations are a synthetic consequence of soil nutrients, moisture, and temperature. It is well known that the absorption of nutrients and water by roots happens simultaneously. Soil nitrogen and moisture are abundant and temperature is favorable in topsoil, which lead fine roots of *L. gmelinii* to accumulate in the topsoil for foraging nutrients and water, and a great deal of carbohydrates may be allocated to roots (Burton et al., 2000). Soil nitrogen and temperature is unlimited in topsoil. Consequently, enough soil moisture perhaps may accelerate fine root growth, for example, living fine root biomass, RLD, and SRL of *L. gmelinii* presenting a positive correlation with soil moisture (Table 1). However, soil nutrients and moisture are deficient in sub-soil (10~20cm), where living fine root biomass, RLD, and SRL have a positive correlation with soil nitrogen and moisture (Table 1). But fine root biomass within this depth accounts for 33%, markedly lower than that in topsoil (50%), suggesting less carbohydrate allocation to roots within this depth because of deficiency in nitrogen and moisture. In deep soil with low nitrogen and temperature, fine root biomass accounts for 17%, and perhaps the main function is to uptake water rather than nutrients (Burton et al., 2000). Yet, excessive moisture in deep soil might lead to higher mortality (r=0.60), while living fine root biomass, RLD, and SRL show significantly negative correlations with moisture (Table 1).

Nevertheless, changes in fine root biomass, RLD, and SRL are controlled by integration of soil moisture, temperature, and nitrogen, and as well as by carbon allocation (Burke et al., 1991; Pregitzer, 2000). This current study suggests that greater metabolic activity of fine roots living in soil with higher resource availability may result in an increasing allocation of carbohydrate to them, but an inverse trend may happen to roots in soil with lower resource availability. Therefore, the pattern of carbon allocation and the diverse physiological function of fine roots reveal a survival strategy of trees adapting to the environment (Eissenstat and Van Rees, 1994; Canadell et al., 1996).

5 Conclusions

Annual average fine root (≤ 2 mm) biomass (live and dead) of *L. gmelinii* was 189.1 $g\cdot m^{-2}\cdot a^{-1}$, with 50% in topsoil (0–10 cm), 33% in sub soil (10–20 cm) and 17% in deep soil (20~30 cm), respectively. Living fine root biomass increased consistent with the decrease in dead fine root biomass from May to October. The highest RLD (7 411.56 $m\cdot m^{-3}$) and SRL (10.83 $m\cdot g^{-1}$) were obtained in the topsoil (0–10 cm) while the lowest, 1,474.68 $m\cdot m^{-3}$ and 8.56 $m\cdot g^{-1}$, respectively, were found in deep soil (20–30 cm). The total RLD and SRL peaked in May (1 0621.45 $m\cdot m^{-3}$ and 14.83 $m\cdot g^{-1}$, respectively), gradually decreased throughout the rest of the growing season, and reached the lowest in September (2 198.20 $m\cdot m^{-3}$ and 3.77 $m\cdot g^{-1}$, respectively). Variations of fine root biomass, RLD, and SRL were consistent with the changes of soil moisture, temperature, and available nitrogen. Correlations based on simple regression indicated that the effects of soil moisture and nitrogen on fine roots were significantly greater than soil temperature, and greater as well to living fine roots than to the dead. The integrative effects of soil moisture, temperature, and available nitrogen on fine roots could explain 58–73% seasonal variation of fine root biomass, RLD, and SRL in *L. gmelinii*.

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