

# Dynamics of fine roots in five Chinese temperate forests

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Received: 29 September 2009 / Accepted: 7 January 2010  
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**Abstract** We used a minirhizotron method to investigate spatial and temporal dynamics of fine roots (diameter  $\leq 2$  mm) in five Chinese temperate forests: Mongolian oak forest, aspen-birch forest, hardwood forest, Korean pine plantation and Dahurian larch plantation. Fine root dynamics were significantly influenced by forest type, soil layer, and sampling time. The grand mean values varied from 1.99 to 3.21 mm cm<sup>-2</sup> (root length per minirhizotron viewing area) for the fine root standing crop; from 6.7 to 11.6  $\mu\text{m cm}^{-2} \text{ day}^{-1}$  for the production; and from 3.2 to 6.1  $\mu\text{m cm}^{-2} \text{ day}^{-1}$  for the mortality. All forests had a similar seasonal “sinusoidal” pattern of standing crop, and a “unimodal” pattern of production. However, the seasonal dynamics of the mortality were largely unsynchronized with those of the production. The minimum values of standing crop, production and mortality occurred in March for all forests, whereas the maximum values and occurrence time differed among forest types. The standing crop, production and mortality tended to decrease with soil depth. The different spatiotemporal patterns of fine roots among the forests highlight the need for forest-specific

measurements and modeling of fine root dynamics and forest carbon allocation.

**Keywords** Minirhizotron · Root biomass · Root mortality · Root production · Seasonality

## Introduction

The biomass of fine roots represents only a small proportion of the total biomass in forest ecosystems (Vogt et al. 1996), but the net primary production (NPP) of fine roots accounts for one-third to three-quarters of annual NPP (Brassard et al. 2009; Gower et al. 2001; Hendrick and Pregitzer 1993b; Jackson et al. 1997; Ruess et al. 1996). In Chinese temperate forests, for example, roots and associated mycorrhizae contribute to 52–83% of the total soil surface CO<sub>2</sub> flux (Wang and Yang 2007). The small diameter, large surface area, short lifespan, and low C:N ratio of fine roots make them disproportionately important in carbon cycling, water and nutrient acquisition, plant survival and reproduction in forest ecosystems (Eissenstat and Yanai 1997; Fornara et al. 2009). A better understanding of fine root production and mortality is urgently needed in order to model forest ecosystem structure and function (Jackson et al. 1997). Fine root dynamics, however, remain one of the least understood aspects of forest ecology (Brassard et al. 2009), mainly because of the inaccessibility of root systems (Fahey and Hughes 1994; Hendricks et al. 2006). To date, few studies on fine roots have been conducted in Chinese temperate forests (Wang et al. 2006b).

Traditional techniques (e.g., soil coring, in-growth core, whole root system excavation, trenching, etc.) have been used to investigate root biomass, but they cannot be applied

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directly to measure root phenology, longevity and turnover (Majdi et al. 2005; Vogt et al. 1998). Minirhizotrons provide a nondestructive in situ method for directly studying fine root dynamics (Johnson et al. 2001). As part of a comprehensive effort to characterize carbon and nutrient budgets in the temperate forests in northeastern China (e.g., Wang and Yang 2007; Wang et al. 2006a), this study aimed at quantifying the spatial and temporal dynamics of fine roots (diameter  $\leq 2$  mm) in five temperate forests: Mongolian oak (*Quercus mongolica* Fisch.), aspen-birch (*Populus davidiana* Dode and *Betula platyphylla* Suk.), hardwood (dominated by *Fraxinus mandshurica* Rupr., *Juglans mandshurica* Maxim., and *Phellodendron amurense* Rupr.) forests, Korean pine (*Pinus koraiensis* Sieb. et Zucc.) and Dahurian larch (*Larix gmelinii* Rupr.) plantations. Because spatiotemporal variations in fine roots closely interact with soil resource availability and forest characteristics, quantifying the fine root production and mortality in these forests will improve our understanding and predictions of carbon and nutrient cycling in the forest ecosystems under changing environmental conditions.

The first objective of this study was to compare standing crop, production and mortality of fine roots among the five temperate forests. Fine root biomass, production and mortality have been reported to be related to soil properties, tree species, stand characteristics, and climatic factors (Brassard et al. 2009; Jackson et al. 1997; Vogt et al. 1996). Recently, Finér et al. (2007) synthesized root biomass data from 150 stands across European countries, and found that correlations between root biomass and site characteristics were species specific. For example, the fine root biomass decreased with stand age for European beech stands, but increased for Scots pine stands. Tierney et al. (2003) also indicated that strong relationships between fine root production and air temperature in hardwood forests vary geographically. Here, we hypothesize that fine root biomass, production and mortality are significantly different among the five forests in this study, even though they have similar stand age and climatic conditions (Wang et al. 2006a).

The second objective was to examine fine root phenology for the five forests. The timing of fine root production and mortality is synchronized with foliage growth and senescence in northern forests (Brassard et al. 2009). Fine root production generally increases in early spring, peaks in late spring to mid-summer, decreases in autumn, and reaches its minimum in winter months (Burke and Raynal 1994; Fahey and Hughes 1994; Hendrick and Pregitzer 1993a; Steele et al. 1997). Nevertheless, fine root mortality is more evenly distributed throughout the year (Burton et al. 2000; Hendrick and Pregitzer 1996), generally peaks in late summer, and is lowest in winter (Burke and Raynal 1994; Hendrick and Pregitzer 1993a; Norby et al. 2004;

Steele et al. 1997). Fine root biomass, as the budget of production and mortality, generally peaks in mid to late summer and is minimal in late autumn to early winter (Ericsson et al. 1996; Fogel 1983; Gower et al. 1992). We hypothesize that the seasonal dynamics of fine roots are coincident to the changes in soil temperature, because the forest phenology is highly coupled with the temperature in this region (Wang et al. 2006a). However, the temporal patterns of fine roots may differ between coniferous and deciduous forests.

The third objective was to examine vertical distribution patterns of fine roots in the five forests. Fine roots mainly absorb water and nutrients from the soil, store reserve food, and synthesize certain growth hormones (Kozłowski and Pallardy 1997). Commonly, fine roots are highly concentrated in the upper soil layer, mainly because water and nutrient availability decline abruptly with soil depth. However, environmental stresses may change fine root distribution patterns. For example, soil temperature controls the vertical distribution of fine roots in Canadian boreal forests (Steele et al. 1997), while soil moisture is the key control in Chinese pine (*Pinus tabulaeformis* Carr.) forests in the arid Loess Plateau (Zhou and Shangguan 2007). We hypothesize that the fine roots in the five forests have different vertical distribution patterns because of divergent species composition and site conditions.

## Materials and methods

### Site description and experimental design

This study was conducted at the Maoershan Forest Ecosystem Research Station, northeastern China (45°20'N, 127°30'E). Forest types and landscape are representative in this region, with an average altitude of 400 m above sea level and an average slope of 10–15°. The parent material is granite bedrock and the soil is Haplumbrepts or Eutroboralfs. The region has a continental monsoon climate with a mean annual precipitation of  $\sim 700$  mm, a mean annual evaporation of  $\sim 880$  mm, and a mean annual air temperature of 2.8°C. The frost-free period is between 120 and 140 days, with an early frost in September and late frost in May. Refer to Wang et al. (2006a) for details.

The experimental design included five forest types, with three random replicate plots in each forest type. The five forest types, which are representative of this region, were Mongolian oak, aspen-birch, hardwood forests, Korean pine and Dahurian larch plantations. The plots were 20 m  $\times$  30 m fixed plots that occurred within an area of 2 km<sup>2</sup>. The stand and site characteristics of the five forests are summarized in Table 1. The understory was mainly composed of *Syringa* spp., *Euonymus* spp., *Spiraea* spp.,

**Table 1** Site and stand characteristics of the five forests

Forest type	Location/slope/aspect	Age (year)	Density (trees ha <sup>-1</sup> )	BA (m <sup>2</sup> ha <sup>-1</sup> )	DBH (cm)	Overstory composition (1/10)
Oak forest	Upper slope/23°/S	59	2111	37.8	15.4	10 QM + TA + BP
Aspen-birch forest	Mid slope/16°/SW	58	2050	29.8	14.7	5 PD 1 FM 1 TA 1 AM 1 QM 1 BP + JM + PA + UP
Hardwood forest	Toe slope/7°/N	53	1889	31.1	18.2	6 FM 2 JM 1 QM 1 UP + AM – PA
Larch plantation	Toe slope/3°/SW	50	1417	32.8	18.6	9 LG 1 UP
Pine plantation	Mid slope/12°/NW	42	2528	38.3	13.9	7 PK 2 BP 1 FM – QM

BA basal area at breast height, DBH mean tree diameter at breast height

PD, *Populus davidiana* Dode; AM, *Acer mono* Maxim.; BP, *Betula platyphylla* Suk.; LG, *Larix gmelinii* Rupr.; QM, *Quercus mongolica* Fisch; JM, *Juglans mandshurica* Maxim.; FM, *Fraxinus mandshurica* Rupr.; TA, *Tilia amurensis* Rupr.; PK, *Pinus koraiensis* Sieb. et Zucc.; PA, *Phellodendron amurense* Rupr.; UP, *Ulmus japonica* (Reh.) Sarg.

The numbers in the overstory composition stand for the proportion of the basal area of each tree species compared to the total, while the “+” and “–” stand for proportions of <5 and <2% compared to the total, respectively

*Deutzia* spp., *Acanthopanax* spp., *Schizandra chinensis*, etc. The ground vegetation mainly consisted of *Carex* spp., *Brachybotrys paridiformis*, *Cardamine leucantha*, *Equisetum* spp., *Ostericum* spp., *Urtica* spp., etc.

#### Monitoring the dynamics of fine roots, leaf area, soil temperature and moisture

The dynamics of fine roots ( $\leq 2$  mm) were monitored with a minirhizotron (MR) method (Johnson et al. 2001). We randomly installed five acrylic minirhizotron (MR) tubes (90 cm length  $\times$  5.1 cm inner diameter) in each plot in the autumn of 2006. The MR tubes were installed at a 45° angle off-vertical (Johnson et al. 2001), and reached a vertical depth of 40 cm, where few roots existed (Wang, personal observation). Each tube was scribed with 40 (1.8 cm  $\times$  1.4 cm) rectangular frames that were sequentially numbered along its length from the bottom to the top, and totaled 100.8 cm<sup>2</sup> of viewing area for each tube. Each tube was permanently sealed at the bottom and extended ~20 cm out of the soil, where it was tied with black adhesive tape and then yellow tape to minimize the effects of light and temperature. The open ends of the tubes were capped with plastic black sheaths between the measurements.

One year after the MR tubes were installed (i.e., October 2007), as recommended in the literature (Johnson et al. 2001), we collected fine root images from each tube. The images were taken with a micro-video camera system (Bartz Technology, Santa Barbara, CA, USA) every 2 weeks from March to October 2008, a total of 14 sampling times. We did not take images during winter because of thick snowpack (~40 cm) and frozen soils. At each

sampling time, 40 MR images were taken from the top to the bottom of each tube.

The images were digitized with the Roottracker software (version 2.0, David C. Tremmel, Duke University Phytron, Durham, NC, USA). Fine roots were classified as woody or herbaceous, live or dead, based on root color and architecture (Belsky 1994; Vogt and Persson 1990). Fine root morphology (length, diameter, order) and type (live, dead, or disappeared) were recorded. We were unable to confidently separate the woody fine roots by tree species. For each MR tube, the length of fine roots for each root category was averaged for each 10-cm soil depth. The whole soil profile was divided into four layers: 0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm. The standing crop of fine roots was presented as the root length per unit MR viewing area (mm cm<sup>-2</sup>). The production and mortality between the sampling points were calculated by summing all new root lengths and dead root lengths, respectively, at the end of the interval for each MR tube. Fine root production and mortality were presented as fine root length per unit MR viewing area per day ( $\mu\text{m cm}^{-2} \text{ day}^{-1}$ ).

Meanwhile, the photosynthetically active radiation (PAR) over and under the canopy of the hardwood forest, the soil temperature ( $T_5$ ) and the moisture ( $M_5$ ) at 5 cm depth were continuously measured at an under-canopy and an adjacent open-area meteorological station with PAR sensors, thermocouples and water content reflectometers, respectively (CS616-L, Campbell Scientific, Logan, UT, USA). These sensors were attached to a Campbell Scientific CR1000 datalogger. The data were recorded at 15 min intervals and averaged daily. The leaf area index (LAI) of the hardwood forest was calculated by Beer's law:

$$\text{LAI} = [-\ln(I_u/I_o)]/k, \quad (1)$$

where  $I_u$  and  $I_o$  are the PAR under and over the canopy, respectively.  $k$  is the light extinction coefficient. We adopted the mean  $k$  value for deciduous broadleaved forests (0.54) as the  $k$  value in this study (White et al. 2000).

### Data analysis

The experimental unit was the plot, and the MR tube was the subsample. Therefore, the means and standard errors of standing crop, production and mortality of fine roots were calculated by averaging plot-level measurements. Based on fine root phenology, we divided the whole growing season into three stages: early growing season (from March to May), when the leaves were out, mid growing season (from June to August), and late growing season (from September to October), when the leaves commenced falling.

The GLM procedure in the SAS 8.2 software package (SAS Institute Inc., Cary, NC, USA) was used to conduct an ANOVA on the main effects on standing crop, production and mortality. Duncan's multiple range test was applied to test significant differences in standing crop, production and mortality among forest types and soil layers by growing season stage.

## Results

### Comparison of fine roots among forest types

The standing crop of fine roots was significantly ( $P < 0.05$ ) different among forest types, soil layers and sampling times

(Table 2). During the early and mid growing season (from March to August), the standing crops in the pine and hardwood forests were significantly greater than those in the larch and oak forests (Fig. 1). In the late growing season (from September to October), however, there was no significant difference in standing crop among the forests. The grand means of the fine root standing crops in the pine, larch, oak, aspen-birch, and hardwood forests across the whole growing season were  $3.05 \pm 0.04$  (mean  $\pm$  SE),  $1.99 \pm 0.14$ ,  $2.16 \pm 0.68$ ,  $2.51 \pm 0.66$ , and  $3.21 \pm 0.58 \text{ mm cm}^{-2}$ , respectively.

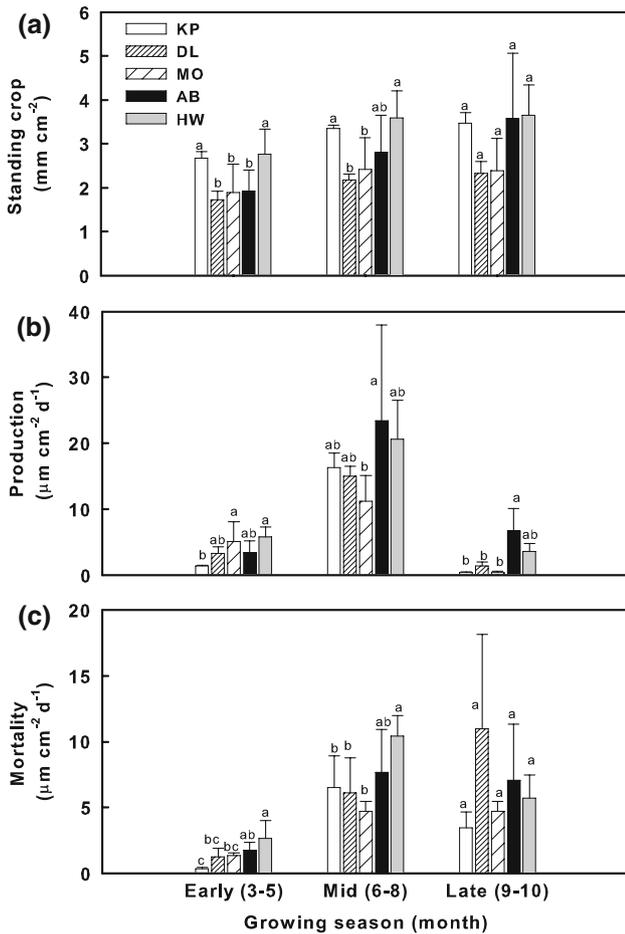
Both production and mortality of fine roots significantly ( $P < 0.05$ ) varied with forest type, soil layer, and sampling time (Table 2). In the early growing season, the production and mortality varied from 1.4 to 5.7 and 0.4 to  $2.7 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$ , respectively. Forests with higher production tended to have a higher mortality (Fig. 1). In the mid growing season, production reached its maximum, ranging from  $11.2 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$  in the oak forest to  $23.4 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$  in the aspen-birch forest. Meanwhile, the mortality substantially increased and varied from  $4.7 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$  in the oak forest to  $10.4 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$  in the hardwood forest. In the late growing season, production substantially declined in all forests and varied from 0.3 to  $6.7 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$ , while mortality remained relatively high and varied from  $3.4 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$  in the pine forest to  $11.0 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$  in the larch forest. For all forests, mortality was higher than production (Fig. 1). The grand means of fine root production in the pine, larch, oak, aspen-birch, and hardwood forests across the whole growing season were 6.9, 7.5, 6.7, 11.6, and  $11.1 \text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$ , respectively, while

**Table 2** Summary of significant main effects on standing crop, production and mortality of fine roots

Root variable	Main effect	df	MSE	F	P
Standing crop ( $\text{mm cm}^{-2}$ )	Forest type	4/3640	223.3	16.7	<0.001
	Soil layer	3/3640	1588.3	119.0	<0.001
	Sampling time	12/3640	55.5	4.2	<0.001
	Forest type * soil layer	12/3640	281.6	21.1	<0.001
Production ( $\text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$ )	Forest type	4/3640	0.0045	4.2	0.002
	Soil layer	3/3640	0.0178	16.6	<0.001
	Sampling time	12/3640	0.0179	16.7	<0.001
	Forest type * soil layer	12/3640	0.0035	3.3	<0.001
	Forest type * sampling time	48/3640	0.0018	1.7	0.002
	Soil layer * sampling time	36/3640	0.0034	3.2	<0.001
Mortality ( $\text{ } \mu\text{m cm}^{-2} \text{ day}^{-1}$ )	Forest type	4/3640	0.0012	4.5	0.001
	Soil layer	3/3640	0.0130	47.9	<0.001
	Sampling time	12/3640	0.0033	12.1	<0.001
	Forest type * soil layer	12/3640	0.0013	4.6	<0.001
	Soil layer * sampling time	36/3640	0.0008	2.9	<0.001

df Degrees of freedom (numerator/denominator), MSE mean square error

F and P values are given. An asterisk denotes the interaction of two main effects



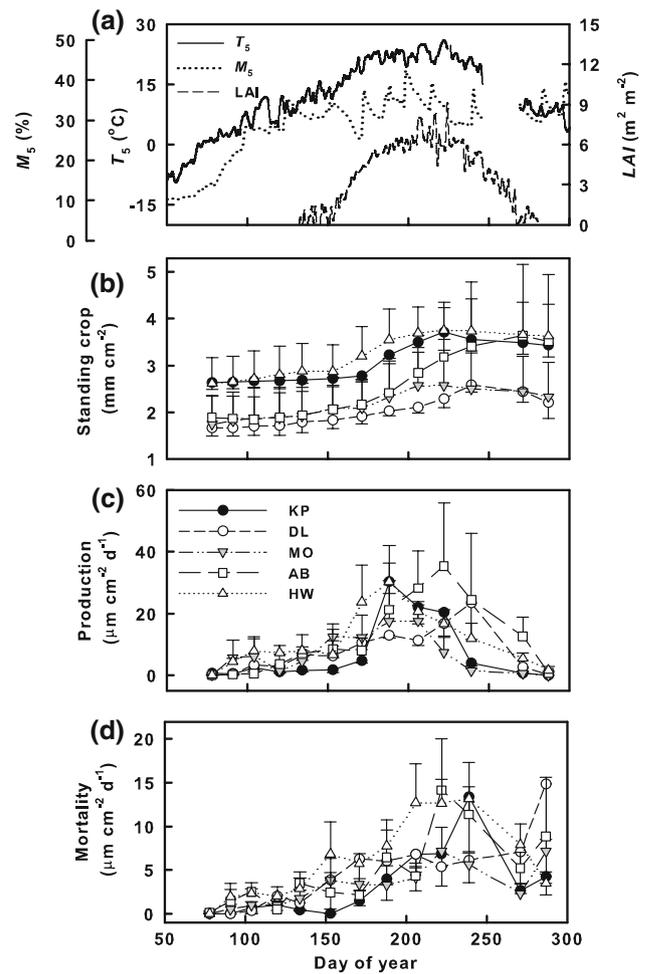
**Fig. 1** Comparison of standing crop (a), production (b) and mortality of fine roots (c) among the five forests during the early (March–May), mid (June–August), and late (September–October) growing season of 2008. The letters *a, b, c* in the figures denote significantly different groups of means among the forest types based on Duncan’s tests at the  $\alpha = 0.05$  level. *KP, DL, MO, AB, and HW* stand for Korean pine, Dahurian larch, Mongolian oak, aspen-birch, and hardwood forests, respectively. The error bars are standard errors ( $n = 3$ )

those of fine root mortality were 3.2, 4.6, 3.2, 4.8, and  $6.1 \mu\text{m cm}^{-2} \text{day}^{-1}$ , respectively.

#### Seasonal dynamics of fine roots, leaf area, soil temperature and moisture

The daily mean soil temperature at 5 cm depth ( $T_5$ ) showed an overall unimodal seasonal trend, peaking in late July to early August (Fig. 2a). The soil moisture content at 5 cm depth ( $M_5$ ) increased in spring when  $T_5$  increased and the snow was melting; it fluctuated during the growing season, largely corresponding to precipitation events. The LAI of the hardwood forest showed a unimodal seasonal pattern, with its maximum value occurring in late July.

All forests had similar “sinusoidal” seasonal patterns of fine root standing crop, but different peak values and



**Fig. 2** Seasonal dynamics of soil temperature ( $T_5$ ), soil moisture ( $M_5$ ) at 5 cm depth, leaf area index (LAI) in the hardwood forest (a), standing crop (b), production (c), and mortality of fine roots (d) in the five forests. *KP, DL, MO, AB, and HW* stand for Korean pine, Dahurian larch, Mongolian oak, aspen-birch, and hardwood forests, respectively. The error bars are standard errors ( $n = 3$ )

occurrence times (Fig. 2b). The minimum standing crop was observed on DOY (day of the year) 78 for all forests (except for the aspen-birch forest, where it was observed on DOY 104), whereas the maximum occurred on DOY 222 in the oak and pine forests, DOY 239 in the larch and hardwood forests, and DOY 271 in the aspen-birch forest. The maximum standing crops for the pine, larch, oak, aspen-birch, and hardwood forests were 3.71, 2.58, 2.57, 3.64, and  $3.76 \text{ mm cm}^{-2}$ , respectively. They were 41, 55, 48, 98, and 44% higher than the minima, correspondingly.

Overall, the fine root production showed a unimodal seasonal pattern for all forests, while the mortality delayed its peak and bounced at the end of the growing season for some forests (Fig. 2c, d). Minimum production and mortality were observed on DOY 78 for all forests, ranging from 0 to  $0.2 \mu\text{m cm}^{-2} \text{day}^{-1}$  and 0 to  $10 \mu\text{m cm}^{-2} \text{day}^{-1}$ , respectively. Maximum production

varied from  $17.5 \mu\text{m cm}^{-2} \text{day}^{-1}$  in the oak forest to  $35.4 \mu\text{m cm}^{-2} \text{day}^{-1}$  in the aspen-birch forest, while maximum mortality varied from  $7.2 \mu\text{m cm}^{-2} \text{day}^{-1}$  in the oak forest to  $14.9 \mu\text{m cm}^{-2} \text{day}^{-1}$  in the larch forest. Maximum production occurred on DOY 188 for the pine and hardwood forests, DOY 206 for the oak forest, DOY 222 for the aspen-birch forest, and DOY 239 for the larch forest. The maximum mortality for the aspen-birch forest was synchronized with the peak production, whereas those for the other forests were delayed ( $\sim 16$  days for the oak forest, and  $\sim 50$  days for the pine, larch and hardwood forests).

Pooling all data across the five forests, the fine root production and mortality were positively correlated to  $T_5$  ( $R^2 = 0.59$ ,  $F_{2,63} = 91.3$ ,  $P < 0.001$  for production;  $R^2 = 0.39$ ,  $F_{2,63} = 39.6$ ,  $P < 0.001$  for mortality), and exponentially increased with  $M_5$  ( $R^2 = 0.36$ ,  $F_{3,62} = 17.5$ ,  $P < 0.001$  for production;  $R^2 = 0.23$ ,  $F_{2,63} = 19.3$ ,  $P < 0.001$  for mortality) (Fig. 3).

#### Vertical distribution of fine roots

The grand mean of standing crop across the five forests significantly ( $P < 0.05$ ) decreased with soil depth across the entire year (Fig. 4a). The mean values ranged from  $3.5$  to  $4.5 \text{ mm cm}^{-2}$  at  $0\text{--}10$  cm depth,  $2.7$  to  $3.6 \text{ mm cm}^{-2}$  at  $10\text{--}20$  cm depth,  $1.7$  to  $2.8 \text{ mm cm}^{-2}$  at  $20\text{--}30$  cm depth, and  $0.9$  to  $1.5 \text{ mm cm}^{-2}$  at  $30\text{--}40$  cm depth, which accounted for 38, 30, 20, and 12% of the total, respectively.

Overall, the fine root production and mortality decreased with soil depth, except during the late growing season

(Fig. 4b, c). Neither production nor mortality differed significantly among the soil layers in the late growing season, varying from 1 to  $4 \mu\text{m cm}^{-2} \text{day}^{-1}$  and 5 to  $9 \mu\text{m cm}^{-2} \text{day}^{-1}$ , respectively. The relative contributions from production at  $0\text{--}10$ ,  $10\text{--}20$ ,  $20\text{--}30$ , and  $30\text{--}40$  cm averaged 46, 22, 17, and 15% of the total, respectively; those from mortality averaged 58, 25, 11, and 6% of the total, correspondingly.

In addition to the effect of sampling time, forest type also significantly affected the vertical distribution patterns of the biomass, production and mortality of fine roots (Table 2; Fig. 5). Generally, the vertical distribution of fine root production exhibited a greater within-forest-type variability than those of standing crop and mortality (Fig. 5b). There was no significant difference ( $P > 0.05$ ) in production among the soil layers for the larch, oak and aspen-birch forests.

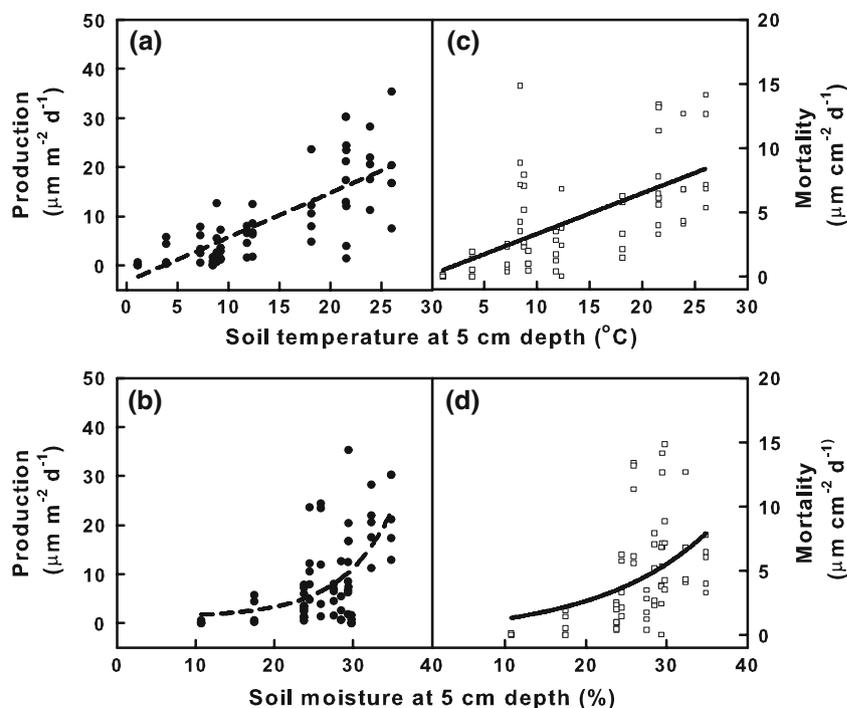
As an exception among the forest types, the standing crop, production and mortality for the larch forest were relatively evenly distributed within the  $0\text{--}40$  cm soil layer; i.e., they did not significantly differ ( $P > 0.05$ ) among the soil layers (Fig. 5a–c).

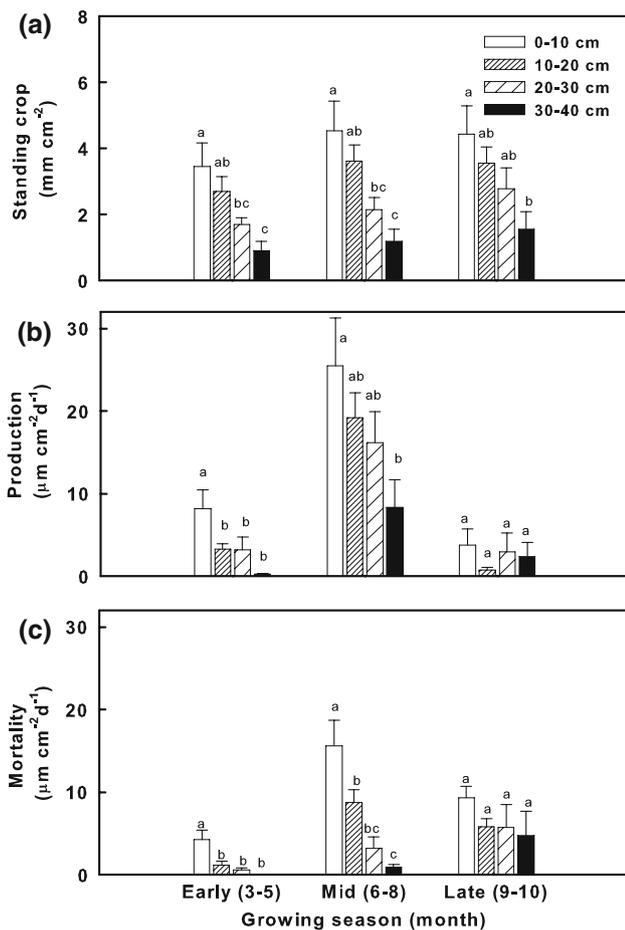
## Discussion

### Fine roots in temperate forests

Our data showed that fine root production and mortality differed significantly among the five forest types (Table 2), especially in the early and mid growing seasons (Fig. 1).

**Fig. 3** Fine root production (a, b) and mortality (c, d) versus soil temperature ( $T_5$ ) and moisture ( $M_5$ ) at 5 cm depth, obtained by pooling data across the five forests

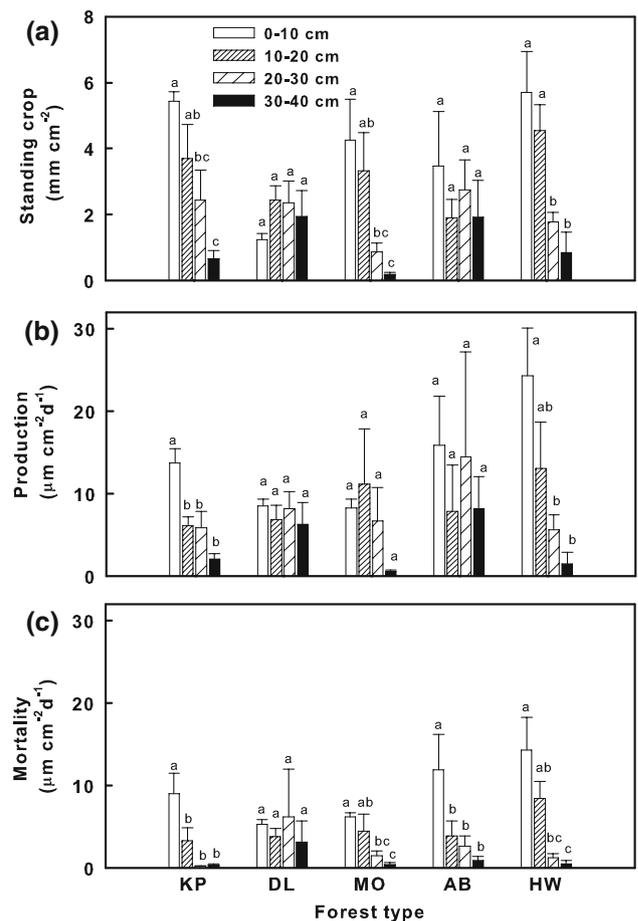




**Fig. 4** Vertical profiles of standing crop (a), production (b) and mortality of fine roots (c) across the five forests during the early (March–May), mid (June–August), and late (September–October) growing season of 2008. The letters *a*, *b*, *c* in the figures represent significantly different groups of grand means among the soil layers based on Duncan’s test at the  $\alpha = 0.05$  level. The error bars are standard errors ( $n = 3$ )

The mean rate of production (6.7–11.6  $\mu\text{m cm}^{-2} \text{day}^{-1}$ ) was almost twice as high as that of mortality (3.2–6.1  $\mu\text{m cm}^{-2} \text{day}^{-1}$ ), leading to a net increase in fine root biomass. This result supports our first hypothesis and is in agreement with previous studies (e.g., Coleman et al. 2000; Steele et al. 1997).

A great variation in fine root measurements exists in our five forest types, in agreement with previous studies of many temperate forests using similar nondestructive methods (Burton et al. 2000; Coleman et al. 2000; Hendrick and Pregitzer 1993b, 1997; Price and Hendrick 1998; Schroerer et al. 1999; Tingey et al. 1995). This variability may be attributed to both biotic and abiotic factors, such as species composition, stand age, mycorrhizal fungi, root herbivores, geographic location, soil resource availability, etc. (Eissenstat and Yanai 1997; Espeleta et al. 2009). Forest type or tree species strongly influences fine root



**Fig. 5** Vertical relative distributions of standing crop (a), production (b) and mortality of fine roots (c) across the whole growing season for the five forests. *KP*, *DL*, *MO*, *AB*, and *HW* stand for Korean pine, Dahurian larch, Mongolian oak, aspen-birch, and hardwood forests, respectively. The letters *a*, *b*, *c* in the figures present significant difference groups of grand means among the soil layers based on Duncan’s tests at the  $\alpha = 0.05$  level. The error bars are standard errors ( $n = 3$ )

characteristics (Eissenstat and Yanai 2002; Fitter 2002). Generally, gymnosperms have greater mean diameters and lower specific root lengths and root length densities than angiosperms (Pregitzer et al. 2002; Wang et al. 2006b). However, fine roots are opportunistic and exploitive in their growth habits, adapting rapidly to changes in climate, nutrient and water supply (Persson 2000). Therefore, the growth, distribution, morphology and architecture of fine roots are also strongly influenced by local environmental conditions (Comas and Eissenstat 2004; Pregitzer et al. 2002). The strong effect of site conditions may overshadow the effect of species composition. We found that the fine root production and mortality were closely related to soil water content (Fig. 3), probably because the water availability influenced nutrient uptake and carbon allocation to the belowground compartment (Persson 2000).

Temperature can influence plant performance indirectly by affecting water and nutrient uptake (Kozłowski and Pallardy 1997). Theoretically, there is an optimum temperature for root growth that varies with genotype (McMichael and Burke 2002). However, we observed a linear relationship between fine root production/mortality and soil temperature (Fig. 3), probably because our temperature did not exceed the optimal temperature limits. This result is consistent with previous studies of boreal forests (Ruess et al. 1996; Steele et al. 1997).

It should be noted that the application of different methodologies may make it difficult to perform a cross-comparison of the fine root data. First, compared to our biweekly sampling intervals, most studies performed with the MR method have used monthly sampling intervals or even longer intervals throughout the growing season (e.g., Hendrick and Pregitzer 1993b; Majdi et al. 2005; Steele et al. 1997). During the sampling intervals, some fine roots with short longevities may disappear (Tingey et al. 2003). Failure to account for such short-lived fine roots could result in a >28% underestimate of the fine root production relative to the 2-week interval (Johnson et al. 2001). Second, many similar studies on fine root biomass have only included tree roots, but our standing crop included both woody and herbaceous fine roots. Third, sampling depths and units vary in the literature. In this study, all standing crops were presented based on a 2.52 cm<sup>2</sup> viewing window. To convert our data into the standing crop per soil area within a soil depth of 0–40 cm, we simply multiplied our values by 40; thus, the standing crop per soil area varied from 0.8 km m<sup>-2</sup> for the larch plantation to 1.3 km m<sup>-2</sup> for the hardwood forest. These values are lower than those reported by Jackson et al. (1997) for temperate deciduous (5.4 km m<sup>-2</sup>) and coniferous forests (6.1 km m<sup>-2</sup>) within various soil depths. Fourth, it is known that the installation of MR tubes will potentially disturb root growth (Johnson et al. 2001). Ideally, the first set of measurements should be taken after an appropriate equilibration time has elapsed in order to allow the system to recover. In this study, we allowed the system to equilibrate for 1.5 years. Collectively, a detailed description of these issues may be required for across-study comparisons.

#### Seasonal and vertical distribution patterns of fine roots

A distinctive characteristic of the forest region of north-eastern China is that high temperature and precipitation coincide with vegetation growth in the summer season (Wang et al. 2006a). During July and early August, temperature and precipitation are high (Fig. 1), and the leaf area simultaneously reaches its maximum (Fig. 2), which provides an abundant supply of carbohydrates for below-ground production and consumption. The overall

seasonality of fine root production in this study was coincident with temporal changes in soil temperature and moisture (Figs. 2, 3; Ruess et al. 1996; Steele et al. 1997). This seasonal pattern agrees well with the general pattern of fine root production in northern forests (Brassard et al. 2009).

However, the fine root mortality was largely unsynchronized with the production (Fig. 3) in that the mortality lagged behind the production and significantly bounced at the end of the growing season for most forests (Fig. 2). As it is the budget of production and mortality, the standing crop of fine roots showed a general “sinusoidal” seasonal pattern, in agreement with previous studies (Ericsson et al. 1996; Fogel 1983; Gower et al. 1992).

Although the general seasonal trends in production and standing crop of fine roots were similar for the five forests, the values and occurrence times of maximum production, mortality and standing crop differed among the forest types (Fig. 2). This result suggests that various belowground carbon allocation patterns exist among forest types, and knowledge of these patterns is urgently required in order to understand and model carbon and nutrient cycling in forest ecosystems (Jackson et al. 1997). This phenomenon may be associated with forest phenology and leaf habits (Fahey and Hughes 1994; Pregitzer et al. 2000). The Korean pine forest had the earliest production peak but next to last (the larch stand was last) mortality peak among the five forests (Fig. 2), which may be related to its evergreen leaf habit. Interestingly, the only deciduous coniferous boreal forest—the Dahurian larch forest—had a unique seasonal pattern of fine root production and mortality (Fig. 2). Its maximum values of both production and mortality occurred last among the five forests. The mortality tended to increase as the growing season proceeded, and reached its maximum before the soil froze (Fig. 2).

Our results on the seasonal patterns of fine root production, mortality and biomass accumulation for various forest types are significant since they will allow errors in fine root estimates introduced by destructive methods to be reduced. The maximum–minimum soil coring method has been widely used to quantify fine root biomass and NPP because it is simple and requires relatively less labor than sequential coring (Gower et al. 1999). Theoretically, the core sampling should be implemented when the fine root mass (both biomass and necromass) reaches its maximum and minimum during the year (Hertel and Leuschner 2002; McClaugherty et al. 1982). However, many previous studies on fine root biomass and NPP have used soil coring methods without knowing the fine root phenology, which undoubtedly introduced biases. The minimum fine root production may occur in the winter (Burke and Raynal 1994; Fahey and Hughes 1994; Hendrick and Pregitzer 1993a; Steele et al. 1997), but it is impractical to take soil

cores at that time because of the frozen soil. Based on this study, coring for minimum values should be implemented in early spring, when production and mortality reach their minima during the year for all forests, while the best time to perform coring for the maximum value would be forest type specific (Fig. 2). Root production in the pine and oak forests reached its maximum on DOY 239 (i.e., the sum of biomass and necromass reached its maximum), whereas those for the other forests reached their maxima on DOY 287 (Fig. 2). Even though fine root production declined afterwards, production did not cease (Fig. 2). If we assume that fine root decomposition is negligible within 1–2 months, then we recommend that the maximum coring should be performed at the end of the growing season.

The production, mortality and standing crop of fine roots tended to decrease vertically along the soil profile, with the greatest production and mortality occurring in the 0–10 cm layer, especially during the early and mid growing season (Figs. 4, 5). This result agrees with previous studies of other forests (Baddeley and Watson 2004; Coleman et al. 2000; Hendrick and Pregitzer 1996; Jackson et al. 1996; Price and Hendrick 1998; Ruess et al. 2003; Steele et al. 1997). The vertical distribution pattern of fine roots is controlled by a myriad of endogenous (i.e., species genetic features) and exogenous (i.e., soil physical, chemical, biological properties) factors (Brassard et al. 2009), among which soil temperature, water and nutrient availability may be the dominant factors in temperate forests (Burton et al. 2000; Hendrick and Pregitzer 1996; Rytter and Hansson 1996). Evidence suggests that shallower fine roots may be more heavily involved in soil nutrient acquisition and carbon cycling, whereas the deeper fine roots may be of greater importance for water capture (Brassard et al. 2009). In this study, soil water limitation was generally not serious for the vegetation due to the coincidence of temperature and precipitation during the growing season. High temperatures in the upper soil are conducive to microbial activity and nutrient mineralization, and thus provide an environment well suited to fine root growth (Fig. 3).

Nevertheless, the vertical distribution patterns of the fine roots varied with growing season and forest type (Figs. 4, 5). During the early and mid growing season, the increased growth of leaf area and aboveground woody tissues demands a large amount of water and nutrients, as supplied by the fine roots (Hendrick and Pregitzer 1996; Rytter and Hansson 1996). Root growth strongly depends on soil water and nutrient availability (Fig. 3), which decreased abruptly with increasing soil depth. In the late growing season, the temperature decreases, tree growth ceases, litterfall occurs, and new fine root growth is no longer necessary. Thus, variability among the soil layers becomes less significant during this time (Fig. 4).

It was not clear why the fine root production of some stands was rather nonuniformly distributed vertically (Fig. 5b). We speculated that the distinctive seasonality of fine root production might result in high production variability (Fig. 5b), and may thus overshadow the vertical distribution pattern. Other possibilities include the effects of various local site conditions and species composition in these forests (Table 1). The larch plantation exhibited a different vertical distribution pattern from the other stands (Figs. 4, 5). We speculate that local site conditions are probably mainly responsible for this pattern. In this study, we classified the soil layer mechanically without considering the natural soil profile. The larch plantation was established at an abandoned crop field, where agricultural activity (plowing) had made the 0–40 cm upper soil a mixed layer. Additionally, a large amount of ground vegetation existed in the larch plantation, which may contribute to the vertical distribution pattern of fine roots. Dawson et al. (2001) reported that there was a marked shift in the distribution pattern of cherry fine root density to shallow depths when grass competition was removed.

In summary, the different patterns of temporal and vertical distributions of fine root production, mortality and standing crop among the five Chinese temperate forests highlight the need for forest-specific measurements and modeling of fine root dynamics and carbon allocation in forest ecosystems. To better understand the fine root dynamics and estimate the belowground NPP, further studies should focus on the longevity and decomposition of the fine roots in these forests.

**Acknowledgments** This research was supported by grants from the National Natural Science Foundation of China (No. 30625010), the Special Foundation for Common Benefits in Forestry (No. 200804001), and the Ministry of Science and Technology of China (No. 2006BAD03A0703). We thank the two anonymous reviewers for their valuable comments.

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