Nitrogen and phosphorus transformations in the rhizospheres of three tree species in a nutrient-poor sandy soil

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ARTICLE INFO

Article history:
Received 23 May 2010
Received in revised form 8 October 2010
Accepted 11 October 2010

Keywords:
Nitrogen mineralization
Phosphorus transformation
Rhizosphere effect
Tree species

ABSTRACT

We examined acid phosphatase activity (APA), N mineralization and nitrification rates, available N and P, and microbial biomass C, N and P in rhizosphere and bulk soils of 18-year-old Siberian elm (Ulmus pumila), Simon poplar (Populus simonii) and Mongolian pine (Pinus sylvestris var. mongolica) plantations on a nutrient-poor sandy soil in Northeast China. The main objective was to compare the rhizosphere effects of different tree species on N and P cycling under nutrient-deficient conditions. All tree species had the similar pattern but considerably different magnitude of rhizosphere effects. The APA, potential net N mineralization and nitrification rates increased significantly (by 27–60%, 110–188% and 106–142% respectively across the three species) in rhizosphere soil compared to bulk soil. This led to significantly higher Olsen-P and NH4+-N concentrations in rhizosphere soil, whereas NO3−-N concentration was significantly lower in rhizosphere soil owing to increased microbial immobilization and root uptake. Microbial biomass C and N generally increased while microbial biomass P remained constant in rhizosphere soil relative to bulk soil, indicating the N-limited rather than P-limited microbial growth. Rhizosphere effects on P transformation were most pronounced for Siberian elm, while rhizosphere effects on N transformation were most pronounced for Mongolian pine, implying the different capacities of these species to acquire nutrients.

1. Introduction

Rhizosphere processes are one of the most important but least understood ways in which plants affect nutrient cycling (Hobbie, 1992; Grayston et al., 1996). Plant roots can influence rhizosphere nutrient cycling by nutrient uptake, rhizodeposition and interactions with microorganisms, which is crucial in maintaining forest growth and ecosystem stability, particularly under nutrient-poor conditions (Gobran et al., 1998; Wang and Zabowski, 1998). Despite rhizosphere processes have been well described for agricultural crops and grasses grown under controlled conditions, information on rhizosphere processes of tree species under natural conditions is limited and opposite (Parmelee et al., 1993; Kuzyakov et al., 2000; Jones et al., 2004). For example, available N and P have been found to be accumulated (Turpault et al., 2005), depleted (Wang et al., 2001; Chen et al., 2002) or unchanged (Parmelee et al., 1993; Ehrenfeld et al., 1997) in rhizosphere soil compared to bulk soil in different studies, which are tightly related to soil conditions and tree species. Moreover, most of published studies of rhizosphere nutrient cycling for trees were conducted on seedlings in microcosms; very few field studies in forests were reported (Phillips and Fahey, 2006). The rhizosphere nutrient cycling of trees under field conditions may differ greatly from that of annual plants and tree seedlings due to their differences in nutrient requirement, soil conditions, as well as growth period (Grayston et al., 1996; Gobran et al., 1998).

Since tree species are very different with respect to root morphology and physiology (such as root biomass, mycorrhizal association, quality and quantity of root exudates) as well as nutrient requirement (Grayston and Campbell, 1996; Wang et al., 2001; Jones et al., 2004), rhizosphere effects on nutrient cycling would be likely to vary with tree species (Richardson et al., 2009). Knowledge of species differences in rhizosphere nutrient cycling is fundamental for characterizing nutrient acquisition capacity of different tree species and for interpreting the influence of tree species on soil processes. To date, very few attempts have been made to compare the rhizosphere nutrient cycling of different tree species (Wang et al., 2001; Kuzyakov, 2002; Phillips and Fahey, 2006). Therefore, there is still a strong need for more field studies on rhizosphere nutrient cycling under different climates and tree species for providing a more realistic view of rhizosphere processes (Gobran et al., 1998; Jones et al., 2004).

The primary objective of this study was to quantify and compare the rhizosphere effects of different tree species on soil N and P transformations under nutrient-deficient field conditions. We examined soil chemical and biological properties associated with...
N and P transformations in rhizosphere and bulk soils under 18-year-old mono-specific Siberian elm (*Ulmus pumila*), Simon poplar (*Populus simonii*) and Mongolian pine (*Pinus sylvestris* var. *mongolica*) plantations on a nutrient-poor sandy soil in Keerqin Sandy Lands of Northeast China. Previously, we have found that these tree species significantly influence soil N and P status (Zeng et al., 2009; Zhao et al., 2009). We hypothesize that rhizosphere effects of all three species would lead to increased N and organic P mineralization by improving microbial activity under nutrient-deficient conditions, but the magnitude of these effects would vary with species due to differences in intrinsic biological characteristics. The results will improve our understanding of nutrient limitation and adaptation of different tree species under nutrient-deficient conditions.

2. Materials and methods

2.1. Site description and sampling

The study site was located at Daqinggou Ecological Station (42°58′N, 122°21′E, 260 m above sea level), Institute of Applied Ecology, Chinese Academy of Sciences in southeastern Keerqin Sandy Lands, Northeast China. The area is within the semiarid region of temperate climatic zone; its annual mean temperature is about 6.4 °C, with the lowest and highest monthly mean temperature occurring in January (−12.5 °C) and July (23.8 °C), respectively; mean annual precipitation is 450 mm, with more than 60% occurring in June to August. The soil is a sandy soil developed from eolian parent material (Typic Ustipsamment) and is characterized by coarse texture and loose structure. The soil is particularly deficient in N and P, with the total N and total P concentrations of 0.30 g kg⁻¹ and 0.15 g kg⁻¹ at 0–30 cm layer, respectively. The textural composition is 90.9% sand, 5.0% silt, and 4.1% clay. Soil water holding capacity is between 10% and 12% (Zeng et al., 2009).

Within the station, three 18-year-old pure even-aged plantations were selected for this study: Siberian elm, Simon poplar and Mongolian pine. These tree species have been widely planted for soil conservation in southeastern Keerqin Sandy Lands, and have contrasting growth rate and foliar nutrient concentrations (Jiao, 1989). Siberian elm, a native, small deciduous tree species, is highly adaptive to semiarid climate and poor soil fertility (Li et al., 2002). Simon poplar is a native, fast-growing, deciduous tree species. Mongolian pine is an evergreen conifer and an introduced species at the study site. All the plantations were located within a 1-km radius of each other, on flat topography, and shared the same soil type. Plantations were established on degraded grassland and at the spacing of 2 m × 5 m, 2 m × 2 m and 3 m × 3 m for Siberian elm, Simon poplar and Mongolian pine, respectively. No management (such as fertilization and pruning) was carried out for all the plantations. For each plantation, five 20 m × 20 m plots were randomly established for soil sampling.

In July 2009, bulk and rhizosphere soils were collected at 10–30 cm layer where tree roots are most dense, and also for the reason to minimize the effects of floor litter decomposition and root activities of understory grasses on soil properties in surface soil. Rhizosphere soil was defined as soil adhering to live fine roots (<1 mm) after gentle shaking. Bulk soil was defined as the soil remaining in the core after removal of rhizosphere soil (Phillips and Fahey, 2006). One composite soil sample consisting of six soil cores (6 cm diameter) was taken randomly within each plot. Live fine roots and adhering rhizosphere soil were picked out in the field. In order to obtain sufficient amount of rhizosphere soil for chemical analyses, additional rhizosphere soil was collected by excavating pits at random locations within each plot, and finally combined with the rhizosphere soil collected by soil cores. All soil and roots were placed in ziplock plastic bags and kept in a cooler until they were brought to the laboratory. In the laboratory, rhizosphere soil was removed from fine roots by brushing. A subsample of fine roots in the soil cores was washed and dried at 65 °C to constant weight for estimating fine root biomass. Another subsample of fine roots was washed gently and stored at 4 °C for 1 day until root surface acid phosphatase activity (APA) was measured. Field moist soil sample was sieved to pass a 2-mm mesh and then was thoroughly mixed and divided into two subsamples. One subsample was stored at 4 °C for measuring APA, Olsen-P, NO3⁻-N, NH4⁺-N, microbial biomass C, N and P, and potential N mineralization and nitrification rates. Another subsample was air-dried for determination of soil pH and soil organic C (SOC).

2.2. Laboratory analyses

Soil pH was measured with a glass electrode (1:2.5 soil:water ratio). The SOC was determined by K2Cr2O7-H2SO4 oxidation method (Nelson and Sommers, 1982). Soil Olsen-P concentration was analyzed colorimetrically using the molybdate blue method after the soil was extracted with 0.5 mol L⁻¹ NaHCO3 at pH = 8.5 (Olsen et al., 1954). Soil APA was measured by the method described by Tabatabai (1994) at pH = 6.5, and was expressed as µg pNP g⁻¹ h⁻¹ (pNP = paranitrophenol). Determination of root surface APA followed the same procedure as soil APA, except that 0.1 g washed fresh fine root (<1 mm) sample was used. Soil NO3⁻-N and NH4⁺-N concentrations were analyzed colorimetrically on an autoanalyzer (AutoAnalyzer III, Bran+Luebbe GmbH, Germany) after the soil was extracted with 2 mol L⁻¹ KCl solution. Potential net N mineralization rate was calculated as the change in soil mineral N (NO3⁻-N plus NH4⁺-N) concentration over the 28-day aerobic incubation at 25 °C. Potential net nitrification rate was calculated as the change in NO3⁻-N concentration during incubation.

Soil microbial biomass C, N and P concentrations were determined by the CHCl₃ fumigation–extraction procedure (Brookes et al., 1982, 1985; Vance et al., 1987). The unfumigated and fumigated soil samples were extracted with 0.5 mol L⁻¹ K2SO4 for microbial biomass C and N, and extracted with 0.5 mol L⁻¹ NaHCO3 for microbial biomass P. Organic C in K2SO4 extracts was determined by K2Cr2O7–H2SO4 oxidation method. Total N in K2SO4 extracts was determined colorimetrically on an autoanalyzer after alkaline persulfate oxidation (Cabrera and Beare, 1993). NaHCO3 extractable inorganic P was determined as the Olsen-P. A spike of KH2PO4 equivalent to 25 µg P g⁻¹ soil was used to correct for inorganic P fixation during the NaHCO3 extraction (Brookes et al., 1982). Correction factors of 0.38 for C, 0.45 for N and 0.40 for P were applied to estimate the recoveries of microbial biomass C, N and P during fumigation (Brookes et al., 1982; Jenkinson et al., 2004). All soil data were expressed on an oven dry weight basis.

2.3. Statistical analyses

All data were tested for normality and homogeneity of error variances prior to comparing means. Paired samples T-test was used to compare the differences in soil variables between the rhizosphere and bulk soil samples for each tree species separately (α = 0.05). The magnitude of the rhizosphere effect was calculated as the percentage difference between paired rhizosphere and bulk soil samples for each soil variable. One-way analysis of variance (ANOVA) was performed to test the effects of tree species on the magnitude of rhizosphere effects as well as on fine root biomass and root surface APA. Tukey’s honestly significant difference (HSD) test was used for post hoc multiple comparisons (α = 0.05). All statistical analyses were performed.
using the SPSS statistical software package version 11.5 (SPSS Inc., 2002).

3. Results

The pH value did not change significantly between bulk and rhizosphere soils in Siberian elm and Mongolian pine plantations, but significantly decreased (by 5.6%) in rhizosphere soil compared to bulk soil in Simon poplar plantation (Table 1). SOC concentration and microbial biomass C (MBC) were significantly higher in rhizosphere soil than in bulk soil in elm and poplar plantations, but no significant rhizosphere effect was observed for SOC and MBC in Mongolian pine plantation. Significant rhizosphere effect on microbial biomass N (MBN) was observed in all plantations, with the greatest rhizosphere effect in Mongolian pine plantation (Table 2). There was no significant difference between rhizosphere and bulk soils for microbial C/N ratio in elm and poplar plantations, but microbial C/N ratio decreased greatly in rhizosphere soil in Mongolian pine plantation. No significant rhizosphere effect on microbial biomass P (MBP) was detected for all plantations (Table 1).

The APA and Olsen-P concentration were significantly enhanced in rhizosphere soil compared to bulk soil in all plantations (Fig. 1). The magnitude of the rhizosphere effects on APA and Olsen-P varied significantly among three species, being the order of Siberian elm > Simon poplar > Mongolian pine (Table 2). There were significant increases in potential net N mineralization and nitrification rates in rhizosphere soil as compared with bulk soil in all plantations (Fig. 2). The magnitude of the rhizosphere effects on N mineralization and nitrification rates differed significantly among three species, being greatest in Mongolian pine plantation and smallest in Simon poplar plantation (Table 2). NO$_3^-$-N concentration decreased significantly while NH$_4^+$-N concentration increased significantly in rhizosphere soil as compared with bulk soil in all plantations, except that NH$_4^+$-N concentration did not differ between bulk and rhizosphere soils in Mongolian pine plantation (Fig. 2). Fine root surface APA was significantly higher in Siberian elm and Mongolian pine than in Simon poplar. Fine root biomass significantly decreased in the order of Simon poplar > Siberian elm > Mongolian pine (Table 3).

Fig. 1. Acid phosphatase activity (APA) and Olsen-P concentration in bulk and rhizosphere soils of different plantations in southeastern Keerqin Sandy Lands, Northeast China (mean ± SE, n = 5). Different letters indicate significant differences between bulk and rhizosphere soils for each tree species by paired-samples T-test (P<0.05).

4. Discussion

4.1. Rhizosphere effects on N and P mineralization and availability

We hypothesized that N and organic P mineralization would be promoted by rhizosphere effects of all tree species. This hypothesis was supported by our results. Potential net N mineralization rate increased by 110–188% and APA increased by 27–60% in rhizosphere soil compared to bulk soil across all plantations (Table 2). Previous studies have demonstrated that the sandy soil is deficient in available N and P at the study site (Chen et al., 2006; Zhao et al., 2002).

Table 1

<table>
<thead>
<tr>
<th>Tree species</th>
<th>pH</th>
<th>SOC (g kg$^{-1}$)</th>
<th>MBC (mg kg$^{-1}$)</th>
<th>MBN (mg kg$^{-1}$)</th>
<th>MBP (mg kg$^{-1}$)</th>
<th>Microbial C/N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Siberian elm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bulk soil</td>
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<td>7.0 (0.1)</td>
<td>1.8 (0.1)</td>
<td>5.2 (0.8)</td>
<td></td>
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</tr>
<tr>
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<td>6.7 (0.2)</td>
<td>2.1 (0.2)</td>
<td>5.6 (1.0)</td>
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</tr>
<tr>
<td>T-test</td>
<td>NS</td>
<td>**</td>
<td>NS</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Simon poplar</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bulk soil</td>
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<td>5.2 (0.8)</td>
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<td>Rhizosphere soil</td>
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<td>1.0 (0.1)</td>
<td>11.1 (1.1)</td>
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<td></td>
</tr>
<tr>
<td>T-test</td>
<td>T-test</td>
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<td>**</td>
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<tr>
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<td></td>
</tr>
<tr>
<td>Bulk soil</td>
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<td>1.8 (0.1)</td>
<td>5.2 (0.8)</td>
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<tr>
<td>Rhizosphere soil</td>
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<td>1.8 (0.1)</td>
<td>5.2 (0.8)</td>
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<tr>
<td>T-test</td>
<td>NS</td>
<td>**</td>
<td>NS</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Data are means with standard errors given in parentheses (n = 5). NS denotes no significant difference (by paired samples T-test).

Table 2

<table>
<thead>
<tr>
<th>Tree species</th>
<th>SOC</th>
<th>MBC</th>
<th>MBN</th>
<th>Microbial C/N</th>
<th>Olsen-P</th>
<th>APA</th>
<th>Net N mineralization</th>
<th>Net nitrification</th>
</tr>
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<td>Siberian elm</td>
<td>43b</td>
<td>43b</td>
<td>33b</td>
<td>NSb</td>
<td>NSb</td>
<td>142a</td>
<td>162a</td>
<td>126b</td>
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<tr>
<td>Simon poplar</td>
<td>58a</td>
<td>23b</td>
<td>22b</td>
<td>NSb</td>
<td>NSb</td>
<td>106b</td>
<td>110b</td>
<td>106b</td>
</tr>
<tr>
<td>Mongolian pine</td>
<td>NSa</td>
<td>NSa</td>
<td>64b</td>
<td>−35b</td>
<td>NSb</td>
<td>48b</td>
<td>27b</td>
<td>188b</td>
</tr>
</tbody>
</table>

Table 3

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Microbial biomass C (MBC)</th>
<th>Microbial biomass N (MBN)</th>
<th>Microbial biomass P (MBP)</th>
<th>APA</th>
<th>Acid phosphatase activity</th>
</tr>
</thead>
<tbody>
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<td>Siberian elm</td>
<td>NSa</td>
<td>64b</td>
<td>−35b</td>
<td>NSb</td>
<td>142a</td>
</tr>
<tr>
<td>Simon poplar</td>
<td>58a</td>
<td>23b</td>
<td>22b</td>
<td>NSb</td>
<td>106b</td>
</tr>
<tr>
<td>Mongolian pine</td>
<td>NSa</td>
<td>NSa</td>
<td>64b</td>
<td>−35b</td>
<td>48b</td>
</tr>
</tbody>
</table>

Values in columns with different superscript letters denote significant differences among tree species at P<0.05. NS, no significant rhizosphere effect; SOC, soil organic carbon; MBC, microbial biomass C; MBN, microbial biomass N; MBP, microbial biomass P; APA, acid phosphatase activity.
significant differences between bulk and rhizosphere soils for each tree species in southeastern Keerqin Sandy Lands, Northeast China.}

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Fine root biomass (g m^{-2})</th>
<th>Root surface APA (mg nPg^{-1} h^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Siberian elm</td>
<td>36.9 (3.2)^a</td>
<td>11.0 (0.9)^a</td>
</tr>
<tr>
<td>Simon poplar</td>
<td>61.0 (5.8)^b</td>
<td>3.5 (0.2)^b</td>
</tr>
<tr>
<td>Mongolian pine</td>
<td>14.0 (2.1)^a</td>
<td>10.7 (0.8)^a</td>
</tr>
</tbody>
</table>

Data are means with standard errors given in parentheses (n = 5). Values in columns with different superscript letters denote significant differences among tree species at P < 0.05.

2009). In addition, mineralization of organic P is the primary source of available P and associated biological processes controlled soil P transformation (Zhao et al., 2009). Under nutrient-poor conditions, enhanced nutrient uptake by trees via rhizosphere processes is an important adaptive strategy to maintain tree growth (Gobran et al., 1998). Increases in APA and net N mineralization in rhizosphere soil compared to bulk soil have been observed in most previous studies on tree seedlings and forests. The increased APA can be attributed to the secretion by both plant roots and rhizosphere fungi (Häussling and Marschner, 1989; Fox and Comerford, 1992; Phillips and Fahey, 2006). The simultaneous increases in potential net N mineralization rate and MBN in rhizosphere soil suggest that tree roots stimulated gross N mineralization in the present study, as net N mineralization rate is the result of gross N mineralization and N immobilization. In general, enhanced gross N mineralization in rhizosphere soil primarily results from the rhizosphere “priming effects” on soil organic matter decomposition (Ehrenfeld et al., 1997; Colin-Belgrand et al., 2003; Phillips and Fahey, 2006). Nitrogen transformation is tightly coupled with soil organic matter decomposition that can be strongly accelerated by rhizodeposition (i.e. root exudates)-activated microbial growth (Jackson et al., 2008). In addition, release of NH_4^+ by soil faunal grazing of rhizosphere microbes has been proposed as another important mechanism for increased rhizosphere N availability (Jackson et al., 2008). However, this was not tested in the present study due to limitations of our experimental design.

The greater net nitrification rate in rhizosphere soil relative to bulk soil did not result in the accumulation of NO_3^-N (Fig. 2). On the contrary, NO_3^-N concentration decreased in rhizosphere soil compared to bulk soil, indicating that the uptake of NO_3^-N by plants and rhizosphere microorganisms exceeded the nitrification. It is suggested that in N-limited soils, the rhizosphere microbial growth is rather N-limited than C-limited, and that rhizosphere C flux may reduce N availability if nutrient-limited rhizosphere microbes immobilize N (Cheng et al., 1996; Phillips and Fahey, 2006). This is confirmed in the present study. Similarly, N availability was increased in the rhizosphere of trees on mineral N concentrations varied among studies. For example, significantly higher NH_4^+ and unchanged NO_3^- concentrations in rhizosphere soil relative to bulk soil were observed by Colin-Belgrand et al. (2003) in three forest sites and by Turpault et al. (2005) in a mature Douglas-fir (Pseudotsuga menziesii) stand. Whereas Wang et al. (2001) observed great depletion of NH_4^+ and NO_3^- in rhizosphere soil of Norway spruce (Picea abies) and European beech (Fagus sylvatica) seedlings. Ehrenfeld et al. (1997) found that NH_4^+ and NO_3^- were not influenced by live roots in mineral soil. The diversity of these results may reflect the diversity of soils and plant species (Ehrenfeld et al., 1997). In general, whether accumulation or depletion of extractable nutrients in rhizosphere soil is determined by the balance between the rates of extractable nutrient release and nutrient uptake by plant roots and microorganisms, which could be largely affected by many factors such as soil fertility, plant nutrient demand and soil moisture (Gahoonie et al., 1994; Zhang and George, 2009).

The NaHCO_3 extraction is a useful method for estimating bioavailable P in soil, which is in good agreement with bioassay experiments (Demetz and Insam, 1999). The increase in Olsen-P in rhizosphere soil in all plantations indicates that the rate of organic P hydrolysis exceeds the P uptake by plant roots and rhizosphere microorganisms. In this sandy soil with low P availability, higher rhizosphere phosphatase activity could therefore largely account for the accumulation of inorganic P in the rhizosphere. In addition, in poplar plantation where soil pH decreased in rhizosphere soil, solubilization of calcium phosphate by decreased pH may in part contribute to the increased Olsen-P in rhizosphere soil. Phosphate ions in soil can form a range of inorganic phosphate compounds in combination with metals such as calcium, iron and aluminum (Hinsinger, 2001). Our previous study found that calcium phosphate is the most abundant form of inorganic P at the study site (accounting for 11–17% of total P) (Zhao et al., 2007). As one of the most important factor influencing soil P availability, the reduction in soil pH can increase the solubility of calcium phosphate (Hinsinger, 2001). Previous studies about rhizosphere effects on extractable P showed contrasting results. For example, significant accumulation of readily available organic P and depletion of available inorganic P were observed in rhizosphere of radiata pine (Pinus radiata) seedlings (Chen et al., 2002) and Norway spruce stand.
(Clegg and Gobran, 1997). Whereas, Chen (2003) and Häussling and Marschner (1989) reported the higher extractable inorganic P and lower hydrolysable organic P concentrations in rhizosphere soil of 18-year-old Chinese fir (Cunninghamia lanceolata) plantation and mature Norway spruce forest, respectively. Being different from MBC and MBN, MBP did not differ between rhizosphere and bulk soils in all plantations (Table 1). This suggests that soil microbial growth is limited by N rather than by P at the present study site, and that rhizosphere microorganisms promote P supply primarily by organic P hydrolysis rather than by microbial biomass turnover.

4.2. Species differences in rhizosphere effects

Consistent with our hypothesis, the magnitude of rhizosphere effects on nutrient transformation varied with tree species. Under the N and P deficient soil conditions, Mongolian pine roots were more effective in facilitating N transformation, whereas Siberian elm roots were more effective in facilitating P transformation, and Simon poplar roots were intermediate for both N and P transformations. This suggests that the extent of nutrient limitation might differ among the three tree species, due to their different capacities to acquire the deficient nutrients. At the ecosystem level, plants have evolved a range of strategies to obtain nutrients under nutrient-limiting conditions (Vance et al., 2003). The combination of these strategies may differ with tree species. So magnitude of rhizosphere effects is not necessarily positively correlated to nutrient requirement. Apart from rhizosphere stimulation of nutrient availability, increased soil exploration by root production is another important strategy for nutrient acquisition (Treseder and Vitousek, 2001; Lambers et al., 2008). In the present study, Simon poplar trees have the greatest nutrient requirement (highest tree growth rate), but intermediate magnitude of rhizosphere effects. The greatest fine root biomass in Simon poplar suggests that increased soil exploration may play a more important role in nutrient acquisition as compared with other two species.

The species difference in the magnitude of rhizosphere effect on soil APA can be ascribed to their different root surface APA and rhizosphere fungi. Phosphatase in rhizosphere soil is secreted by both plant roots and rhizosphere fungal hyphae (Häussling and Marschner, 1989). In the present study, the relative contribution of plant roots and rhizosphere fungi to increased rhizosphere soil APA may differ among three species, since the magnitude of rhizosphere effect on soil APA is not proportional to root surface APA across all plantations (Table 3). The greater magnitude of rhizosphere effect on soil APA in Siberian elm plantation may largely result from the higher root surface APA. While in Simon poplar plantation, the lowest root surface APA and intermediate magnitude of rhizosphere effect on soil APA suggest that rhizosphere fungi may contribute more to rhizosphere P acquisition than in other two plantations. This proposition is further supported by the data on microbial biomass C/N ratio (Table 1). Microbial biomass C/N ratio has been used as an indicator of changes in microbial community structure (Paul and Clark, 1989). The greatly higher microbial biomass C/N ratio in Simon poplar plantation (11.1) than in Siberian elm (5.6) and Mongolian pine (6.1) plantations indicates that rhizosphere microbial biomass is more dominated by fungi in Simon poplar plantation, while in Siberian elm and Mongolian pine plantations, it is more dominated by bacteria.

Differences in the amount and type of root exudates among three species could be largely responsible for the variation in the magnitude of rhizosphere effect on N mineralization. As discussed above, increased rhizosphere N mineralization primarily results from rhizosphere “priming effects” on soil organic matter decomposition by microbes. The magnitude of rhizosphere “priming effects” has been known to be largely determined by the amount and type of C released from the roots, as well as intrinsic soil characteristics (Kuzyakov and Domanski, 2000; Jones et al., 2004). Though there is almost no quantitative information about root exudates of mature trees growing under natural conditions due to numerous technical difficulties, experiments on tree seedlings have revealed that tree species differ greatly in amount and type of root exudates (Grayston et al., 1996). In the present study, different magnitude of rhizosphere effects on MBC, MBN and microbial biomass C/N ratio among three species suggest that amount and quality of root exudates may differ among Siberian elm, Simon poplar and Mongolian pine. In Mongolian pine plantation, greatly decreased microbial biomass C/N ratio in rhizosphere soil may reflect the root exudates with lower C/N ratio.

Root exudates influence nutrient cycling not only by stimulating rhizosphere microbial growth but also by altering microbial community structure (Hernesmaa et al., 2005). Rhizosphere microbial community structure also varies with tree species, as a result of the differences in amount and type of root exudates (Grayston and Campbell, 1996). In Mongolian pine plantation of the present study, MBC did not differ between rhizosphere and bulk soils, while microbial biomass C/N ratio decreased significantly in rhizosphere soil compared to bulk soil, indicating that the stimulation of N mineralization may result from the altered rhizosphere microbial community structure (an increase of bacterial biomass with respect to fungal biomass) rather than from increased total microbial biomass. Conversely, in Siberian elm and Simon poplar plantations, significantly increased MBC and unchanged microbial biomass C/N ratio in rhizosphere soil suggest that enhanced N mineralization in rhizosphere soil may result from the increased rhizosphere microbial biomass. These results reflect that mechanisms of rhizosphere effects on nutrient cycling may differ among tree species.

To date, very few studies have investigated the effects of different plant species on rhizosphere nutrient cycling, especially for tree species (Priha et al., 1999; Phillips and Fahey, 2006). Though differences in root exudates among tree species have been recognized as the important mechanism responsible for tree species differences in rhizosphere effects, how tree species regulate root exudation is poorly understood (Pinton et al., 2001; Kuzyakov, 2002). Nutrient status and root type have been thought to be the two main aspects controlling root exudates, but involved physiological processes still await further study (Pinton et al., 2001; Kuzyakov, 2002). In the present study, under the same climatic and nutrient-deficient soil conditions, tree species with contrasting nutrient requirement and root characteristics had the similar pattern of rhizosphere effects on N and organic P mineralization rates and available N and P concentrations, but the magnitude of rhizosphere effects varied considerably among tree species. The similar pattern and greatly varied magnitude of rhizosphere effects on nutrient cycling for different tree species have also been observed in limited studies (e.g. Priha et al., 1999; Wang et al., 2001; Phillips and Fahey, 2006). For example, Wang et al. (2001) observed that Norway spruce had the similar pattern but more pronounced rhizosphere effects on soil chemistry than European beech. Phillips and Fahey (2006) observed that the magnitude of rhizosphere effects on C and N mineralization rates and phosphatase activity ranged from 10% to 35% across different arbuscular mycorrhizal and ectomycorrhizal tree species. Soil conditions and plant species are the two main factors influencing rhizosphere effects (Kuzyakov, 2002; Hinsinger et al., 2009). Taken together, these results suggest that the direction of rhizosphere effects on nutrient transformation and availability mainly depends on soil conditions, while the magnitude of these effects depends on tree species. Certainly, this should be verified by more comparative studies on the rhizosphere effects of different tree species.
5. Conclusions

Siberian elm, Simon poplar and Mongolian pine trees had the similar pattern but considerably different magnitude of rhizosphere effects on N and P transformations, suggesting different capacities of these species to acquire the deficient nutrients. N mineralization and nitrification rates and APA were significantly stimulated in rhizosphere soil. This led to the accumulation of Olsen-P and NH$_4^+$-N in rhizosphere soil. However, NO$_3^-$-N was depleted in rhizosphere soil owing to the root uptake and rhizosphere microbial immobilization. The microbial growth is N-limited rather than P-limited as indicated by the increased microbial biomass N and unchanged microbial biomass P in rhizosphere soil at the study site. Additionally, the differential responses of microbial biomass and C/N ratio to rhizosphere effects among different species reflect that the relative contribution of rhizosphere microbial biomass and microbial community structure to nutrient cycling varies with tree species.

Acknowledgments

This work was funded by the National Natural Science Foundation of China (Nos. 30800887 and 30872011). The authors thank Pei-Yong Lian for his assistance in field work, and Gui-Yan Ai and Jing-Shi Li for their help in laboratory analyses. We gratefully acknowledge two reviewers and Fu-Sheng Chen for their insightful comments for manuscript revision.

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