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RESEARCH ARTICLE

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Impact factors on fine root seasonal dynamics in *Fraxinus mandshurica* plantations

Abstract Fine root turnover plays important roles in carbon allocation and nutrient cycling in forest ecosystems. Seasonal dynamics of fine roots is critical for understanding the processes of fine root turnover. From May to October 2002, soil core method was used for estimating the seasonal pattern of fine root (diameter <1 mm) parameters (biomass, specific root length (SRL) and root length density (RLD)) in a Manchurian ash (*Fraxinus mandshurica*) plantation located at the Maoershan Experiment Station, Heilongjiang Province, northeast of China. The relationships of fine root biomass, SRL and RLD with available nitrogen in soil, average soil temperature per month in 10 cm depth and soil moisture content were analyzed. Seasonal variation of fine root biomass was significant ($P<0.05$). The peak values of fine root biomass were observed both in spring and in autumn, but SRL and RLD were the highest in spring and lowest in autumn. Specific root length and root length density were higher in spring and summer, which means that fine root diameter was thinner. In autumn, both parameters decreased significantly due to secondary incrassation of fine root diameter or the increase of tissue density. Seasonal dynamics of fine roots was associated with available nitrogen in soil, soil temperature in 10 cm depth and moisture content. Fine root biomass has a significant relationship with available NH_4^+-N in soil. Available NO_3^--N in soil, soil temperature in 10-cm depth and moisture content have a positive correlation with fine root biomass, SRL and RLD, although these correlations are not significant ($P>0.05$). But the compound effects of soil available N, soil temperature and soil moisture content are significant to every root parameter. The variations of these three root parameters in different seasons show different physiological and ecological functions in different growing periods.

Keywords *Fraxinus mandshurica*, fine root, biomass, root length density (RLD), specific root length (SRL), seasonal dynamics

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1 Introduction

Forest fine roots follow a dynamic process of growth, senescence, death and regrowth (fine root turnover) (Norby and Jackson, 2000). This process consumes 10%–75% of the primary production of a terrestrial ecosystem (Bloomfield et al., 1996), and in many forest ecosystems, this consumption of fine roots accounts for more than one half of net primary production (Vogt et al., 1996). Thus, this consumption of primary production caused by fine root turnover will have an influence on the carbon allocation process and pattern between above and below-ground in ecosystems (Nadelhoffer, 2000). Studying the seasonal pattern of fine roots will help us understand fine root turnover and the roles carbon plays in nutrient cycling in forest ecosystems (Norby and Jackson, 2000).

Fine root dynamics exhibit as the seasonal dynamics of biomass, which is influenced by climate (Pregitzer et al., 2000) and soil (Hendrick and Pregitzer, 1993). Such dynamics reflect fine root sensitivity to soil moisture content, temperature and nutrients (Vogt et al., 1996; Huang et al., 1999; Zhang and Wu, 2001). The climate and soil of temperate zones have typical rules in different seasons; fine root biomass in some forest ecosystems peaks in spring (Burke and Raynal, 1994) or in summer (Hendrick and Pregitzer, 1993). Fine root biomass may have two peaks both in autumn and in spring (Chen et al., 2004), which means that more carbon was allocated to the root system (Nadelhoffer and Raich, 1992). Many researchers conclude that the increase of fine root biomass is related to moisture and nutrients absorbed during boom season (Hendrick and Pregitzer, 1993; Chapin et al., 2002), although the reason why it increases in autumn remains unexplained. The seasonal variation of fine root biomass in temperate zones is not only controlled by some external factors (such as the climate and soil) but also influenced by the variation of trees' physiological function (such as the allocation and accumulation of nutrients and photosynthetic products). Root length density (RLD) and specific root length (SRL) are important structural parameters, which reflect more functions of roots than biomass (Robinson et al., 2003). When considering seasonal dynamics of fine roots, it is necessary to account for functions that fine roots show at different stages, i.e. to explain the increase or decrease of fine root biomass by analyzing the variation of RLD and SRL.

Ash (*Fraxinus mandshurica*) is a kind of valuable broad-leaved tree whose roots begin to grow very early while its leaves start to spread very late in spring. The seasonal variation of biomass of fine roots and carbon consumption are very complicated. This paper analyzes the characteristics of the seasonal variation of biomass and its relationship with available nitrogen in soil, soil temperature and moisture content by sampling root biomass regularly from the beginning to the end of the growing period. Moreover, we associated biomass with RLD and SRL to analyze carbon allocation and the physiological and ecological relationships of seasonal dynamics of fine roots by the seasonal variation of RLD and SRL.

2 Methods

2.1 Site description

The research plots are located in the Maoershan Experiment Station of Northeast Forestry University (127°30′–127°34′E, 45°21′–45°25′N), which is in the temperate zone with a continental monsoon climate. The annual average temperature is 2.8°C, annual average precipitation 723 mm, annual average evaporation 1,094 mm, frost-free period 120–140 days, and cumulative temperature more than 10°C is 2,526°C. The plots are upside the hill, with elevation of 506.3 m, slope of 15°, dark brown soil and average soil thickness about 40 cm. The pure forest has 17-year-old ash trees and the area of research plot is 20 m × 30 m. The average height of the ash tree is 10.4 m and the average diameter at breast height is 9.1 m.

2.2 Sampling and classification

In the middle of the months from May to October, 2004, we sampled in every plot (20 m × 30 m) six times, 24 soil cores were sampled each time with a drill, for a total of 144 sampling points. In each sampling point, a soil core with inner diameter of 60 mm is divided into three layers from top to bottom of soil (together), each layer is 10 cm (0–10 cm, 10–20 cm, 20–30 cm) (Smit et al., 2000). Then these samples were swilled by running water in a sieve and the clear roots refrigerated at low temperature. When the samples were brought back to the laboratory, we distinguished the roots of ash tree from the roots of shrub and weed which will be removed later. These samples were classified according to their diameters (< 1 mm, 1–2 mm, 2–5 mm, >5 mm) (Smit et al., 2000). In this research, the roots whose diameters are less than 1 mm were defined as fine roots. Both living and dead roots will be distinguished by analyzing their external form, colour and elasticity (Wang et al., 1995; Smit et al., 2000).

2.3 Fine root biomass, root length density and specific root length

Every month, fine root samples of 2/3 times biomass were dried in each layer for 48 h and later weighed by electronic scale. The other 1/3 samples were put on a glass pane with gridding paper on it and the length of roots was measured with the assistance of forceps (precision of 0.1 mm), after which they were dried and weighed respectively. This allows us to get the SRL according to the ratio of the length to dry weight of these samples. Then, the dry weight of these two samples was used to get the biomass of each layer. Root length density of each layer can be obtained by the product of SRL and biomass of each sample. The sum of biomass or RLD in the three layers is the biomass or RLD of each soil sample. We then calculate SRL of soil samples with different diameters. Finally, we calculate the average of the parameters of those 24 soil samples and change them into the biomass per area units (g/m^2), RLD per area units (m/m^2) and SRL per units (m/g).

2.4 Available nitrogen in soil, temperature and moisture content

Sampling of some soil was done using a 20-mesh sieve, then later sealed and refrigerated quickly. Moisture content, available NH_4^+-N and NO_3^--N in the soil were analyzed. Phenol disulfonic acid colorimetry was used to analyze the content of available NO_3^--N in soil and KCl lixiviation-amylon colorimetry to analyze the content of the available NH_4^+-N. Available NO_3^--N and NH_4^+-N in soil in this research are the average of the 24 soil samples. The average temperatures over the recent six years are used to present soil temperature each month. Taking into consideration that 70%–80% roots distribute in the soil layer 0–20 cm deep, we adopt the data of temperature and soil moisture content in the 10-cm soil layer.

2.5 Root order sampling and measurement

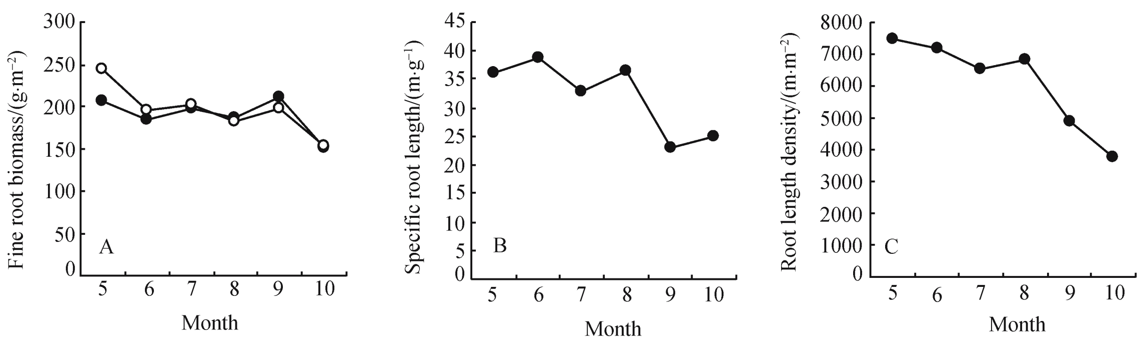
Three random sampling points were chosen in the plot on May 15, July 15 and September 15, 2003. Samples were collected with flat shovels (20 cm × 20 cm × 20 cm) in the two soil layers (0–10 cm and 11–20 cm). We wiped off soil on the roots, picked out the whole root, put them in plastic bags and finally subjected them to cold preservation (1–3°C). All the samples will be brought back to the lab and put into the refrigerator (–20°C). Any soil particles adhering to the roots will be very carefully removed with forceps and the root rinsed clean with deionized water. Then different orders of roots will be distinguished at a low temperature (2–3°C). According to Pregitzer et al. (2002), roots sampled in each sampling point will be divided into different segments, and then these roots can be analyzed according to those root segments. The distal roots will be defined as the first order, the second order, the third order, the fourth and the fifth order fine roots. Forceps will be used to pick off each root, which will be put into a medium dish with ice water according to their order, respectively, and the number of roots in each order will be counted. At the same time, the length and diameter of each root (precision of 0.001 m) will be measured by microscope (× 20) with micrometer.

3 Results and analysis

3.1 Seasonal dynamics of fine roots

Two peak values appeared in May (205 ± 8.5 g/m^2) and September (211 ± 19.7 g/m^2) in a growing period (Fig. 1 A), and they reach their minimum in October (150 ± 11.3 g/m^2). There was no significant difference between the biomass of live roots from May to September ($P > 0.05$). Except for June, biomass of all the months had a significant difference from the biomass of October ($P < 0.05$). Both dead and live fine root biomass have the same seasonal patterns, the dead biomass in May was significantly higher and dead biomass in October was significantly lower than the other months, but there was no significant difference between June, July and August ($P < 0.05$). Specific root length and root length density have different seasonal patterns with biomass (Fig. 1B and C). From May to August, the average SRL of live fine roots is 36.4 ± 1.7 m/g without any significant difference. From September to October, SRL experienced a sharp decline to 24.9 ± 1.8 m/g (average decline of 30%), which led to the major difference between SRL in spring and summer ($P < 0.05$) (Fig. 1B). Root length density is on a decline during May to October (Fig. 1C), but statistically shares the same rule of variation with SRL. The biomass of September is the largest (Fig. 1A), but the diameter and RLD of September is much smaller than they previously were ($P < 0.05$) (Fig. 1B and C), which indicates that the structural components and functions of the fine roots in autumn can be different from spring and summer (Eissenstat and Yanai, 1997).

The fine roots of ash (diameter < 1 mm), including the first to the fourth order, are mainly occupied by 90% of the first order roots (diameter less than 0.26 ± 0.08 mm) (Table 1). From spring (May) to autumn (September), the first order roots declined by 2%, the third order roots (average diameter of 0.47 ± 0.13 mm) increased by 13%, and the fourth order roots (average diameter of 0.86 ± 0.33 mm) increased by 40% (Table 1). The research on different order roots shows that the average root length of these four orders in the 0–10 cm layer declined from 36.65 ± 2.24 mm in May to 27.26 ± 3.06 mm in September (decline by 25%), while that in the 10–20 cm layer declined from 29.91 ± 2.24 mm to 27.19 ± 2.37 mm (decline by 10%). These indicate that the decline of RLD and SRL (Fig. 1) in autumn is mainly caused by an increase in the number of big-diameter roots and decrease in individual root length.



● Live fine root, ○ Dead fine root.

Fig. 1 Seasonal dynamics of fine root biomass (A), SRL (B) and RLD (C) in *Fraxinus mandshurica* plantation

Table 1 Mean number proportions (%) of fine roots of five orders in different months and soil layers

Month	Soil depth	Percent of fine roots number /%				
		First-order	Second-order	Third-order	Fourth-order	Fifth-order
May 15	0–10 cm	91.1	6.4	1.7	0.6	0.1
	10–20 cm	87.3	9.1	2.5	0.8	0.3
July 15	0–10 cm	90.9	5.6	2.5	0.7	0.3
	10–20 cm	87.3	8.2	3.2	0.9	0.4
Sep. 15	0–10 cm	88.4	8.0	2.2	1.0	0.4
	10–20 cm	87.2	8.3	2.6	1.3	0.6

3.2 Impact of available nitrogen in soil on seasonal dynamics of fine roots

Available nitrogen in soil has significant variations during the growing season due to different mineralization rates (Table 2). This differentiation controls the dynamic process of fine roots (Nadelhoffer, 2000; King et al., 2002). In the ash plantation, the available nitrogen in soil is high in summer and low in spring and autumn (8.8–22.4 mg/kg), the variation of available NH_4^+-N (2.3–6.7 mg/kg) is less than the variation of available NO_3^--N (5.5–19.5 mg/kg). Regression analysis showed that the impact of available NH_4^+-N on fine root seasonal dynamics is greater than available NO_3^--N, and the biomass of fine root has a significantly positive correlation with available NH_4^+-N (live root: $R^2 = 0.647$, $P < 0.05$; dead root: $R^2 = 0.704$, $P < 0.05$) (Table 2). Though RLD and SRL have a positive correlation with available NH_4^+-N, this correlation is not significant. Bivariate linear regression indicates that the compound effects of available NH_4^+-N and NO_3^--N influence the seasonal biomass variation of both dead and live fine roots, with impact forces at 87% and 75%, respectively. The impact forces of available nitrogen in soil on SRL and RLD are only 50% and 17%. It is clear that the seasonal variation of available nitrogen in soil has an impact on the growth and death of fine roots (Nadelhoffer, 2000; Norby and Jackson, 2000). Moreover, available NH_4^+-N plays a main role.

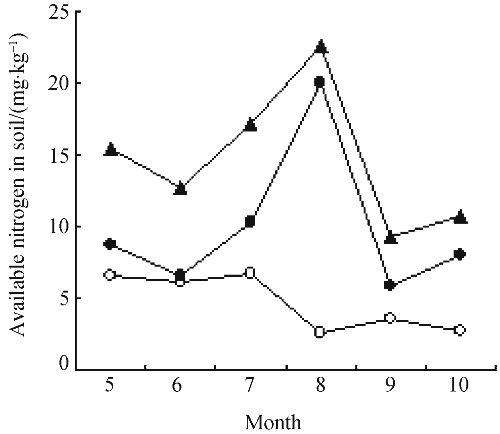


Fig. 2 Seasonal variation of available nitrogen in *Fraxinus mandshurica* plantation soil

3.3 Impact of soil temperature and moisture content on seasonal dynamics of fine roots

Soil temperature and moisture content influence the availability of soil nutrients and the growth of fine roots (Pregitzer et al., 2000; Zhang and Wu, 2001). The seasonal variation of soil temperature is greater than soil moisture content (Fig. 3). The soil moisture content in the plot (0–30 cm) is higher (35%–40%) during growing season (except for autumn because of drought). In addition, rainfall has little impact on the seasonal variation of soil moisture content. Seasonal dynamics of fine roots and soil moisture content in the 0–10 cm layer have some influence on the biomass of live roots ($R^2 = 0.405$) and little impact on other parameters (Table 2). The seasonal variation of soil temperature is very obvious. Average temperature in 10–cm layer in growing

Table 2 Correlation of fine root parameters (biomass, RLD and SRL) seasonal dynamics and soil resources of *Fraxinus mandshurica* plantation

Parameters	R^2						
	NH_4^+	NO_3^-	$NH_4^+ + NO_3^-$	ST	SM	ST+SM	$NH_4^+ + NO_3^- + ST + SM$
Live fine root biomass /(g·m^{-2})	0.647*	0.085	0.874*	0.312	0.405	0.701	0.981*
Dead fine root biomass /(g·m^{-2})	0.704*	0.001	0.746*	0.135	0.053	0.184	0.930*
Root length density /(m·m^{-2})	0.390	0.039	0.505	0.551	0.068	0.628	0.859*
Specific root length /(m·g^{-1})	0.129	0.013	0.166	0.420	0.333	0.770*	0.863*

* $P < 0.05$; ST and SM are soil temperature and soil moisture content respectively.

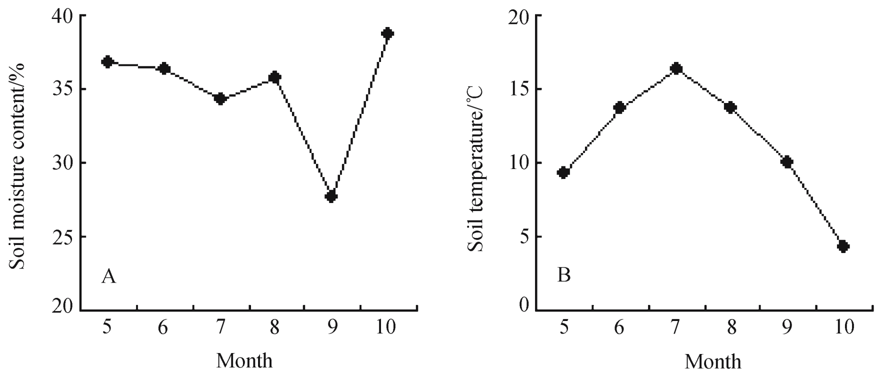


Fig. 3 Variations of soil moisture content (A) and temperature (B) in 10-cm soil depth during the growing period

season is 4–17°C. The impact of this monthly average temperature on fine roots (average $R^2 = 0.354$) is greater than that of moisture content (average $R^2 = 0.215$), and the impact on RLD and SRL (55% and 42%, separately) is greater than the impact on biomass (31% and 13%, separately), but these impacts are not significant. Bivariate linear regression has indicated that the compound effects of the soil temperature and moisture content in 10-cm layer have a significant influence on dynamics of live fine roots; the impact on biomass, RLD and SRL of fine roots are 70%, 63% and 77%, respectively ($P < 0.05$), while the impact on biomass of dead roots is only 18%.

3.4 Synthetic effect of available soil resources on the seasonal pattern of fine roots

Unitary analyses indicate that the impacts of different kinds of soil resources on seasonal dynamics of fine roots are quite different. Linear multianalysis shows that available nitrogen in soil (available NH_4^+-N and NO_3^--N), average soil temperature of each month and moisture content have remarkable influences on biomass of both live and dead fine roots, RLD and seasonal dynamics of SRL ($P < 0.05$) (Table 2). The seasonal dynamics of the available soil sources can reasonably explain 98% biomass of live fine roots, 93% biomass of dead roots, 86% RLD and seasonal dynamics of SRL (Table 2). These show that the growth, death, density, form and structure of ash roots are mainly controlled by the comprehensive impact of the available soil sources (Norby and Jackson, 2000).

4 Discussion

4.1 Seasonal dynamics of fine roots of an ash tree

Growth of fine roots is a complicated physiological and ecological process (Eissenstat and Yanai, 1997) in two modes: 1) fine roots grow earlier than leaves (mainly broad-leaf species); 2) fine roots grow simultaneously with leaves (mainly evergreen conifer tree) (Pregitzer et al., 2000). The former mode needs carbohydrate stored in roots from the previous year (Pregitzer, 2003). While the latter needs photosynthetic products by new leaves, the growth of fine roots peaks when leaves spread out completely.

There are two fine root biomass peaks of ash during its growing season (Fig. 1A). In terms of the observation of ash roots in Maoershan, it is clear that roots start growing in April when the upper soil layer begins to unfreeze and leaves start to spread out in the last ten days of May. The growth of roots is 20–25 days earlier than that of leaves. Before leaves spread out, carbon consumed by the growth of roots is supplied mainly by carbohydrate stored in roots from the previous year. After the new leaves can produce carbohydrate, the production of photosynthesis will be allocated to the growing parts of fine roots. In the middle and last ten days of September, when all the leaves have fallen off, the biomass and the number of the third and fourth order roots increased by 13%–40% (Table 1) while SRL and RLD decreased (Fig. 1B and C). These mean that diameters of roots or density have increased. The research of Pregitzer et al. (2002) indicates that the amount of nitrogen in the cells of roots with larger diameters is small and respiration is very weak with a large amount of non-structural carbohydrate, which will do support the growth of roots in early spring and the respiration of roots during the period between defoliation and dormancy (Langley et al., 2002).

The increase of biomass caused by the increase of the diameters of ash roots or density may have two functions: one is to store more carbohydrate to meet root growth requirement during the long period before leaves start spreading out. Another is the secondary incrassation of root tissues (including the increase of root tissue density), the decrease of root respiration, and the increase of resistance and lifespan to accommodate the decrease of temperature (Eissenstat and Yanai, 1997; Pregitzer et al., 2000). Similar results can also be concluded from the research of Hendrick and Pregitzer (1993). In spring, the SRL and biomass of ash fine roots is large, which addresses the need for more nutrients and moisture content during growth (Eissenstat and Yanai, 1997). The increase of biomass in autumn (as the SRL is small, the diameters are large) is to store more carbohydrate for growth next spring. Those conditions show that in different seasons, roots play different physiological functions through the regulation of biomass, RLD and SRL.

4.2 The relationship between fine root seasonal dynamics and environmental factors

Available nitrogen in soil mainly comes from mineralization of organic matter. Because of the seasonal change of temperature and moisture content, mineralization of nitrogen varies with the seasonal rotation (Pregitzer et al., 2000). When the soil moisture content of Maoershan is adequate for years, mineralization of nitrogen will increase with the increase of temperature. Consequently, available nitrogen in soil (especially the available NH_4^+-N) will be the leading factor that can influence the seasonal dynamics of fine roots (Table 2). Research on *Acer saccharum* by Burton et al. (2002) shows that in spring, the growth of fine roots of ash will increase with increasing temperature and has a positive correlation with the availability of nitrogen. The seasonal dynamics of ash is controlled by the comprehensive impact of soil available resources (Table 2), which can account for 93%–98% biomass change and 86% of the change in RLD and SRL.

In spring (May and June), the soil temperature is low (6–10°C) while the fine roots grow very fast. Pregitzer et al. (2000) maintain that soil cumulative temperature is the main factor accounting for those developments. The biomass of dead roots reaches its peak in May, due to the accumulation of dead roots as they decompose very slowly in winter (Yang et al., 2001). In summer (July and August) soil temperature and available nitrogen in soil reach their peaks (the total amount of available nitrogen is 17.5–22.4 mg/kg). At this time, tree crowns grow steadily and biomass stabilizes, which indicates that the growth of roots is related to the photosynthetic ability of leaves (Eissenstat and Yanai, 1997). In autumn, the soil temperature falls (4–10°C) and mineralization rate of nitrogen begins to slow down gradually (total amount of nitrogen 9.5–10.5 mg/kg). The biomass of live fine roots in a forest ecosystem gets smaller with defoliation while biomass of dead roots increases (Hendrick and Pregitzer, 1993; Eissenstat and Yanai, 1997). Biomass of live roots reaches its second peak in September (Fig. 1A) while SRL and RLD decrease dramatically (Fig. 1B and C), which shows the thinner roots die and the short, thick roots come out. This also explains the large biomass of fine roots in September. In October, the biomass of fine roots decreased sharply (Fig. 1A), due partly to decreases in temperature and nutrients. That relationship has a direct connection with the lack of supply of carbon after the defoliation (Pregitzer et al., 2002).

The dynamics of fine roots from late autumn to next spring are often neglected (Pregitzer et al., 2000). The average temperature of Maoershan in April is 4.8°C. The difference between the highest and lowest temperatures is –1.9 –11.2°C, the average soil temperature in 10-cm layer is 1–2°C. The biomass of ash fine roots begins to increase in April. The biomass of live fine roots (179 g/m) and dead fine roots (129 g/m^2) in the middle ten days of April, 2003 is 16% and 18% higher respectively than those of October, 2002; and 13% (205 g/m^2) and 47% (243 g/m^2) lower than those of May, 2002. The research conducted by Wang et al. (2002) shows that roots of *Picea mariana* begin to respirate when the soil (10-cm depth) temperature is 2°C. When the soil temperature is 3°C, the fine roots of white oak (*Quercus alba*) grow at a rate of 1.8 mm/d (Teskey and Hinckley, 1981), which means that fine roots of forests in boreal and temperate zones begin to grow and act physiologically at low temperatures.

5 Conclusions

There are two notable peaks of fine root biomass in ash plantation with soil core method: one is in spring, and the other is in autumn. However, both SRL and RLD have only one peak, respectively. In spring and summer, the parameters of SRL and RLD are high, which means that fine roots are thin. Those two parameters decrease sharply in autumn, reflecting different physiological functions in different growing seasons.

A simple relativity analysis indicates that the impacts of available nitrogen, soil temperature and moisture content on seasonal dynamics of fine roots are different from each other. Biomass of fine roots has a notable correlation with available NH_4^+-N in soil. Available NO_3^--N, soil temperature (10-cm depth) and moisture content have a correlation with biomass of fine roots, SRL and RLD, but this correlation is not notable.

The compound impacts of available nitrogen, soil temperature and soil moisture content on all the parameters of fine roots are very significant, accounting for 93%–98% variation of biomass, 86% of RLD and 86% of SRL, which shows that seasonal dynamics of ash fine roots are mainly controlled by the comprehensive impacts of soil sources availability.

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