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RESEARCH ARTICLE

Estimation of fine root production, mortality and turnover with Minirhizotron in *Larix gmelinii* and *Fraxinus mandshurica* plantations

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Abstract Fine root turnover is a major pathway for carbon and nutrient cycling in forest ecosystems. However, to estimate fine root turnover, it is important to first understand the fine root dynamic processes associated with soil resource availability and climate factors. The objectives of this study were: (1) to examine patterns of fine root production and mortality in different seasons and soil depths in the *Larix gmelinii* and *Fraxinus mandshurica* plantations, (2) to analyze the correlation of fine root production and mortality with environmental factors such as air temperature, precipitation, soil temperature and available nitrogen, and (3) to estimate fine root turnover. We installed 36 Minirhizotron tubes in six monospecific plots of each species in September 2003 in the Mao'ershan Experimental Forest Station. Minirhizotron sampling was conducted every two weeks from April 2004 to April 2005. We calculated the average fine root length, annual fine root length production and mortality using image data of Minirhizotrons, and estimated fine root turnover using three approaches. Results show that the average growth rate and mortality rate in *L. melinii* were markedly smaller than in *F. mandshurica*, and were highest in the surface soil and lowest at the bottom among all the four soil layers. The annual fine root production and mortality in *F. mandshurica* were significantly higher than in *L. gmelinii*. The fine root production in spring and summer accounted for 41.7% and 39.7% of the total annual production in *F. mandshurica* and 24.0% and 51.2% in *L. gmelinii.* The majority of fine root mortality occurred in spring and summer for *F. mandshurica* and in summer and autumn for *L. gmelinii*. The turnover rate was 3.1 a^{-1} for *L. gmelinii* and 2.7 a^{-1} for *F. mandshurica*. Multiple regression analysis indicates that climate and soil resource factors together could explain 80% of the variations of the fine root seasonal growth and 95% of the seasonal mortality. In conclusion, fine root production and mortality in *L. gmelinii* and *F. mandshurica* have different patterns in different seasons and at different soil depths. Air temperature, precipitation, soil temperature and soil available nitrogen integratively control the dynamics of fine root production, mortality and turnover in both species.

Keywords *Larix gmelinii*, *Fraxinus mandshurica*, fine root production, fine root mortality, fine root turnover, Minirhizotron

1 Introduction

Fine roots (< 2 mm in diameter) serve a major function in absorbing water and nutrient from soil for trees. Fine root turnover, including fine root production and mortality, will cost a great amount of carbohydrates, and meanwhile, return substantial nutrients to the soil (Bloomfield et al., 1996; Huang et al., 1999; Zhang et al., 2000). Therefore, fine root turnover plays an important role in carbon (C) budget and nutrient cycling in forest ecosystems (Eissenstat and Yanai, 1997; Gill and Jackson, 2000). For example, 40%–73% of net primary production (NPP) was allocated to belowground in some forest ecosystems (Fogel, 1985; Vogt et al., 1986), and most of them were allocated to fine root turnover (Raich and Nadelhoffer, 1989; Vogt et al., 1996; Gill and Jackson, 2000). Apparently, accurate estimation of fine root turnover is key to understanding carbon allocation patterns and processes in terrestrial ecosystems (Gill and Jackson, 2000; Matamala et al., 2003).

It is, however, important to understand fine root dynamics in order to estimate fine root turnover (Eissenstat and Yanai, 1997; Mei et al., 2004). Many studies have revealed that an affinity exists between fine root production/mortality and soil resource availability

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(Bloomfield et al., 1996; Norby and Jackson, 2000; Pregitzer et al., 2000), which leads to big differences in fine root turnover among tree species, or for the same species in different environmental conditions (Raich and Nadelhoffer, 1989). For instance, the fine root turnover rate in the *Pinus banksiana* and *Picea mariana* forests were 1.75 a^{-1} and 2.9 a^{-1} at the same site, respectively (Steele et al., 1997). Moreover, the *Acer saccharum* located at different sites exhibited different fine root turnover rates of 0.76 a^{-1} and 0.66 a^{-1}, respectively (Burton et al., 2000). Gill and Jackson (2000) thought that fine root dynamics were closely related to environmental factors. However, it is still unclear how soil resource availability influences the process of fine root production and mortality. Moreover, previous studies only focused on different soil or climate conditions, while the correlation between fine root dynamics and environmental factors was neglected. Nevertheless, such a correlation is critical for estimating the pattern and process of carbon allocation in global change studies (Schenk and Jackson, 2002). In the temperate forest ecosystem, the major characteristic of soil resource availability is seasonality (Pregitzer et al., 2000). Therefore, fine root production and mortality also show substantial seasonal variations (Burke and Raynal, 1994; Zhang and Wu, 2001; Cheng et al., 2005). However, how soil resource availability (e.g. soil nitrogen availability, soil temperature) and climate factors (e.g., air temperature, precipitation) affect fine root production and mortality is poorly understood. The minirhizotron method has been widely used in studying fine root dynamics and estimating fine root turnover in the past decades, yet there are few studies in China. We conducted an investigation with Minirhizotron in the *Larix gmelinii* and *Fraxinus mandshurica* plantations at the same site in an effort to provide useful information for the regulation of fine root production and mortality in these two species based on the soil resource availability and seasonal variations. Specifically, we aimed (1) to investigate the seasonality of fine root production and mortality in different soil layers; (2) to reveal the relationship between fine root production/mortality and environmental factors such as soil nitrogen availability, soil temperature, air temperature and precipitation; and (3) to estimate fine root turnover for each species.

2 Materials and methods

2.1 Study site

This study was carried out at the Jianlagou Silviculture Station in the Mao'ershan Forestry Center (127°30′–127°34′E, 45°21′–45°25′N) of the Northeast Forestry University in the Heilongjiang Province, China. The study area was located at the northeastern edge of the Zhangguancai Mountains, which belong to the Changbai Mountain range. The topography shows a slow elevation from the south to the north. The average elevation is 300 m, with a slope of 10°–15°. The study area has a continental cold temperate monsoon climate with mean January, July, and annual temperatures of −23°C, 20.9°C and 2.8°C, respectively. It is characterized by a long and cold winter, a dry spring with little rain, and a short and hot summer. The mean annual precipitation is 723 mm. The average annual evaporation is 1094 mm. The frost-free period is 120–140 days. The accumulated temperature ⩾10°C amounts to 2526°C.

2.2 Methods

2.2.1 Plots and Minirhizotron tubes installation

The study plots were located above the middle of the hills, with an elevation range from 450 to 500 m above sea level and in the south-west-facing slope (approximately 10°). The soil is classified as Hap-Boric Luvisols, with an average soil depth of about 40 cm. Both plantations, *F. mandshurica* and *L. gmelinii*, were established in 1986 by planting 2-year-old seedlings using a 1.5 m × 2.0 m planting grid. Three 20 m × 30 m plots were randomly placed in each of the *F. mandshurica* and *L. gmelinii* plantations. In sampling year 2003, for *F. mandshurica*, the average height and diameter at breast height of the trees were 10.4 m and 9.1 cm respectively, and the corresponding values for *L. gmelinii* were 10.3 m and 10.6 cm, respectively.

In September 2003, the Minirhizotron tubes (Bartz Technology Corporation, USA) were installed at six random locations in each plot. The installation methods were based on Johnsons' descriptions (Johnson et al., 2001). Tubes (5.5 cm inside diameter, 90 cm long) were installed at a 45-degree angle to the soil surface to a minimum of 45 cm vertical depth. The aboveground length of the tube was about 20 cm. A total of 36 tubes were installed in six plots for both trees. The bottoms of the tube were tightly obturated before installation. For the aboveground portions of the tubes, black adhesive tape was firstly adhibited, and then yellow tape was adhibited again. Finally, the tube was capped by using a plastic cap (20 cm long), which was painted white. Minirhizotron sampling was conducted every two weeks from the middle of May, 2004 to May 29, 2005. It stopped when the soil froze in winter. Thus, one year's fine root dynamics were measured completely.

2.2.2 Image analysis and data collection

The system of BTC (Bartz Technology Corporation) was used for sampling. The area of the sampling frame was 1.4 cm × 1.8 cm. The number of images was about 40–45 for each tube. The sampling began on May 18, 2004 and stopped on May 29, 2005, for a total of 13 days. Every image was analyzed by the RooTracker 2.0 (Craine and Tremmel, 1995), and relative data were obtained. Fine roots were classified with reference to Hendrick and Pregitzer's method (1992). Roots were defined as: new roots, roots observed for the first time; white roots, roots previously observed but still white in windows. If the root color became brown, it was defined as brown roots. If the roots became black, or disappeared between two measurements, they were defined as dead roots. During the process of image analysis, the database of fine roots was established according to tree species, including plot number, tube number, location frame, sampling time and fine root number for subsequent data analysis.

The changes in root length could be continuously measured, which is the major characteristic of the Minirhizotron. The root length was expressed as root length density (*RLD*, $\mathrm{mm \cdot cm^{-2}}$), and root production and mortality were expressed as RLD_P and RLD_M, respectively. Moreover, we assumed that the rate of growth and death showed consistency at every interval between two consecutive sampling days (usually 15 days). The RLD_P ($\mathrm{mm \cdot cm^{-2} \cdot d^{-1}}$) and RLD_M ($\mathrm{mm \cdot cm^{-2} \cdot d^{-1}}$) were calculated according to the following methods: when the root length showed an increase in the interval between two consecutive sampling days, it was defined as fine root production. Otherwise, it was considered fine root mortality. Thus, the ratio of fine root production or mortality per unit tube area ($\mathrm{cm^{-2}}$) to the interval time (d) was expressed as RLD_P ($\mathrm{mm \cdot cm^{-2} \cdot d^{-1}}$) or RLD_M ($\mathrm{mm \cdot cm^{-2} \cdot d^{-1}}$). The calculation formula is as follows:

$$RLD_{P(M)} = \frac{RLD_{n+1} - RLD_n}{T} \left(\mathrm{mm \cdot cm^{-2} \cdot d^{-1}}\right)$$

where $RLD_{P(M)}$ shows fine root production and mortality at an interval time; RLD_{n+1} and RLD_n show the numerical value of fine root length density ($\mathrm{mm \cdot cm^{-2}}$), which was measured at time $n+1$ and n, respectively; and, T is the interval time (d) between two consecutive sampling days. Fine root production and mortality were calculated at each soil depth, which was divided into 0–10, 10–20, 20–30, 30–40 cm layers, respectively. The RLD_P ($\mathrm{mm \cdot cm^{-2} \cdot d^{-1}}$) and RLD_M ($\mathrm{mm \cdot cm^{-2} \cdot d^{-1}}$) of each soil depth were calculated using all images measured at this depth.

Annual fine root production, mortality and standing crop were calculated by using Burtons' method (Burton et al., 2000). Annual fine root production was the net increment in fine root length at all sampling time points over a year. It summed up both new root length and the extension growth of all the previously existing roots. At the same time, annual fine root mortality was the net decrease in length of fine roots at all sampling times over a year, including dead roots and other disappeared roots, which resulted from fine root shedding and insect feeding. Annual fine root production and mortality were also expressed as root length per unit tube area in a year ($\mathrm{mm \cdot cm^{-2} \cdot a^{-1}}$). The standing crop referred to live root length per unit tube area at every sampling time. Moreover, fine root turnover was estimated using three methods: (1) the ratio of the annual fine root production to the average annual standing crop; (2) the ratio of annual fine root mortality to the average annual standing crop; (3) the ratio of annual fine root production to the maximal standing crop. These three methods were compared for estimation of fine root turnover.

2.2.3 Measurement of soil nitrogen, temperature and moisture, air temperature and precipitation

Soil nitrogen availability ($\mathrm{NO_3^-}$-N and $\mathrm{NH_4^+}$-N) was measured during April–October 2003. The soil samples were excavated using soil core (60 mm inside diameter) at each month interval. There were 8 sampling points at three soil depths (0–30 cm at 10 cm interval) for each plot. Soil samples (about 80 g) at each soil depth were carefully collected using a 0.84 mm mesh and immediately put into plastic bags, and then stored in a refrigerator(−4°C). The $\mathrm{NO_3^-}$-N and $\mathrm{NH_4^+}$-N concentrations were analyzed in the lab. Soil moisture content was measured during the analysis of soil nitrogen concentration. The concentration of the $\mathrm{NO_3^-}$-N was measured by the colorimetric method with phenol-two-sulfonic acid, and the $\mathrm{NH_4^+}$-N concentration was measured by the colorimetric method with 2 M KCL and starch blue. All climate data were obtained from the Laoyeling Ecosystem Experimental Station in Mao'ershan (500 m away), including air temperature, precipitation and soil temperature (5, 15, 20, and 40 cm of soil depths). Then, they were calculated as the average for six years' data (1995–2000).

2.2.4 Statistical analysis

Data for the Minirhizotron images were analyzed by using Microsoft Excel. Then, the ANOVA method was used to determine the differences in fine root production and mortality at different soil depths. Simple regression was used to examine the relationships between fine root production and mortality and available soil nitrogen, soil temperature, air temperature and precipitation. Furthermore, stepwise regression was also used to examine the integrative effects of available soil nitrogen, soil temperature, air temperature and precipitation on fine root production and mortality.

3 Results

3.1 Fine root production at different soil depths

Species, season, and soil depth all had a significant influence on fine root production ($P < 0.05$, Fig. 1). The mean RLD_P of *L. gmelinii* ($0.0045 \pm 0.0022\ \mathrm{mm \cdot cm^{-2} \cdot d^{-1}}$) was

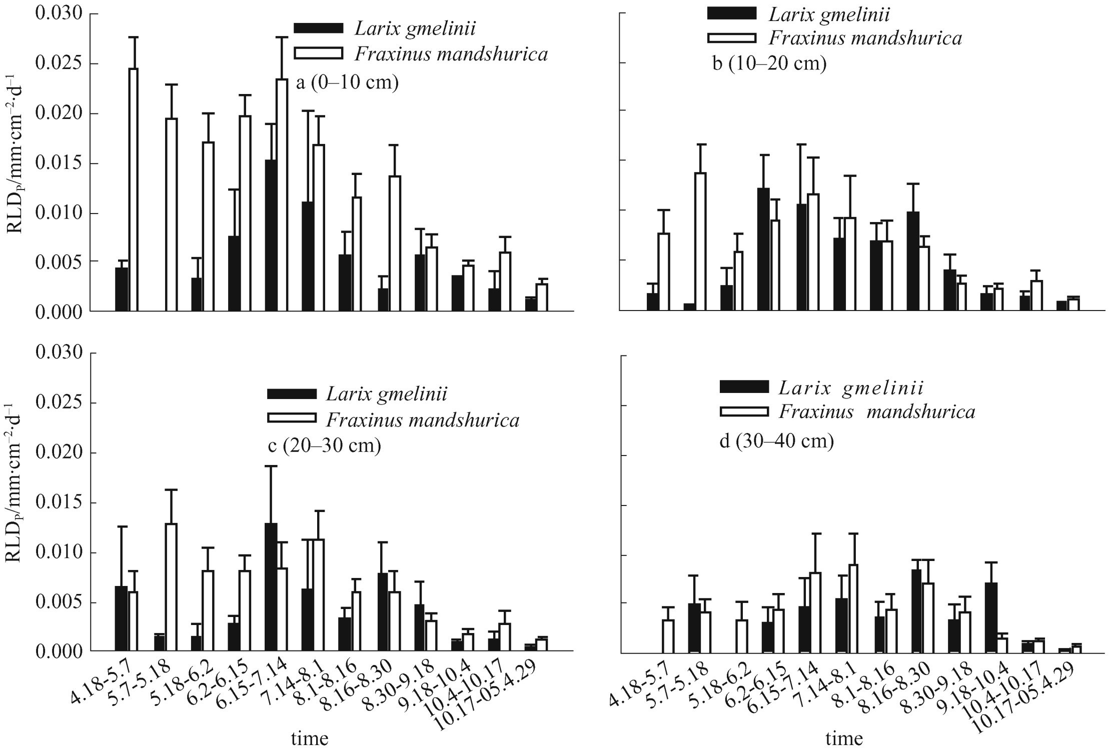

Fig. 1 Dynamics of fine root length production in *Larix gmelinii* and *Fraxinus mandshurica* plantations

markedly lower than that of *F. mandshurica* (0.0077 ± 0.0001 mm·cm^{-2}·d^{-1}), with a difference of 41.6%. In the growing season, for both species at four soil depths, the mean RLD_P in the surface (0–10 cm) was the largest (0.0056 ± 0.0029 mm·cm^{-2}·d^{-1} and 0.0138 ± 0.0022 mm·cm^{-2}·d^{-1} for *L. gmelinii* and *F. mandshurica*, respectively. Fig. 1a), and the lowest occurred at the bottom (30–40 cm) (0.0034 ± 0.0017 mm·cm^{-2}·d^{-1} and 0.0042 ± 0.0008 mm·cm^{-2}·d^{-1} for *L. gmelinii* and *F. mandshurica*, respectively. Fig. 1d). For *L. gmelinii*, at the 0–20 cm soil depth, the RLD_P peaked in late spring and early summer (June 15–July 14, Fig. 1a, b). At the 20–30 cm depth and at the bottom (30–40 cm), the peaks occurred in summer (July 14–August 1, Fig. 1c) and late summer (August 16–August 30, Fig. 1d), respectively. For *F. mandshurica*, in the 0–20 cm soil layer, the maximum RLD_P occurred in spring (April 18–May 18, Fig. 1a, b), and a similar pattern occurred in the 20–30 cm soil layer (May 7–May 18, Fig. 1c). At the bottom (30–40 cm), the maximum RLD_P happened in summer (July 14–August 1, Fig. 1d). Moreover, 24.0% and 51.2% of fine root production in *L. gmelinii* occurred in spring (April 18–June 15) and summer (June 15–August 30), respectively (Fig. 2). As for *F. mandshurica*, 41.7% and 39.7% of the fine root production happened in spring and summer, respectively (Fig. 2). For both species, the fine root production were both small in winter (October 17, 2004–April 29, 2005). The values were 4.6% and 5.7% of the annual fine root production for *L. gmelinii* and *F. mandshurica*, respectively.

The degree of correlation differed between RLD_P and soil nitrogen availability, soil temperature, air temperature and precipitation (Table 1). RLD_P was not correlated with available soil nitrogen at any soil layer ($P > 0.05$). The soil temperature only significantly influenced RLD_P at the 20–40 cm and 30–40 cm soil depths for *L. gmelinii* and *F. mandshurica*, respectively ($R = 0.81$–0.89, $P < 0.05$). Moreover, the air temperature and precipitation were significantly correlated with RLD_P at the 20–30 cm ($R = 0.82$–0.95, $P < 0.05$) and 30–40 cm ($R = 0.91$–0.92, $P < 0.01$) soil depths for *L. gmelinii* and *F. mandshurica*, respectively. These indicate that fine root growth at the bottom layer might be strongly controlled by temperature (Table 1).

The multiple correlation analysis suggests that the integrative effect of soil nitrogen availability, soil temperature, air temperature and precipitation on the fine root dynamics differed between the two species. Further, there were no clear patterns (Table 2). Except for *L. gmelinii* at the 10–20 cm depth, RLD_P was significantly influenced by the integration of all the factors mentioned above for both species ($R^2 = 0.79$–0.99, $P < 0.05$ or $P < 0.01$). Furthermore, the major variations($> 80\%$) in fine root production in both species might be attributed to all these above- and belowground factors together (Table 2).

3.2 Fine root mortality at different soil depths

Similar to RLD_P, RLD_M also was significantly different between different species, seasons, and soil depths

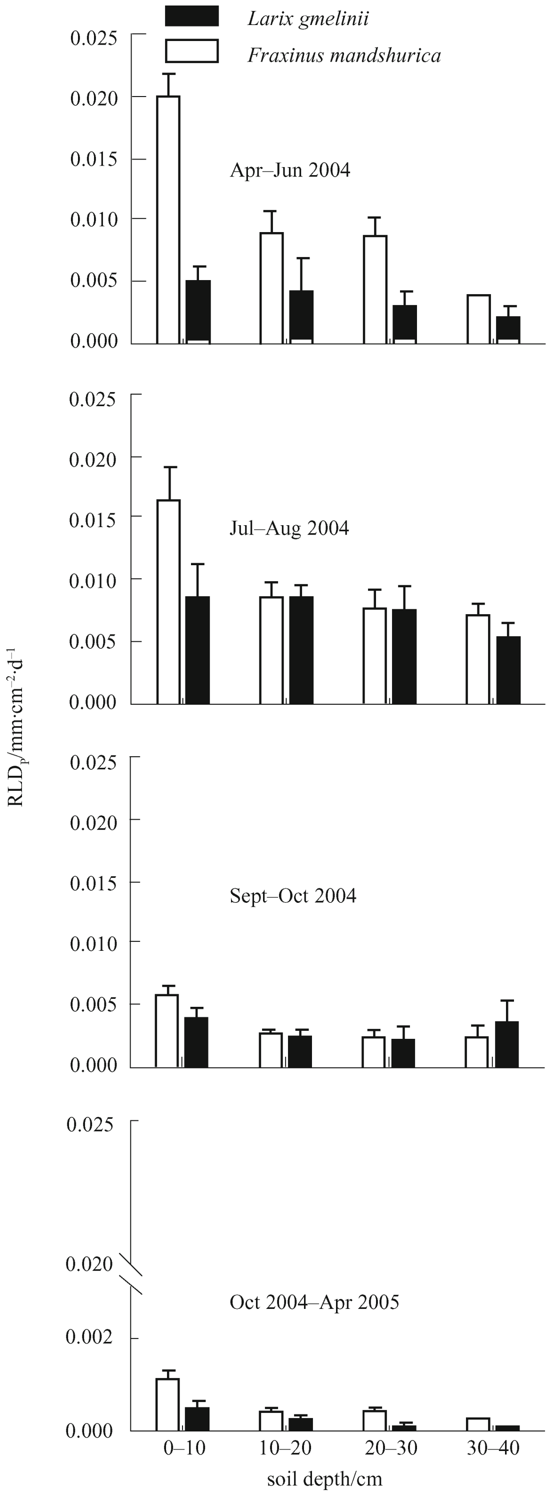

Fig. 2 Dynamics of fine root length production at four soil depths in different seasons in the *Larix gmelinii* and *Fraxinus mandshurica* plantations

($P < 0.05$, Fig. 3). The mean RLD_M of *L. gmelinii* ($0.0069 \pm 0.0022\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) was 4.2% lower than that of *F. mandshurica* ($0.0072 \pm 0.0007\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$). For *L. gmelinii*, RLD_M was largest at the surface ($0.0075 \pm 0.0040\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$, Fig. 3a), and lowest at the bottom ($0.0061 \pm 0.0013\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$, Fig. 3d). The RLD_M of *F. mandshurica* also showed a similar pattern to *L. gmelinii*, which gradually decreased from the surface ($0.0131 \pm 0.0021\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) to the bottom ($0.0052 \pm 0.0008\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$). Moreover, the fine root mortality in *F. mandshurica* mainly occurred in spring (34.3%) and summer (34.0%), while it happened in summer (28.5%) and autumn (32.3%) for *L. gmelinii*. For both species, the RLD_M was small in winter (8%–12%, Fig. 4).

There were no correlations between RLD_M and any single factor such as soil nitrogen availability, soil temperature, air temperature and precipitation (the table of simple correlation was not shown), which is different from RLD_P. Multiple correlation analysis indicates that RLD_M in the sub-surface soil layer (10–20 cm) was only affected by soil nitrogen availability and temperature ($R^2 = 0.67$, $R^2 = 0.85$–0.87, $P < 0.05$), while air temperature and precipitation exerted influences on RLD_M in the sub-surface and bottom layers. For both species, except for the surface layer (0–10 cm), RLD_M was significantly affected by these factors together ($R^2 = 0.95$–0.98, $P < 0.01$; Table 3). This suggests that more than 95% of the dynamics in fine root mortality was controlled by such factors combined together.

3.3 Annual fine root production, mortality and turnover

The annual fine root production, mortality and turnover differed between the *L. gmelinii* and *F. mandshurica* (Table 4). The annual fine root production and mortality for *L. gmelinii* were about 40% lower than that for *F. mandshurica*. In *L. gmelinii*, the annual fine root production and mortality were $0.94 \pm 0.33\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{a}^{-1}$ and $0.72 \pm 0.12\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{a}^{-1}$, respectively; while the corresponding values were $1.52 \pm 0.19\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{a}^{-1}$ and $1.21 \pm 0.08\ \text{mm}\cdot\text{cm}^{-2}\cdot\text{a}^{-1}$ for *F. mandshurica*, respectively. In both species, the annual fine root production and mortality were largest in the surface and lowest in the bottom. The fine root turnover also differed between the two species due to large differences in the mean standing crop, fine root production and mortality (Table 4). The fine root turnover in *L. gmelinii*, based on the three methods, was 3.1 a^{-1} (based on the annual fine root production), 2.4 a^{-1} (based on the annual fine root mortality) and 1.8 a^{-1} (based on the largest standing crop), respectively; while the corresponding values in the *F. mandshurica* were 2.7, 2.2 and 2.1 a^{-1}, respectively. Accordingly, the difference in fine root turnover was approximately 12% between *L. gmelinii* and *F. mandshurica*.

4 Discussion

4.1 Annual fine root production and mortality

Fine roots (< 1 mm in diameter) usually show weak lignification, maintaining their functions of nutrient and

Table 1 Correlation coefficients of fine root length production with soil nitrogen availability, soil temperature, air temperature and precipitation at different soil depths in the *Larix gmelinii* and *Fraxinus mandshurica* plantations

soil depth/cm	soil nitrogen availability			soil temperature/°C				air temperature/°C	precipitation/mm
	0–10	11–20	21–30	5	15	20	40		
L. gmelinii									
0−10	−0.22	0.78	0.42	0.57	0.45	0.40	0.27	0.60	0.48
10–20	0.00	0.45	0.30	0.59	0.52	0.52	0.45	0.56	0.31
20–30	0.49	0.01	−0.26	0.85*	0.89*	0.89*	0.88*	0.82*	0.95**
30–40	0.70	−0.06	−0.62	0.79	0.87*	0.84*	0.84*	0.77	0.67
F. mandshurica									
0–10	0.49	0.24	0.28	0.52	0.30	0.27	0.08	0.60	0.31
10–20	0.55	0.31	0.29	0.65	0.44	0.42	0.25	0.71	0.49
20–30	0.44	0.22	−0.07	0.63	0.45	0.44	0.29	0.71	0.65
30–40	0.56	0.38	0.12	0.89*	0.81*	0.81*	0.71	0.91**	0.92**

$^*P < 0.05$; $^{**}P < 0.01$

water absorption as well as consuming carbohydrates (Hendrick and Pregitzer, 1992; Eissenstat and Yanai, 1997). Production and mortality are the typical characteristics in fine root dynamics (Eissenstat and Yanai, 2002). The Minirhizotron method is a reliable approach for studying fine root population dynamics, with the advantage of consecutive observations of individual roots. The present study indicates that fine root production and mortality synchronously occurred in *L. gmelinii* and *F. mandshurica* over one year's observation. The annual fine root production of *F. mandshurica* was higher than that of *L. gmelinii*, and so was the annual fine root mortality. Moreover, the annual fine root production and mortality mainly occurred in the surface (0–10 cm) and sub-surface (10–20 cm) layers (Fig. 1, 3), together accounting for 59.2% (*L. gmelinii*) and 66.9% (*F. mandshurica*) of the annual fine root production, and 58.0% (*L. gmelinii*) and 60.3% (*F. mandshurica*) of the annual fine root mortality. Only about 15% of the annual fine root production and mortality occurred at the bottom (30–40 cm) layer in both species. Hendrick and Pregitzer's (1996) study, conducted in a temperate deciduous broad-leaved forest in the North America with the minirhizotron method, showed that 44% of the total fine root production occurred in the surface, and only 11% happened at the bottom(> 70 cm). The corresponding values of fine root mortality were 49% and 4%, respectively. In the *Quercus alba* forest, Joslin and Henderson (1987) found that 50% of the fine root production and mortality occurred in the surface (0–22 cm), and 13% was contributed by the bottom layer(> 75 cm). Such a phenomenon, i.e. fine root production and mortality decreasing with increasing soil depth, was considered as a universal pattern in forest ecosystems in many studies (Powell and Day, 1991; Hendrick and Pregitzer, 1996). The most probable reason was that the distribution of fine root systems was strongly controlled by soil physical and chemical characteristics (Jackson and Reynolds, 1996; Vogt et al., 1996; Schenk and Jackson, 2002). It has been proven that there are large differences in available soil resources at different soil depths (Canadell et al., 1996). In the surface soil layer, soil resource availability was high but variable. On the contrary, it was poor and stable at the bottom soil layer. Therefore, such a pattern would result in a large discrepancy in fine root lifespan among different soil layers (Eissenstat and Yanai, 1997; Pregitzer et al., 2000).

Table 2 Multiple correlation coefficients (R^2) of fine root production with soil nitrogen availability, soil temperature, air temperature and precipitation at different soil depths in the *Larix gmelinii* and *Fraxinus mandshurica* plantations

soil depth/cm	R^2_{N+T}	$R^2_{T\ air+P}$	$R^2_{N+T+Tair+P}$
L. gmelinii			
0–10	0.89**	0.36	0.99**
10–20	0.47	0.41	0.50
20–30	0.84**	0.89**	0.98**
30–40	0.74*	0.59	0.79*
F. mandshurica			
0–10	0.30	0.52	0.83*
10–20	0.20	0.57	0.92**
20–30	0.23	0.51	0.99**
30–40	0.52	0.90**	0.98**

$^*P < 0.05$; $^{**}P < 0.01$

4.2 Fine root production dynamics

Due to climatic influences, the production processes aboveground and belowground, showed obvious seasonal dynamics in the temperate forest (Pregitzer et al., 2000; Fahey and Hughes, 1994). Our results indicate that the fine root production was affected by the integrative influence of available soil nitrogen, soil temperature, air temperature and precipitation (Table 2). However, there were significant differences between the two species. Particularly at the 0–30 cm soil depth, the fine root production of the *F. mandshurica* peaked in early spring, but for the *L. gmelinii* it was in late spring and early summer (Fig. 1). At the bottom, the peaks for both species happened in summer. This pattern of seasonal dynamics in fine root growth at different soil depths in temperate forest ecosystems has been proven in some forest studies

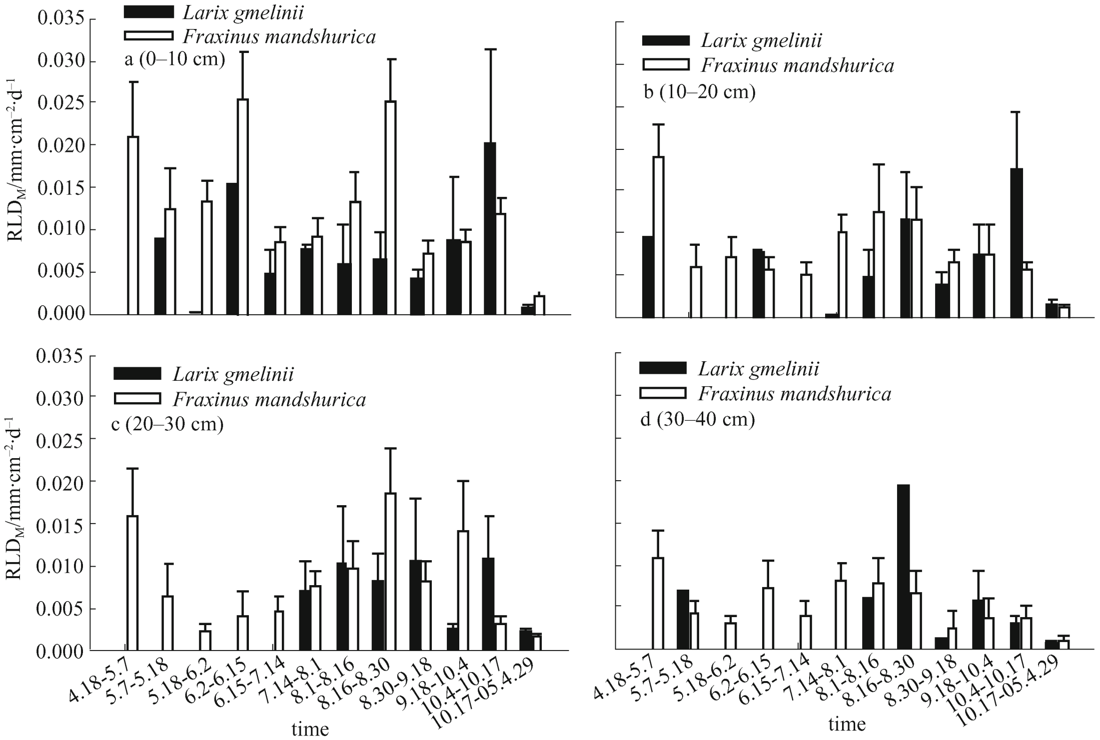

Fig. 3 Seasonal dynamics of fine root length mortality in the *Larix gmelinii* and *Fraxinus mandshurica* plantations

(Hendrick and Pregitzer, 1993; Burk and Ranyal, 1994; Fahey and Hughes, 1994), suggesting that the seasonality of the temperature, coupled with fine root seasonal dynamics for many species, might be the most important factor in controlling fine root dynamics (Pregitzer et al., 2000). In the Mao'ershan region, the leaves of the *L. gmelinii* unfold in the middle of May, but for the *F. mandshurica* it occurs in late May. New fine root growth in *L. gmelinii* was nearly synchronous with that of the leaves, but the fine root growth in *F. mandshurica* occurred earlier than the leaves (Fig. 1). Such a pattern indicates that the fine root growth in early spring for *F. mandshurica*, mainly depended on the stored carbohydrates of the previous year; however, the fine root production in *L. gmelinii* employed the current photosynthate in spring. There are two possible reasons: firstly, the photosynthate stores in the root systems were different in both species (more for *F. mandshurica* and less for *L. gmelinii*); secondly, the lowest temperature restricted fine root growth in the study site. The suitable temperature for the onset of growth of the roots was higher for *L. gmelinii* than for *F. mandshurica*. In the field sampling, it was found that new root growth for *F. mandshurica* began in the middle of April (Mei et al., 2006), during which time the surface soil had thawed and the top soil temperature was around 0°C–2°C. Therefore, except for the 10–20 cm soil depth, the multiple correlations between the fine root production in *L. gmelinii* and soil nitrogen availability and temperature was significant ($R^2 = 0.74$–0.89, $P < 0.05$). However, the correlation was not significant in *F. mandshurica* ($R^2 = 0.20$–0.52).

4.3 Fine root mortality dynamics

Fine root mortality is a complex eco-physiological process (Eissenstat and Yanai, 1997). Physiologically, fine root mortality is related to photosynthate allocation in the root system (Bloomfield et al., 1996; Farrar and Jones, 2000). In an ecological context, it is strongly influenced by soil resource availability (Eissenstat and Yanai, 1997; Mei et al., 2004). The present study, based on the minirhizotron observation, indicates that the dynamics in fine root mortality at each season or soil depth show large discrepancies between the two species (Fig. 3, 4). Fine root mortality for *F. mandshurica* decreased with increasing soil depth, showing a relatively stable pattern in the growing season (spring, summer and autumn). However, most of the fine root mortality for *L. gmelinii* occurred in the middle soil depth (10–30 cm), and more were distributed in summer and autumn than in spring. Fine root mortality in spring, especially for *F. mandshurica*, might be related to the consumption of stored carbohydrates (Anderson et al., 2003; Pregitzer, 2003). Although soil resource availability in summer was suitable for fine root physiological activity, the pattern of carbohydrate allocation changed, most of which were allocated to portions of the branch and trunk (Pregitzer, 2003). Therefore, competition for the carbon source between the aboveground and belowground parts, contributes largely to the fine root mortality in a tree (Farrar and Jones, 2000; Cheng et al., 2005). Moreover, defoliation and decreased temperature in autumn might result in large quantities of fine root senescence (Pregitzer

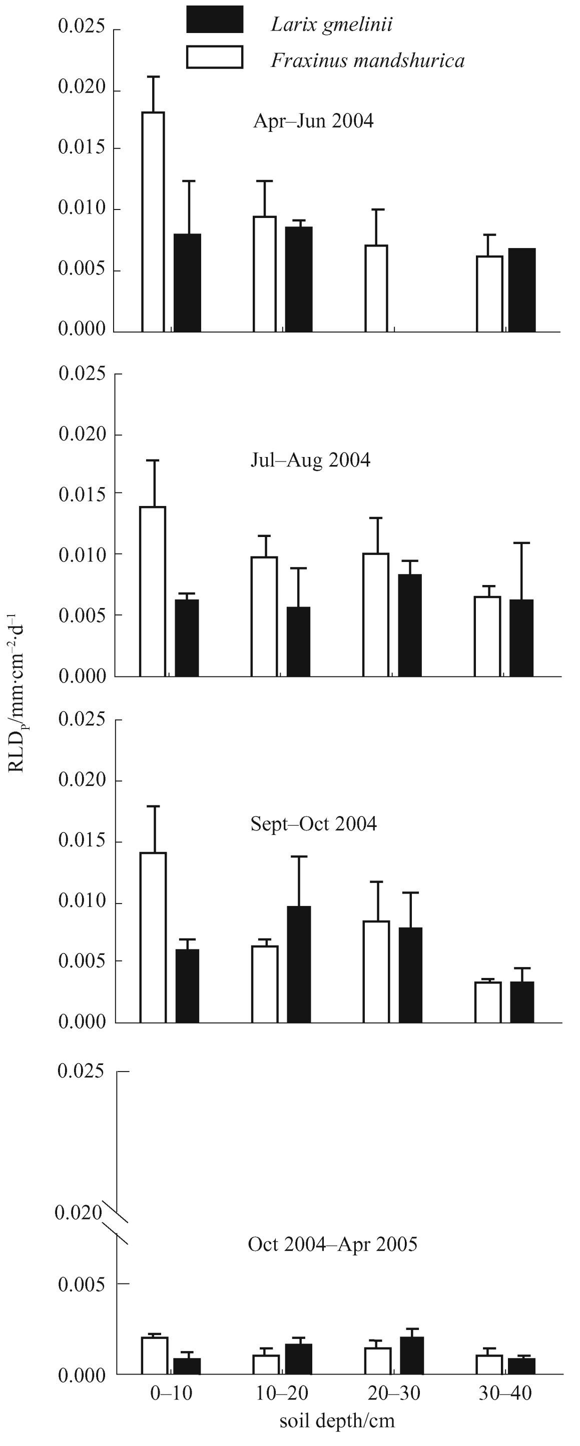

Fig. 4 Dynamics of fine root length mortality at different seasons in the *Larix gmelinii* and *Fraxinus mandshurica* plantations

et al., 2000). In temperate regions, the growth rhythm of trees (e.g. phenology) and the pattern of photosynthate allocation are both affected by the seasonal changes in climate factors (available soil nitrogen, soil temperature, air temperature and precipitation, etc). For instance, in the present study, 95%–98% of fine root mortality could be explained by such factors (Table 3). To our surprise, the dynamics of fine root mortality in the surface (0–10 cm) was not related to these factors (Table 3). One possible reason is that fine root death might result from colonization of pathogens and feeding by herbivores (e.g. nematodes) or insects. The potential causes of such phenomena deserve further study in the future.

Table 3 Multiple correlation coefficients (R^2) of fine root mortality with soil nitrogen availability, soil temperature, air temperature and precipitation at different soil depths in the *Larix gmelinii* and *Fraxinus mandshurica* plantations

soil depth/cm	R^2_{N+T}	R^2_{Tair+P}	$R^2_{N+T+Tair+P}$
L. gmelini			
0–10	0.28	0.44	0.44
10–20	0.67*	0.85**	0.98**
20–30	0.60	0.28	0.95**
30–40	0.56	0.82*	0.98**
F. mandshurica			
0–10	0.44	0.28	0.44
10–20	0.67*	0.87**	0.97**
20–30	0.60	0.29	0.95**
30–40	0.55	0.82*	0.98**

*$P < 0.05$; **$P < 0.01$

4.4 Fine root turnover

Fine root turnover is a major pathway for carbon and nutrient return to soil (Norby and Jackson, 2000). The Minirhizotron method provides a nondestructive, *in situ* observation of fine roots dynamics. In recent years, this method has been widely employed to study the dynamics of fine roots in the ecosystems of crops, grass, desert community, orchard and forest (Johnson et al., 2001). It is advantageous in that it is capable of monitoring the process of birth to death for individual roots in a continuous way, without large disturbances. Thus, a reliable estimation of the fine root turnover could be achieved using this method (Majdi, 1996; Huang et al., 1999; Tierney and Fahey, 2001). The fine root turnover was calculated by the ratio of annual fine root production (or mortality) to the mean standing crop (Johnson et al., 2001; Shi et al., 2006), or the ratio of annual fine root production to the maximum of standing crop (Gill and Jackson, 2000), which indicates the mean turnover and the minimal turnover, respectively. The quantities of biomass and length were both used in the estimation of fine root turnover. In the biomass method, root length must be transformed into biomass data depending on the factor of specific root length (SRL), in which the SRL is usually obtained by soil core. The estimation of fine root turnover was directly calculated from the fine root length in the current study. In each species, the annual fine root production and mortality were similar among different soil depths. As a result, the turnover estimations were similar either based on the production or mortality data (Table 4). Given that the fine root turnover was calculated in the whole soil profile (0–40 cm), the turnover calculated from the annual fine

Table 4 Average fine root length, annual length production, annual length mortality and turnover in the *Larix gmelinii* and *Fraxinus mandshurica* plantations

soil depth/cm	average length/mm·cm^{-2}	annual length production/ mm·cm^{-2}·a^{-1}	annual length mortality/mm·cm^{-2}·a^{-1}	turnover^1/a^{-1}	turnover^2/a^{-1}	turnover^3/a^{-1}
L. gmelinii						
0–10	0.60 (0.21)	1.39 (0.05)	1.35 (0.07)	2.31	2.23	1.38
10–20	0.68 (0.26)	1.15 (0.04)	1.25 (0.06)	1.69	1.83	0.87
20–30	0.77 (0.29)	1.00 (0.05)	1.15 (0.07)	1.30	1.50	0.76
30–40	0.33 (0.10)	0.75 (0.03)	0.73 (0.03)	2.26	2.20	1.15
0–40	0.30 (0.09)	0.94 (0.33)	0.72 (0.12)	3.09	2.37	1.79
F. mandshurica						
0–10	1.10 (0.11)	3.30 (0.05)	2.80 (0.05)	2.99	2.54	2.32
10–20	0.59 (0.13)	1.53 (0.04)	1.79 (0.04)	2.59	3.04	2.03
20–30	0.46 (0.10)	1.40 (0.03)	1.81 (0.05)	3.02	3.91	2.42
30–40	0.32 (0.09)	0.99 (0.03)	1.21 (0.04)	3.10	3.79	2.43
0–40	0.55 (0.03)	1.52 (0.19)	1.21 (0.08)	2.74	2.20	2.13

Turnover^1: Annual length production/Average length; Turnover^2: Annual length mortality/Average length; Turnover^3: Annual length production/Max average length

root production was larger than that from the fine root mortality. In the same site condition, the fine root turnover for *L. gmelinii* was slightly higher than that for *F. mandshurica*. Compared with other studies on fine root turnover in northeast China, our results on fine root turnover was markedly higher for both *L. gmelinii* and *F. mandshurica* (2–3 a^{-1}) than that for *Pinus koraiensis* (0.9 a^{-1}) in the Changbai Mountain (Shan et al., 1993) and the *Populus maximowiczii* plantation in the Liaoning Province (1.4 a^{-1}, Li et al., 2001). The difference in methods used might be a major reason causing such a result, because the soil core method (collecting root $\leq$ 2 mm in diameter) was used in their studies, while the minirhizotron method was used in ours. There is a major difference between the two methods in estimating fine root turnover (Huang et al., 1999). Moreover, our results on fine root turnover are also higher than the value of 0.56 a^{-1} for broad-leaved deciduous forests in the same latitude (Hendrick and Pregitzer, 1993). The fine roots with diameters less than 2 mm were all included to calculate the fine root turnover in their study. However, the mean diameter of fine roots in our study was less than 0.50 mm (most of them were less than 0.40 mm). Therefore, our turnover result is higher than theirs. In addition, Wells et al. (2002) also found that fine root lifespan increased from 70 to 131 d with the fine root diameter increasing from 0.25 to 0.5 mm for *Prunus persica*, and when the diameter was more than 0.5 mm, the lifespan might be extended to 213 d. Therefore, the estimation of fine root turnover was substantially affected by different diameter criteria. Generally, fine root turnover decreases with increasing diameter (Eissenstat and Yanai, 1997; Gill and Jackson, 2000). It should be noted that the current observation was only conducted within one year, and the result might be a short-term phenomenon. However, the annual fine root production and mortality and turnover reflect indefinitely the dynamics of fine roots in *L. gmelinii* and *F. mandshurica* species. Thus, they may shed new light on understanding of the processes of carbon allocation between the above- and belowground parts in these two species.

5 Conclusions

(1) The mean RLD_P of *L. gmelinii* (0.0045 ± 0.0022 mm·cm^{-2}·d^{-1}) was markedly lower than that of *F. mandshurica* (0.0077 ± 0.0001 mm·cm^{-2}·d^{-1}). The mean RLD_P was largest in the surface (0–10 cm), and lowest at the bottom (30–40 cm) for both species. The mean RLD_M also showed a similar pattern for both species. Moreover, fine root production and mortality showed seasonal dynamics. A total of 41.7% and 39.7% of fine root production for *F. mandshurica* occurred in spring and summer, respectively, while the corresponding values were 24.0% and 51.2% for *L. gmelinii*. On the other hand, for *F. mandshurica*, the fine root mortality mainly occurred in spring (34.3%) and summer (34.0%). However, for *L. gmelinii*, it mainly occurred in summer (28.5%) and autumn (32.3%). For both species, fine root production and mortality were relatively small in winter.

(2) The annual fine root production and mortality were lower for *L. gmelinii* than for *F. mandshurica*. The annual fine root production and mortality for *L. gmelinii* were 0.94 ± 0.33 mm·cm^{-2}·a^{-1} and 0.72 ± 0.12 mm·cm^{-2}·a^{-1}, respectively, compared with the values of 1.52 ± 0.19 mm·cm^{-2}·a^{-1} and 1.21 ± 0.08 mm·cm^{-2}·a^{-1} for *F. mandshurica*, respectively. The annual fine root production and mortality were both largest in the surface, but smallest at the bottom at different soil depths. On the other hand, the rates of fine root turnover showed small differences between the two species. The turnover of *L. gmelinii* was 3.1 a^{-1} (based on annual fine root production) and 2.4 a^{-1} (based on annual fine root mortality), respectively. As to *F. mandshurica*, the corresponding values were 2.7 a^{-1} and 2.2 a^{-1}, respectively.

(3) Analysis of single-factor correlation indicates that fine root production is influenced by soil nitrogen availability, soil temperature, air temperature and precipitation. However, the degrees are different and depend on the factors examined. Moreover, no obvious correlations are found between fine root mortality and those factors. Multiple correlation analysis suggests that an integrative influence including aboveground (air temperature and precipitation) and belowground (soil nitrogen availability and soil temperature) factors, largely contributes to the dynamics in fine root production (more than 80% of the variations) and mortality (more than 95% of the variations) in both species.

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References

Anderson L J, Comas L H, Lakso A N, Eissenstat D M (2003). Multiple risk factors in root survivorship: a 4-year study in Concord grape. New phytologist, 158: 489–501

Bloomfield J, Vogt K A, Wargo P M (1996). Tree root turnover and senescence. In: Wiasel Y, Bshel A, Kafkafi U, eds. Plant Roots: The Hidden Half (second edition, revised and expanded). New York: Marcel Dekker, Inc., 363–381

Burke M K, Raynal D J (1994). Fine root growth phonology, production, and turnover in a northern hardwood forest ecosystems. Plant and Soil, 162: 135–146

Burton A J, Pregitzer K S, Hendrick R L (2000). Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forest. Oecologia, 125(3): 389–399

Canadell J, Jackson R B, Ehleringer J B, Mooney H A, Sala O E, Schulze E D (1996). Maximum rooting depth of vegetation types at the global scale. Oecologia, 108(4): 583–593

Cheng Y H, Han Y Z, Wang Q C, Wang Z Q (2005). Seasonal dynamics of fine root biomass, root length density, specific root length and soil resource availability in a *larix gmelini* plantation. Acta Phytoecologica Sinica, 29: 403–410 (in Chinese)

Craine J, Tremmel D (1995). Improvements to the minirhizotron system. Bulletin of the Ecological Society of America, 76: 234–235

Eissenstat D M, Yanai R D (1997). The ecology of root lifespan. Advances in Ecological Research, 27: 1–60

Eissenstat D M, Yanai R D (2002). Root Lifespan, efficiency, and turnover. In: Waisel Y, Eshel A, Kafkafi U, eds. Plant Roots: The Hidden Half. 3rd Edition. New York: Marcel Dekker, Inc., 221–238

Fahey T J, Hughes J W (1994). Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest. Journal of Ecology, 82: 533–548

Farrar J F, Jones D L (2000). The control of carbon acquisition by roots. New Phytologist, 147: 43–53

Fogel R (1985). Roots as primary producers in below-ground ecosystems. In: Fitter A H, Atkinson D, Read D J, Usher MB, eds. Ecological interactions in soil: Ecological interactions in soil: plants, microbes and animals. Oxford (UK): Blackwell, 23–36

Gill R A, Jackson R B (2000). Global patterns of root turnover for terrestrial ecosystems. New phytologist, 147: 13–31

Hendrick R L, Pregitzer K S (1992). The demography of fine roots in a northern hardwood forest. Ecology, 73: 1094–1104

Hendrick R L, Pregitzer K S (1993). The dynamics of fine root, length, biomass, and nitrogen content in two northern hardwood ecosystems. Canadian Journal of Forest Research, 23: 2507–2520

Hendrick R L, Pregitzer K S (1996). Applications of minirhizotrons to understand root function in forests and other natural ecosystems. Plant and Soil, 185: 293–304

Huang J H, Han X G, Chen L Z (1999). Advances in the research of (fine) root biomass in forest ecosystems. Acta Ecologica Sinica, 19: 270–277 (in Chinese)

Jackson R B, Reynolds H L (1996). Nitrogen and ammonium uptake for single- and mixed-species communities grown at elevated CO_2. Oecologia, 105(1): 74–80

Johnson M G, Tingey D T, Phillips D L, Storm M J (2001). Advancing fine root research with minirhizotrons. Environmental and Experimental Botany, 45(3): 263–289

Joslin J D, Henderson G S (1987). Organic matter and nutrients associated with fine root turnover in a white oak stand. Forest Science, 33: 330–346

Li P Z, Fan S H, Wang L H, Xu S M (2001). Productivity and turnover of fine roots in poplar tree and grass roots. Chinese Journal of Applied Ecology, 12: 829–832 (in Chinese)

Majdi H (1996). Root sampling methods–applications and limitations of minirhizotron technique. Plant and Soil, 185: 255–258

Matamala R, Gonzàlez-Meler M A, Jastrow J D, Norby R J, Schlesinger W H (2003). Impacts of Fine Root Turnover on Forest NPP and Soil C Sequestration Potential. Science, 302(5649): 1385–1387

Mei L, Han Y Z,Yu S Q, Shi J W, Wang Z Q (2006). Impact Factors on Fine Roots Seasonal Dynamics in Manchurian ash Plantation. Scientia Silvae Sinicae (in Chinese), (in press)

Mei L, Wang Z Q, Cheng Y H, Guo D L (2004). A review: factors influencing fine root longevity in forest ecosystem. Acta Phytoecologica Sinica, 28(5): 704–710 (in Chinese)

Norby R J, Jackson R B (2000). Root dynamics and global change: seeking an ecosystem perspective. New Phytologist, 147: 3–12

Powell S W, Day F P Jr (1991). Root production in four communities in the Great Dismal Swamp. American Journal of Botany, 78 (2): 288–297

Pregitzer K S (2003). Woody plants, carbon allocation and fine roots. New Phytologist, 158(3): 421–423

Pregitzer K S, Zak D R, Maziasz J, DeForest J, Curtis P S, Lussenhop J (2000). Fine root growth, mortality, and morphology in a factorial elevated atmospheric $CO_2 \times$ soil N availability experiment. Ecological Applications, 10: 18–33

Raich J W, Nadelhoffer K J (1989). Belowground carbon allocation in forest ecosystems: Global trends. Ecology, 70: 1346–1354

Schenk H J, Jackson R B (2002). The global biogeography of roots. Ecological Monographs, 72(3): 311–328

Shan J P, Tao D L, Wang M, Zhao S D (1993). Fine roots turnover in a broadleaved Korean pine forest of Changbai Mountain. Chinese Journal of Applied Ecology, 4: 241–245 (in Chinese)

Shi J W, Yu S Q, Yu L Z, Han Y Z, Wang Z Q, Guo D L (2006). Application of Minirhizotron in Fine Root Studies. Chinese Journal of Applied Ecology (in Chinese) (in press)

Steele S J, Gower S T, Vogel J G, Norman J M, (1997). Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiology, 17(8–9): 577–587

Tierney G L, Fahey T J (2001). Evaluation of minirhizotron estimates of fine root longevity in the forest floor of a temperate broadleaf forest. Plant and Soil, 229: 167–176

Vogt K A, Gxier C C, Vogt D J (1986). Production, turnover and nutrient dynamics of above-and belowground detritus of world forests. Advances in Ecological Research, 15: 303–377

Vogt K A, Vogt D J, Palmiotto P A, Boon P, O'Hara J, Asbjornsen H (1996). Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and soil, 187(2): 159–219

Wells C E, Glenn D M, Eissenstat D M (2002). Soil insects alter fine root demography in peach (*Prunus persica*). Plant, Cell and Environment, 25(3): 431–439

Zhang X Q, Wu K H (2001). Fine root production and turnover for forest ecosystem. Scientia Silvae Sinicae, 37(3): 126–138 (in Chinese)

Zhang X Q, Wu K H, Murach D (2000). A review of methods for fine-root production and turnover of trees. Acta Ecologica Sinica, 20(5): 875–883