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Belowground carbon pools and dynamics in China's warm temperate and sub-tropical deciduous forests

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Abstract

We report the first estimates of pools and dynamics of microbes, roots, plant litter and soil organic carbon (SOC) in three dominant types of China's vast deciduous forest area: *Betula platyphylla*, *Quercus liaotungensis*, and *Quercus aliena varacuteserrata*. Organic matter degradation rates overshadowed litter inputs as the main determinant of the soil carbon stocks. Across the three forests, rates of litter decomposition were also indicative for turnover rates of SOC. Litter and SOC decay was faster in the sub-tropical than in the warm-temperate forests. Among the latter, SOC turnover was highest in the forest producing the higher-quality litter. Microbial biomass was, as expected, correlated with SOC content. Microbial activity, in contrast, was highest at the sub-tropical forest, despite the lower SOC availability, lower fraction of labile SOC, and lower soil microbial biomass. These results may contribute to increased understanding of controls over belowground carbon cycling in deciduous forests.

1 Introduction

With the significant increase in atmospheric greenhouse gas concentrations and the potential for global climate change, studies of the terrestrial carbon cycle have gained attention over the last 20 years (Houghton et al., 2001; Callesen et al., 2003). Soil carbon is an important terrestrial carbon reservoir and plays a key, yet poorly understood role in the global carbon cycle and its feedback to climate change (Post et al., 1982; Davidson and Janssens, 2006). Therefore, the study of soil organic carbon (SOC) dynamics is critically important to our ability to understand the global carbon cycle and its response to future global change (Davidson et al., 2000).

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Deciduous broad-leaved forests are an important forest type and the status of these forests as carbon sources or sinks has previously been assessed (Curtis et al., 2002; Stephenson and van Mantgem, 2005). Asia white birch (*Betula platyphylla* ; about 22°–53° N, 90°–135° E), East-Liaoning oak (*Quercus liaotungensis* ; about 26°–53° N, 90°–135° E) and Sharptooth oak (*Quercus aliena var. acuteserrata* ; about 22°–39° N, 92°–125° E) are widely distributed in mountainous areas in the temperate and sub-tropical zone of China (Delectis Flora Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita, 1979, 1998) and dominate important forest types in China (Chen, 1997). However, despite their high importance for the carbon budget of east Asia (Fang et al., 2007; Feng et al., 1999), soil carbon dynamics, including soil carbon pool sizes and turnover rates, have so far not been reported for these kinds of forests.

In this study, we therefore compared pools and dynamics of fine roots, soil carbon pools, and soil microbes among Asia white birch, East-Liaoning oak, and Sharptooth oak forests. The overall objective of this study was to examine soil carbon quantity and quality in these important forest types. The specific objectives of this study were: (1) to determine the total SOC pool and its components in the three forest types, and (2) to determine the rates of carbon cycling through the litter and SOC pools.

2 Materials and methods

2.1 Site description

Three deciduous broad-leaved forest types were assessed in this study: (1) Asia white birch forest; (2) East-Liaoning oak forest; and (3) Sharptooth oak forest. All three forests were growing on clay-poor soils (less than 5%), a prerequisite for allowing comparisons of SOC pools. The study sites of Asia white birch and East-Liaoning oak were located in the Donglingshan Mountains, Beijing (39°48′–40°00′ N, 115°24′–115°36′ E). These two sites were situated in the warm temperate climate zone, and the two sites were characterized by a warm temperate, semi-wet monsoon climate. Long-term mean

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annual precipitation in this area was 612 mm and mean annual air temperature was 4.8°C. The soil in both stands was classified as a Eutric cambisol (FAO-UNESCO, 1988), with a depth of about 60 cm. The Sharptooth oak forest was located in the Shennongjia Mountains, Hubei Province (31°15′–31°57′ N, 109°56′–110°58′ E). This forest was located in the sub-tropical zone, and was characterized by a sub-tropical monsoon climate, with mean annual precipitation of 1514 mm and mean annual air temperature of 10.6°C. The sandy-loam soil in this forest is classified as mountainous brown soil (FAO-UNESCO, 1988) with a depth of some 100 cm.

A 0.25 ha plot of 60-year-old Asia white birch forest (39°57′01″ N, 115°25′07″ E, elevation 1380 m a.s.l.) was selected for this study. The inclination of the site was 32°. The Asia white birch forest was dominated by Asia white birch, admixed with associated species (*Betula utilis* and *Populus alba*), and an abundance of shrubs including *Sorbus pohuashanensis*, *Lonicera japonica*, *Prunus armeniaca*, *Corylus mandshurica*, *Acer mono*, *Abelia biflora*, *Leptodermis oblonga*, *Spiraea sargentiana*, *Macrocarpium officinalis*. Tree density at the plot was 1234 trees ha^{-1}, with a mean diameter at breast height (DBH) of 13.2 cm and a mean tree height of 8.5 m.

We also selected a 0.25 ha plot of 60-year-old East-Liaoning oak forest (39°57′04″ m, 115°25′04″ E, elevation 1200 m a.s.l.), with an inclination of 28°. This East-Liaoning oak forest was dominated by East-Liaoning oak, and admixed with *B. utilis* as associated tree species and some shrubs (*Spiraea sargentiana*, *Acer mono*, *Lespedeza bicolor*, *Lonicera japonica*, *Corylus mandshurica*, and *Deutzia scabra*). Tree density was 1262 stems ha^{-1}, with a mean diameter at breast height (DBH) of 12.2 cm and a mean tree height of 6.8 m.

Last, a 0.25 ha plot of 55-year-old Sharptooth oak forest (31°30′09″ N, 110°30′29″ E, elevation 1994 m a.s.l.) was selected for the study. The inclination of the site was 30°. The Sharptooth oak forest was dominated by Sharptooth oak, admixed with associated tree species such as: *Cornus japonica* var. *Chinensis, Platyearya strobilacea, Carpinus lurczaninowii,* and *Viburnum betulifolium*, and shrubs including: *Indocalamus lessellalus*, *Viburnum* SP., *Lilsea* SP., *Rhus Chinensis, Abelia* SP., *Lespedeza* SP., and

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Coriaria sinica. Tree density was 1296 trees ha^{-1}, with a mean diameter at breast height (DBH) of 12.4 cm and a mean tree height of 7.5 m.

Primary forests of Asia white birch and East-Liaoning oak have been intensely disturbed by human activities and disappeared completely. The contemporary Asia white birch and East-Liaoning oak forests are secondary and are currently protected and naturally regenerating (Chen, 1997). Sharptooth oak forests were much less disturbed by human activities, and although our study site was not a primary forest, it has been less intensively managed/disturbed than the other two study sites. For all three species, leaves tend to appear by the end of April, and most of the litterfall occurs between early September and end of October.

2.2 Soil analyses

Five soil cores for the determination of bulk density at different depths (0–5, 5–15, 15–30, 30–45, 45–55 cm) were taken in all plots in May 2006. In July 2006, five soil columns were collected in each plot for the determination of LF-OC, HF-OC and total SOC. Samples were randomly taken with a sharp-edged metal cylinder with an inner diameter of 3 cm and a length of 10 cm. Samples were separated according to depth (0–5, 5–15, 15–30, 30–45, 45–55 cm) and the fresh samples were passed through a 2-mm sieve and manually cleaned off any visible plant tissues.

The LF-OC was determined using the density fractionation method (Sollins et al., 1984). Air-dried soils were passed through a 2 mm mesh sieve and 5.0 g (dry weight equivalent) of air-dried soils was transferred to a tube and dispersed in 20 mL of NaI solution adjusted to a density of 1.7 gmL^{-1}. The suspension in the tube was shaken thoroughly for 15 min, and after overnight standing, separated light and heavy fractions. The light fractions at the surface of the density liquid were aspirated, and trapped onto a membrane filter paper (Whatman, Grade 1:11μm), rinsed with deionized water, and then oven-dried at 50°C and weighed. Total SOC and LF-OC were determined with the dichromate oxidation method (Lovell et al., 1995). Briefly, 0.2 g of grinded soil

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was digested with 5 ml of 2 M $K_2Cr_2O_7$ and 5 ml of concentrated H_2SO_4 at 170°C for 10 min, followed by titration of the digests with 2 M standardized $FeSO_4$. The HF-OC was determined by subtracting LF-OC from the total SOC.

2.3 Soil microbial biomass carbon and activity

Five soil core samples per plot were randomly collected for determination of soil microbial biomass carbon (SMB-C) and soil microbial activity (SMA) in May, July and September 2006. Samples were taken from the 0–15 cm soil layer using a sharp-edged metal cylinder with an inner diameter of 10 cm and a length of 15 cm. Each sample was labeled, and then stored at 2°C in a cooler for transport to the laboratory. In the laboratory, the fresh samples were passed through a 2-mm sieve and manually cleaned off any visible plant tissues.

Soil microbial biomass carbon (SMB-C) was measured using the fumigation–extraction method (Vance et al., 1987). Twenty grams (dry weight equivalent) of fumigated and non-fumigated soil samples were extracted with 0.5 M K_2SO_4. Extracts were filtered through 0.45-μm filters and frozen at −20°C before analysis of extractable carbon by dichromate digestion as described by Lovell et al. (1995). SMB-C was calculated as the difference in extractable carbon of fumigated and non-fumigated soil samples. To correct for incomplete extractability, a conversion factor (Kec) of 0.38 was used to obtain SMB-C (Vance et al., 1987).

Soil microbial activity (SMA), i.e. soil microbial respiration, was estimated by determining CO_2 evolution over a 2-week incubation period. First, 20.0 g (dry weight equivalent) of soil was brought to 60% of the water holding capacity and incubated at 25°C for 2 weeks. Respired CO_2 was captured in 5.0 ml of 0.5 M NaOH suspended inside a Mason jar, and the NaOH solution was subsequently titrated to determine the amount of CO_2 evolved (Hu and van Bruggen, 1997).

2.4 Forest floor mass and litterfall

The three forests exhibited a moder type of litter layer (Müller, 1889). Forest floor mass was measured on five randomly located, 0.5 m×0.5 m subplots from each plot in May, June, July, August, September, and October 2006 and in April 2007. Forest floor mass was sorted into coarse woody debris and surface organic matter. Litterfall was trapped and collected in May, June, July, August, September, and October 2006 and in April 2007 using five randomly located 0.45 m×0.35 m rectangular baskets, and sorted into woody- and non-woody fractions. Dry litter mass was determined after oven-drying at 75°C for 2–3 days.

2.5 Fine root biomass, production and turnover rate

Fine root (<2 mm) biomass was determined in each plot by core sampling (Roberts, 1976) to a depth of 55 cm in May, July and September 2006. At each sampling date, 10 sample columns were randomly excavated using a sharp-edged metal cylinder with an inner diameter of 10 cm and a length of 20 cm. Samples from different depths (0–5, 5–15, 15–30, 30–45, 45–55 cm) were separated and labeled. Fine roots were manually removed from the soil samples and washed. Live and dead root fragments were subsequently separated by visual inspection. The xylem of dead roots looks darker and deteriorated, the degree of cohesion between the cortex and the periderm decreases, and root tips become brittle and less resilient. Dry biomass was determined after oven-drying at 75°C for 2–3 days.

Fine root (<2 mm) production during the growing season was estimated with a modified in-growth core technique (Lund et al., 1970). The 10 holes created by the root biomass in each plot were refilled early May 2006 with native soil obtained from the root biomass experiment and their boundaries were marked with sticks. The in–growth cores were harvested at the end of October 2006. Soil samples from different depths (0–5, 5–15, 15–30, 30–45, 45–55 cm) for each in-growth core were labeled, and fine root biomass was subsequently estimated using exactly the same procedures

as described above. Total fine root production was estimated as the sum of live and dead roots present in the in-growth core in end October 2006.

Fine root turnover is defined here as the rate of the total amount of fine root produced in the growing season over the mean standing biomass of fine roots (Aber et al., 1985). Mean fine root biomass was estimated as the average of live root biomass on May, July and September 2006.

2.6 Decomposition of leaf litter, fine roots, LF-OC, HF-OC and SOC

Decomposition rates of leaf litter and fine root, LF-OC, HF-OC and SOC were determined using the nylon bag (or litterbag) method (Wen, 1984; Lin et al., 1992; Arunachalam et al., 1996; Li et al., 2005). Recently fallen leaves, fine root and soil from the 0–10 cm soil layer were collected from the forests. The fresh soil samples were processed with a 2-mm sieve. Each nylon bag had a dimension of 10 cm×15 cm and a mesh of 1 mm for leaf litter and fine roots, and of 48μm for soil. 40 nylon bags for Asia white birch and East-Liaoning oak forests and 35 nylon bags for Sharptooth oak forest containing 3 g of air-dried leaves and fine roots, and 100 g of air-dried soil were placed in nylon bags and the edges heat-sealed, respectively. These nylon bags were collected after 0, 30, 59, 91, 123, 151, 179 and 365 days for Asia white birch and East-Liaoning oak forests, and after 0, 29, 66, 90, 121, 174, 365 days for Sharptooth oak forest. Five nylon bags were collected at each sampling date. Mass of leaf litter and fine roots in each nylon bag was determined after oven-drying at 75°C for 2–3 days. LF-OC, HF-OC and total SOC of soil in each litterbag were determined using the density fractionation method described above.

At the onset of the decomposition experiments, we also determined total C and N of leaf and fine root material, and total N of LF-OC, HF-OC and of total SOC. Total C was determined by the standard method of wet-combustion, and total N by semi-micro Kjeldahl method (Bao, 1999). Lignin was determined with the thioglycolic acid method (Dean, 1997). Soluble phenol concentrations were analyzed using a combination of methanol extraction and the Folin-Ciocalteau assay (Waterman and Mole, 1994).

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Initial chemical characteristics for the substrates used in the decomposition studies are shown in Table 1.

2.7 Statistical analysis

Data management and statistical analyses were performed using SPSS software (SPSS, Chicago, IL). The decay constant (K) and the average rate of litter loss were determined by fitting the following exponential function: $X_t = X_0\ e^{-kt}$ (Olson, 1963). One-way ANOVA was used to test for significant differences of initial chemical content of leaf litter, fine root, and LF, HF and total soil, soil bulk density, surface organic, coarse woody debris, LF-OC, HF-OC and total SOC, fine root biomass, production and turnover rate. Repeated Measures Analysis of Variance was used to detect the significant differences of seasonal variation of forest floor mass, SMB-C, SMA and fine root biomass.

3 Results

3.1 Soil carbon pools

The seasonal evolutions of the forest floors in the three investigated forests were relatively similar (Fig. 1), exhibiting a continuous slow decrease interrupted in October because of the annual leaf litterfall. Nonetheless, total forest floor mass was significantly ($P<0.05$) higher in the temperate Asia white birch and East-Liaoning oak than in sub-tropical Sharptooth oak forest (Table 2); a difference that was mainly related to differences in the non-woody fraction of the surface organic horizon (Fig. 2). There was no significant difference in coarse woody debris among the three forests (Fig. 2). In the Asia white birch and East-Liaoning oak forest, coarse woody debris comprised about 30% of the forest floor mass, whereas in the less disturbed Sharptooth oak forest coarse woody debris accounted for 36% of the forest floor mass. In contrast to the

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non-woody fraction of the forest floor, seasonal fluctuation of woody debris was very little (data not shown).

In the various soil layers down to 55 cm, LF-OC, HF-OC and total SOC differed significantly among the studied forests ($P<0.05$, Fig. 2; Table 2). In accordance with the carbon stores in the surface horizon, we observed the largest SOC pool in Asia white birch and the lowest in Sharptooth oak forests.

Although LF-OC and HF-OC differed among these forests in parallel to total SOC, the differences in LF-OC were more pronounced than those in HF-OC (the proportion of labile components was lower where total SOC was lowest; Fig. 2 and Table 2). Hence, the differences in SOC availability to microbial decay were larger than those in SOC content.

3.2 Microbial biomass and activity

In accordance with the SOC availability, mean SMB-C of the two temperate forests was significantly higher than that of the sub-tropical Sharptooth oak forest ($P<0.05$, Fig. 3a). In contrast, SMA exhibited exactly the opposite trend, and this throughout the entire growing season ($P<0.05$, Fig. 3b). In all three forests, both SMB-C and SMA were significantly higher in July than in May and September 2006 ($P<0.05$, Fig. 3a and b).

The mass loss patterns of decomposing leaf litter, fine roots, LF-OC, HF-OC and total SOC are shown in Fig. 4. Fine roots decomposed fastest (42–58% mass loss per year; Table 3), followed by leaf litter, LF-OC, Total OC, and last HF-OC that decomposed with an annual mass loss of 4.1–5.5%. Across all litter and SOC types, the decay constant and mass loss rates decreased from Sharptooth oak, Asia white birch to East-Liaoning oak. Differences in decomposition rates were, however, significant only for leaf litter mass, fine root mass, LF-OC and total SOC, and not for HF-OC (Table 3, Fig. 4).

3.3 Fine root biomass and production

As with microbial biomass, fine root biomass in the soil layers down to 55 cm was significantly higher in July than in May and September ($P<0.05$, Fig. 5) in all three forests. Statistically significant differences in fine root biomass among the forests occurred in the 0–35 cm soil layers in May, and in the 5–25 cm soil layers in July and September ($P<0.05$, Fig. 5).

Integrated over all depths and averaged over the growing season, mean fine root biomass was 0.33±0.02, 0.30±0.02 and 0.26±0.01 kg C m^{-2} in Asia white birch, East-Liaoning oak and Sharptooth oak forests, respectively. However, it should be kept in mind that in the first two forests, almost the entire soil profile was sampled, whereas in the Sharptooth oak forest, where soil depth was around one meter, total fine root biomass was underestimated by sampling only to a depth of 55 cm.

Fine root production in the 0–55 cm soil layer decreased from Sharptooth oak, Asia white birch to East-Liaoning oak forests, and significant differences were observed in the 0–25 cm soil layers (Fig. 6). Integrated over all depths, fine root production was lowest in East-Liaoning oak forests (Table 2).

Fine root turnover rate was thus significantly higher in the sub-tropical Sharptooth oak forest (0.67±0.06 $year^{-1}$) than in the temperate Asia white birch (0.50±0.04 $year^{-1}$) and East-Liaoning oak forests (0.44±0.04 $year^{-1}$).

3.4 Soil carbon inputs and their residence times

The seasonal patterns of litterfall were very similar among the different forests, with the majority of the annual litter production in September and October. Seasonal fluctuations in branch litterfall were, however, very little. Annual above-ground litter inputs were significantly ($P<0.05$) higher in Asia white birch and Sharptooth oak forests than in the East-Liaoning oak forest (Table 2). In agreement with above-ground litterfall, below-ground litter production, estimated as being equal to fine root production (under the assumption of interannual steady state in fine root biomass), was also higher in

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Asia white birch and Sharptooth oak than in East-Liaoning oak (Table 2).

The quality of leaf litter for decomposition decreased in the same order as the quantity of litter inputs. For every measured proxy for the quality of leaf litter for decomposition (soluble phenolics, C:N ratio, lignin:N ratio, lignin content), East-Liaoning oak exhibited the lowest quality litter and Asia white birch the highest (Tables 1 and 3). In contrast to leaf litter, however, fine root quality differed only very slightly among the three tree species.

The residence time of the surface litter inputs in the forest floor (calculated as the ratio of the maximum carbon content in October over the carbon loss between October and September), is much smaller in the sub-tropical Sharptooth oak forest (3.6 years) than in the Asia white birch forest (4.3 years). The East-Liaoning oak forest (5.4 years) has the longest residence time in the forest floor. This pattern is also obtained when the forest floor residence time is calculated from the ratio of forest floor mass over leaf litter inputs. According to this computation, the Sharptooth oak forest exhibited a mean residence time of less than three years, whereas carbon resides for more than four years in the forest floor of the East-Liaoning oak forest.

When considering the total unprotected SOC (surface litter + LF-SOC), the residence times calculated as the ratio of the carbon stock over the total litter inputs (above + root litter inputs) follow the same pattern as those in the surface layer. According to these calculations, labile carbon resides in the litter and LF-OC for slightly more than 4 years in the Sharptooth oak forest, up to 6.5 years in the East-Liaoning oak forest, with Asia white birch as an intermediate (5.8 years).

4 Discussion

4.1 Decomposition of various SOC types

Decomposition of litter and SOC is an important process contributing to carbon and nutrient cycling (Vogt et al., 1991; Christensen, 2001; Cornelissen et al., 2007) and is

mediated primarily by climate and organic matter quality (Harmon et al., 1990; Sinsabaugh et al., 2002; Fioretto et al., 2007). In all three forests, the quality of the SOC for microbial decay decreased in the sequence fine roots, leaf litter, LF-OC and HF-OC, as indicated both by decay constants as by the chemical analyses. Moreover, independent of the type of SOC (from fresh litter to HF-SOC), Sharptooth oak always exhibited the fastest decay rates and East-Liaoning oak the slowest. Thus, it appears that the decomposability of the litter is transferred to the SOC derived from it. The observed C:N ratio's of the LF-OC were 31–38, and thus within but in the lower end of the range (24–86) observed in forest soils (Strickland and Sollins, 1987; Swanston and Myrold, 1997). The C:N ratio's of HF-OC (16–17) were much lower than those of LF-OC, consistent with other studies (Whalen et al., 2000; Tan et al., 2007), and indicated that the microbial communities were probably fungal dominated (Swift et al., 1979).

Albeit in agricultural ecosystems, Post and Kwon (2000) pointed out that the turnover of LF-OC varies from a few months to a few years, while the HF-OC is stabilized through microaggregation and its turnover time is on the order of decades. In agreement with observations in other studies (Sollins et al., 1996; Swanston et al., 2002), and as expected from the differences in C:N ratio, the decay constants of LF-OC were indeed considerably higher than those of HF-OC in all three studied forests.

4.2 What determines the differences in SOC stocks?

The observed total soil organic carbon stocks (14–17 $kg\,m^{-2}$) were within, but at the low end of the range reported for forest ecosystems (8–48 $kg\,m^{-2}$; Dixon et al., 1994). The relatively small pools compared to other forests is, however, probably due to the shallower soils in our study compared to the review by Dixon et al. (1994). Total soil carbon stocks were lowest in Sharptooth oak forest, highest in Asia white birch, and intermediate in East-Liaoning oak forests. However, it should be kept in mind that in the two temperate forests, the entire soil profile was sampled (bedrock at about 55 cm), whereas in the sub-tropical Sharptooth oak forest, where soil depth was around one meter, total SOC was underestimated by sampling to the same depth as in the other

forests.

In soils with similar clay contents (as the three study sites included in this study), where stabilization potential of SOC is similar, SOC densities are determined by the balance of soil carbon inputs and carbon losses. Would it then be possible to explain the observed differences in the SOC stocks with those in the litter inputs and decomposition rates?

The sub-tropical Sharptooth oak and temperate Asia white birch forest exhibited very similar amounts of litter input, both above- and below-ground. Given the higher quality for decomposition in the Asia white birch forest, as indicated by the chemical composition and decay constants of the litter and LF-OC, one would expect lower SOC stocks in the Asia white birch forest. However, the opposite is observed. Both in the forest floor as in the LF-OC, the residence time in the Asia white birch forest is 50% higher than in the Sharptooth oak forest and hence, the SOC stocks are 22% higher in the Asia white birch forest (despite the similar litter inputs). This result indicates that the negative effects of the poorer SOC quality on its decay in the Sharptooth oak forest are overshadowed by the positive effects of the better sub-tropical climatic conditions.

Does this imply that the differences in chemical composition are unimportant in these deciduous forests? When comparing the two temperate forests, it becomes clear that chemical quality does play a primordial role. Here, climate is very similar and thus does not confound the observations. Total litter inputs are 33% higher in the Asia white birch – than in the East-Liaoning oak forest. Nonetheless, the total SOC content is only 11% higher, and this discrepancy is related solely to differences in the surface organic layer. Below-ground, the 25% difference in root litter inputs is reflected in the LF-OC pool, which exhibits a very similar relative difference between both forest types (+29%). In contrast, above-ground litter fall is 40% higher in the Asia white birch – than in the East-Liaoning oak forest. Because leaf litter is of much higher quality in the Asia white birch forest, leaf litter decomposition proceeds much faster and hence the forest floor does not really differ in mass between both forest types (statistically insignificant difference of 7%). Hence, we can conclude that the difference in above-ground carbon

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inputs is quasi completely offset by the higher carbon losses due to the difference in above-ground litter quality. Thus, litter quality is a very important determinant of SOC cycling in these temperate forests, but among our study sites less so than the effect of climate.

4.3 Soil microbial biomass and activity

Soil microbial biomass represents an important labile pool of nutrients and carbon (Henrot and Robertson, 1994). Changes in the size of the microbial biomass pool may indicate changes in the substrate availability that are otherwise not easily detectable. In this study, SMB-C and SMA were higher in July than in May and September in all three forests, reflecting that substrate availability must have varied considerably during the growing season. Similar findings were also observed in other studies (Wardle, 1998; Michelsen et al., 2004; Shishido et al., 2008).

Soil microbial biomass of the sub-tropical Sharptooth oak forest was lower than that of East-Liaoning oak and Asia white birch forests. This pattern reflected well that of the labile SOC pools, confirming that substrate availability might be an important control over the size of the SMB-C pool (Wardle, 1992).

In contrast to SMB-C, SMA was higher in the Sharptooth oak forest than in the Asia white birch and East-Liaoning oak forests. This pattern was very surprising given that SMA was determined in the lab under similar climatic conditions, and that the Sharptooth oak soil contained the least available SOC, which also was less degradable than the SOC in the Asia white birch soil. Based on the observed SOC quantity and quality, we would have expected the highest SMA in the Asia white birch, and lower ones in the Sharptooth oak forest because of the lower SOC availability. We can only speculate why the SMA observations contrasted our expectations. One potential explanation could be that the environmental conditions in the lab during the SMA experiments resembled the climatic conditions in the sub-tropical Sharptooth oak forest much better (both in terms of temperature and soil moisture) than in the two temperate-zone forests. Perhaps the warm and moist conditions were more optimal for the microbial

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populations in the subtropical soil, and supra-optimal for those in the temperate soils, but this remains pure speculation.

4.4 Fine root dynamics

Our estimates of mean fine root biomass (between 510 and 660 g dry matter m^{-2}) were well within the range reported by Vogt et al. (1996) for fine root biomass in temperate broadleaved forests (243–999 g dry matter m^{-2}). Fine root growth at our study sites (270 to 350 g dry matter m^{-2} $year^{-1}$) was much higher relative to that of a temperate oak forest in a more moderate, maritime climate (Quercus robur; fine root productivity of 180 g dry matter m^{-2} $year^{-1}$; Curiel Yuste et al., 2005). Luyssaert et al. (2007) reported a fine root productivity average across 52 temperate deciduous forests of 440 g dry matter m^{-2} $year^{-1}$ (recalculated from carbon units assuming that dry matter contains 50% carbon). Although our sites are all below this global average, they are all well within the 25–75% percentile range (204–460 g dry matter m^{-2} $year^{-1}$) reported in the review by Luyssaert and co-workers.

Fine root biomass and - production both decreased with soil depth. Similar findings have been observed in many studies (Vogt et al., 1981; Olsthoorn, 1991; Xiao et al., 2003; Konôpka et al., 2006) and have been attributed to declining nutrient availability and changing physical conditions with depth. Also fine root turnover declined with depth (data not shown). Averaged over all depths, turnover of roots <2 mm at our sites (0.45 to 0.67 $year^{-1}$) was lower than the global mean turnover rate (0.8 $year^{-1}$) for forest fine roots <2 mm reported in the review by Gill and Jackson (2000), but nonetheless well within the range for broadleaf forests in similar climates (0.2–1.4 $year^{-1}$).

Rates of root turnover are influenced by climate (Vogt et al., 1986; Hendrick and Pregitzer, 1993; Pregitzer et al., 2000) and nutrient availability (Crick and Grime, 1987; Schoettle and Fahey, 1994; Janssens et al., 2002), amongst others. The faster root turnover in the Asia white birch forest relative to the East-Liaoning oak forest, however, cannot be climate driven and might thus be related to faster decomposition rates and thus nutrient cycling. The higher turnover rate observed in the sub-tropical Sharptooth

oak forest might be due merely to the warmer and wetter conditions, that favour root production. However, the more favourable climate also accelerates decomposition and thus nutrient availability to roots (Wardle, 1992; Zaman et al., 1999; Gill and Jackson, 2000; Tu et al., 2003; Xiao et al. 2007). Hence, it is impossible to state from this limited number of forest sites whether climate or nutrient cycling is the dominant control over root turnover.

In conclusion, our results show that there are obvious differences in pool size and decomposition rates of litter and SOC, SMB-C and SMA, and fine root biomass, production and turnover rate among Asia white birch, East-Liaoning oak and Sharptooth oak forests. These results provide basic information in estimating the effectiveness of belowground carbon dynamics and sequestration in the three forests.

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Table 1. Initial chemical content of leaf litter, fine root, light fraction organic carbon (LF-OC), heavy fraction organic carbon (HF-OC) and total soil organic carbon used in the decomposition experiments in Asia white birch-, East-Liaoning oak- and Sharptooth oak forests. Values represent mean ± standard error (n=5). Different letters in each column are significantly different (P<0.05) according to the least significant difference test.

		Asia white birch	East-Liaoning oak	Sharptooth oak
Leaf litter	C ($g\,kg^{-1}$)	458±9	441±9	450±8
	N ($g\,kg^{-1}$)	12.4±0.8a	9.1±0.4b	10.7±0.6ab
	Lignin ($g\,kg^{-1}$)	219±10b	263±12a	253±11a
	Soluble Phenolics ($g\,kg^{-1}$)	36.3±1.5b	44.8±2.2a	42.2±1.8a
	C:N	37.3±1.6b	48.9±2.0a	42.4±1.7b
	Lignin:N	18.0±1.6b	29.4± 2.4a	24.0± 2.1ab
Fine root	C ($g\,kg^{-1}$)	443±9	434±9	448±9
	N ($g\,kg^{-1}$)	7.4±0.4	6.6±0.3	7.0±0.3
	Lignin ($g\,kg^{-1}$)	308±10	332±16	321±15
	Soluble Phenolics ($g\,kg^{-1}$)	20.3±0.9	23.4±1.1	22.6±1.1
	C:N	60.7±2.8	65.9±2.5	64.1±2.2
	Lignin:N	42.1±1.7	50.4±2.7	46.3±3.5
LF-OC	C ($g\,kg^{-1}$ soil)	14.2±0.2a	10.1±0.2b	7.9±0.1c
	N ($g\,kg^{-1}$ soil)	0.45±0.01a	0.27±0.01b	0.23± 0.01c
	C:N	31.8±0.8b	37.6±0.9a	35.2±1.1a
HF-OC	C ($g\,kg^{-1}$ soil)	40.9±0.4a	35.2±0.3b	30.8±0.3c
	N ($g\,kg^{-1}$ soil)	2.52±0.06a	2.06±0.03b	1.84±0.02c
	C:N	16.2±0.3b	17.1±0.2a	16.7±0.3ab
Total SOC	C ($g\,kg^{-1}$ soil)	55.1±0.5a	45.3±0.3b	38.7±0.2c
	N ($g\,kg^{-1}$ soil)	2.97±0.07a	2.33±0.03b	2.07±0.03c
	C:N	18.6±0.3	19.4±0.2	18.8±0.3

Table 2. Soil organic carbon inputs and pools in the Asia white birch-, East-Liaoning oak- and Sharptooth oak forests. Values represent mean ± standard error (inputs in g C $m^{-2}yr^{-1}$; pools in in kg C m^{-2}; n=5). Different letters in each column are significantly different at P<0.05). Labile carbon was assumed to include non-woody surface litter and light-fraction SOC. Recalcitrant carbon was estimated as woody debris plus heavy-fraction SOC.

	Asia white birch	East-Liaoning oak	Sharptooth oak
Carbon inputs			
Woody debris	30±3a	23±2b	28±2a
Above ground litter fall	142±8a	100±6b	134±7a
Fine root turnover	165±15a	133±12b	173±17a
Total	337±23a	256±18b	335±24a
SOC pools			
Surface layer	0.6±0.1a	0.6±0.1a	0.5±0.1b
SOC	16.1±0.4a	14.5±0.3b	13.2±0.2c
Total	16.7±0.4a	15.1±0.3b	13.7±0.2c
Proportion labile	0.19	0.16	0.15
Proportion recalcitrant	0.81	0.84	0.85

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Table 3. Mean annual decay/mineralization constants (k) of leaf litter and fine root, and light fraction organic carbon (LF-OC), heavy fraction organic carbon (HF-OC) and total soil organic carbon (SOC) in Asia white birch and East-Liaoning oak forests of warm temperate zone and Sharptooth oak forest of sub-topical zone. Values represent mean ± standard error derived from eight-time sampling with five replicates for Asia white birch and East-Liaoning oak forests, and seven-time sampling with five replicates for Sharptooth oak forest. Different letters in each column are significantly different ($P<0.05$) according to the least significant difference test. R^2, multiple coefficient of determination. Significance level: $*P<0.05$; $**P<0.01$.

		k	R^2	Loss% year^{-1}
Leaf litter	Asis white birch	0.399±0.100	0.728**	33.05±1.28b
	East-Liaoning oak	0.267±0.069	0.715**	23.14±1.12c
	Sharptooth oak	0.483±0.125	0.751*	39.26±1.37a
Fine root	Asis white birch	0.623±0.132	0.787**	45.93±1.29b
	East-Liaoning oak	0.556±0.110	0.810**	42.14±1.01b
	Sharptooth oak	0.845±0.214	0.757*	58.49±1.48a
LF-OC	Asis white birch	0.162±0.042	0.715**	14.81±0.80b
	East-Liaoning oak	0.151±0.038	0.725**	13.80±0.64b
	Sharptooth oak	0.224±0.061	0.732*	20.71±0.98a
HF-OC	Asis white birch	0.0475±0.012	0.710**	4.67±0.67
	East-Liaoning oak	0.0431±0.011	0.729**	4.13±0.62
	Sharptooth oak	0.0547±0.016	0.710*	5.49±0.77
Total SOC	Asis white birch	0.0758±0.02	0.711**	7.29±0.69ab
	East-Liaoning oak	0.0662±0.017	0.726**	6.29±0.62b
	Sharptooth oak	0.0868±0.024	0.716*	8.60±0.79a

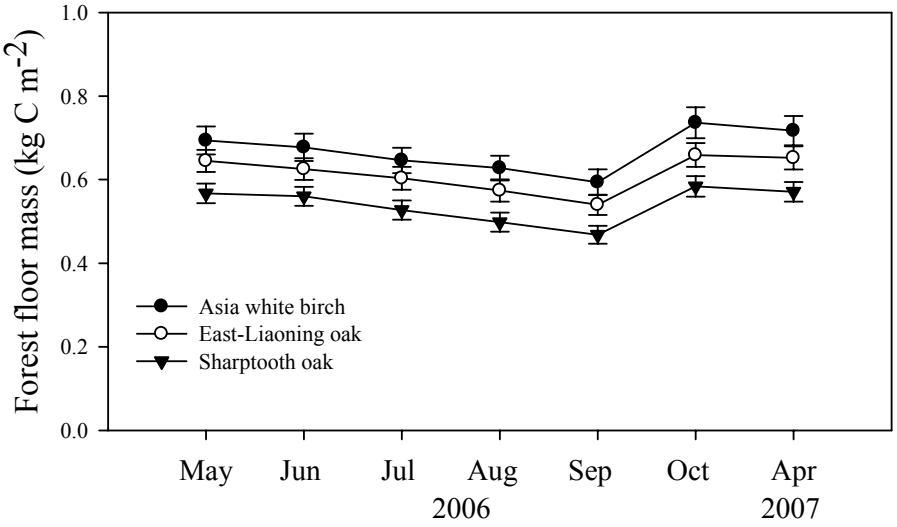

Fig. 1. Seasonal changes of forest floor mass in Asia white birch and East-Liaoning oak forests of warm temperate zone and Sharptooth oak forest of sub-topical zone from May 2006 to April 2007. Vertical bars indicate standard errors of means (n=5).

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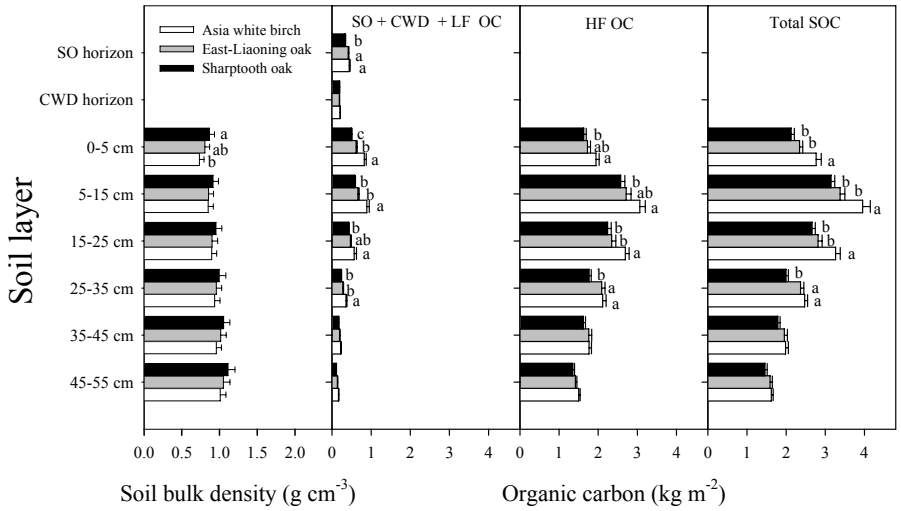

Fig. 2. Vertical distribution of soil bulk density, light fraction organic carbon (LF-OC), heavy fraction organic carbon (HF-OC) and total soil organic carbon (SOC), and carbon of coarse woody debris (CWD) and surface organic (SO) horizon in Asia white birch and East-Liaoning oak forests of warm temperate zone and Sharptooth oak forest of sub-topical zone. Horizontal bars indicate standard errors of means (n=5). Different letters within a soil layer are significantly different (P<0.05) according to the least significant difference test. Absence of letters implies that no significant differences were detected.

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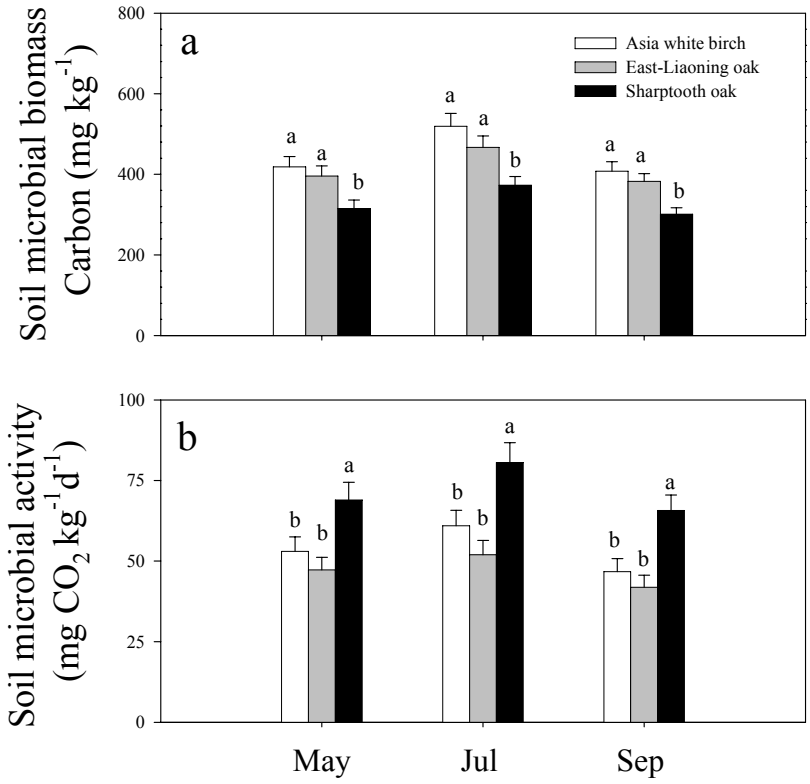

Fig. 3. Soil microbial biomass carbon and soil microbial activity in Asia white birch and East-Liaoning oak forests of warm temperate zone and Sharptooth oak forest of sub-topical zone in May, July and September 2006. Vertical bars indicate standard errors of means (n=5). Different letters within a month are significantly different (P<0.05) according to the least significant difference test.

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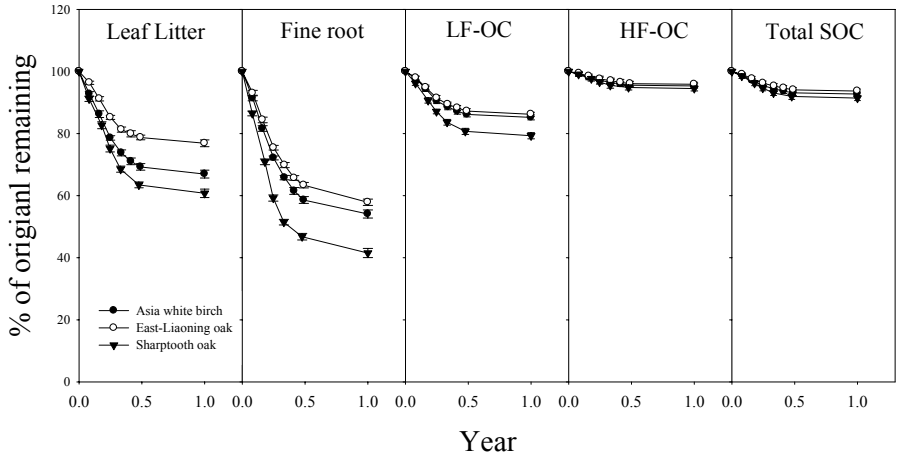

Fig. 4. Leaf litter mass, fine root mass, light-fraction organic carbon (LF-OC), heavy-fraction organic carbon (HF-OC) and total soil organic carbon (SOC) remaining (% of initial) in Asia white birch and East-Liaoning oak forests of warm temperate zone and Sharptooth oak forest of sub-topical zone during the 1-year period. Vertical bars indicate standard errors of means (n=5).

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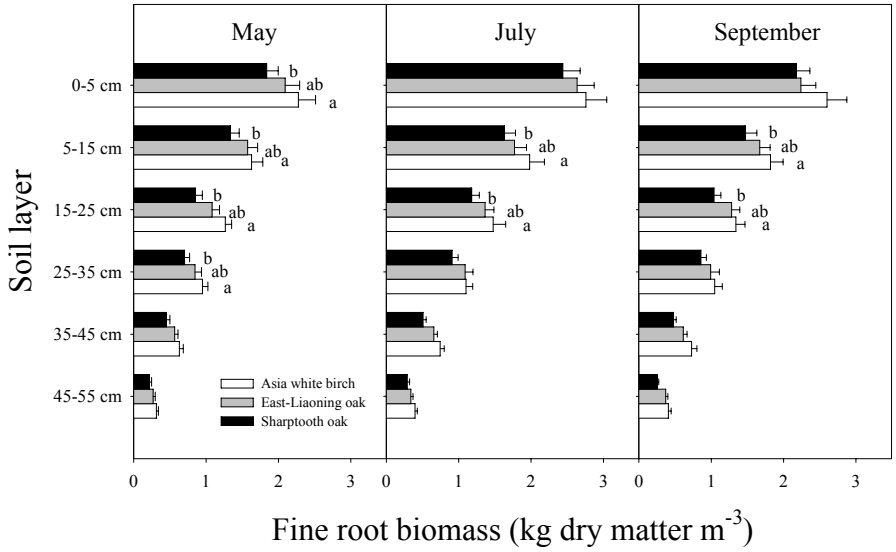

Fig. 5. Vertical distribution of fine root biomass in Asia white birch and East-Liaoning oak forests of warm temperate zone and Sharptooth oak forest of sub-topical zone in May, July and September 2006. Horizontal bars indicate standard errors of means (n=5). Different letters within a soil layer are significantly different (P<0.05) according to the least significant difference test. Absence of letters implies that no significant differences were detected.

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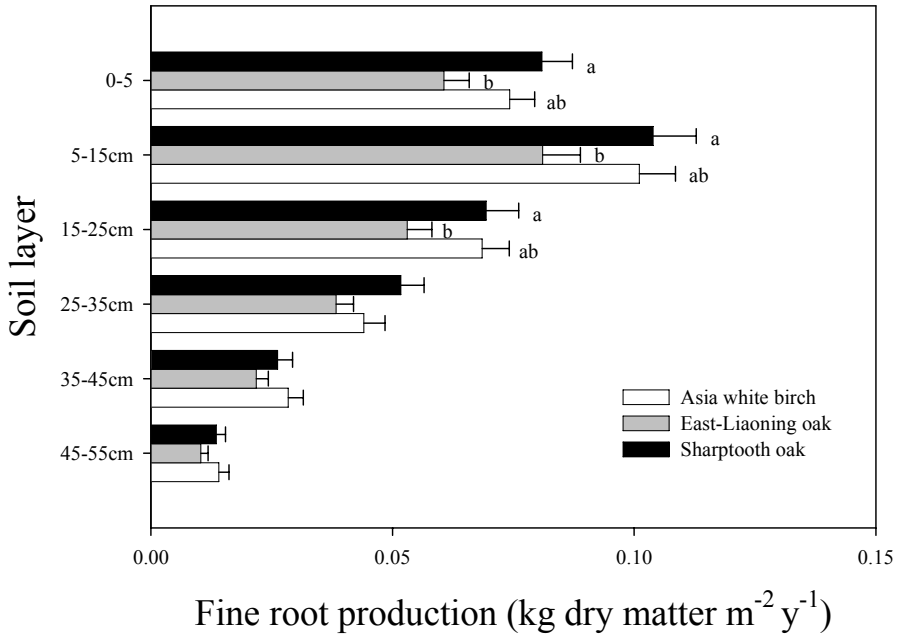

Fig. 6. Vertical distribution of fine root production in Asia white birch and East-Liaoning oak forests of warm temperate zone and Sharptooth oak forest of sub-topical zone. Horizontal bars indicate standard errors of means (n=5). Different letters within a soil layer are significantly different (P<0.05) according to the least significant difference test. Absence of letters implies that no significant differences were detected.

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