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The influence of tree species on small scale spatial heterogeneity of soil respiration in a temperate mixed forest

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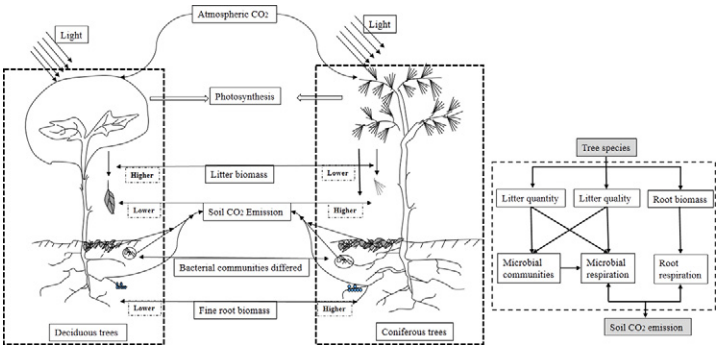
HIGHLIGHTS

- Soil respiration rates were higher under pine than oak and ash trees.
- Soil respiration variation among tree species was not caused by soil temperature.
- Higher carbon and nutrition retention in soil under pine than oak and ash trees.
- Tree species strongly affected bacterial rather than fungal communities.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil respiration is the largest terrestrial carbon flux into the atmosphere, and different tree species could directly influence root derived respiration and indirectly regulate soil respiration rates by altering soil chemical and microbial properties. In this study, we assessed the small scale spatial heterogeneity of soil respiration and the microbial community below the canopy of three dominant tree species (Korean pine (*Pinus koraiensis*), Mongolian oak (*Quercus mongolica*), and Manchuria ash (*Fraxinus mandshurica*)) in a temperate mixed forest in Northeast China. Soil respiration differed significantly during several months and increased in the order of oak < ash < pine, while soil temperature was greater in the order of pine < oak < ash, suggesting that soil respiration variations among tree species were not mainly regulated by soil temperature. In addition, the lower N and higher C concentrations of pine litter resulted in a higher C/N ratio than ash and oak, which might lead to a higher recalcitrance and slower decomposition rate, and decreased heterotrophic respiration under pine. By contrast, fine root biomass was significantly higher under pine than ash and oak, which induced higher soil autotrophic respiration under pine compared to ash and oak. Tree species sharply regulated the bacterial communities through altering the litter and soil properties, while the fungal communities were relatively consistent among tree species. This study revealed the connection between species specific traits and soil respiration, which is crucial for understanding plant-soil feedbacks and improving forecasts of the global carbon cycle.

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1. Introduction

Soil respiration as a major constituent in the terrestrial carbon cycle (Davidson et al., 2006b; Li et al., 2012), is the second largest carbon source to the atmosphere (Schlesinger and Andrews, 2000). Therefore, small changes in soil respiration can largely affect atmospheric CO_2 concentration, which in turn influence the global warming processes. In addition, soil respiration rates have large spatio-temporal variation (Makiranta et al., 2008; Xu and Qi, 2001), and the high spatial variability were reported within the one ecosystem (Saiz et al., 2006), and even within one measurement site (Raich and Schlesinger, 1992). Hence understanding the small scale spatio-temporal variation in soil CO_2 efflux at stand level is critical for accurate evaluating total annual soil CO_2 efflux rates under climate change scenarios (Jordan et al., 2009).

The spatio-temporal variations of soil respiration are generally caused by soil abiotic and biotic factors (Ceccon et al., 2011). Temporal and spatial variability of soil respiration has been shown to be influenced by seasonal fluctuations in both soil temperature and soil moisture (Adachi et al., 2009; Inoue and Koizumi, 2012; Song et al., 2013). Soil temperature and moisture interact to affect the decomposition rate of soil organic matter and productivity of terrestrial ecosystems, which in turn lead to soil respiration variation (Wiseman and Seiler, 2004). In addition, greater spatial heterogeneity of soil respiration generally exhibit due to the differences of soil organic matter quantity and quality (Couteaux et al., 1995; Taylor et al., 1989), soil texture and fertility (Schwendenmann et al., 2003; Xu and Qi, 2001), and microbial biomass (McCarthy and Brown, 2006).

Soil abiotic and biotic factors may explain most of the spatial variation in soil respiration (Longdoz et al., 2000). However, complicated interaction of those factors limits our understanding of the underlying mechanisms and thus make it harder to accurately estimate soil respiration by models (Adachi et al., 2005). Tree species generally differ in productivity, canopy structure and litter quality and quantity (Olsson et al., 2012), and thus alter soil properties, which in turn results in the spatial variation of soil respiration. Previous studies have confirmed that tree species could strongly affect soil temperature and moisture (Liu et al., 2014), soil fertility (Aponte et al., 2012; Cardelus et al., 2009; Eisalou et al., 2013), and microbial communities (Kiikkila et al., 2014; Ushio et al., 2010) in mixed forest. Besides these indirect effects of tree species via influencing the mentioned soil properties, tree species could directly affect soil respiration via influencing autotrophic respiration due to their distinct fine root traits and biomass (Ryan et al., 1996), rhizosphere effects (Phillips and Fahey, 2006) and as well as phenology (Hogberg et al., 2001; Migliavacca et al., 2015). Therefore, the spatial distribution of tree species may cause small-scale heterogeneity of soil respiration.

As yet, some studies have reported soil respiration and soil microbial community with consideration of forest types (Mitchell et al., 2010; Vesterdal et al., 2012). For example, Raich and Tufekciogul (2000) reviewed the effect of tree species on soil respiration and indicated that broadleaf stands have higher soil respiration rates than coniferous stands at the same site. By contrast, Subke et al. (2006) conducted a meta-analysis and did not find significant difference in soil respiration between temperate deciduous and coniferous forests. However, less studies addressed tree species effects on soil respiration in mixed forest where the site-related confounding effects could be minimized (e.g. Liu et al., 2014). In addition, mechanisms of how differing tree species affect soil respiration have not been clearly demonstrated.

This study was conducted with three main tree species (Korean pine (*Pinus koraiensis*), Mongolian oak (*Quercus mongolica*), and Manchuria ash (*Fraxinus mandshurica*)) in a temperate mixed forest in Northeast China to evaluate the effects of tree species on soil respiration via influencing soil properties and microbial community. The specific objectives of this study were (1) to evaluate differences in soil respiration rates and the microbial community under different tree species canopy in a mixed forest, (2) to investigate main control factors on in situ soil respiration rate.

2. Materials and methods

2.1. Site description and experimental setup

This study was conducted in Changbai Mountain Nature Reserve (42°24′10″N, 128°05′46″E, at an elevation of 740 m a.s.l.), which is located in Jilin province, northeastern China. The region is characterized by a monsoon-influenced, temperate, continental climate, with long and cold winters, and warm summers. Mean annual temperature is 3.6 °C, with the highest temperature in mid-August, and the lowest temperature in early February. Mean annual precipitation is 690 mm, mainly falling between May and September. The study site is located in a flat area, with slope ranging from 1° to 5°. The forest is covered with 300 year-old mixed stand of pine, oak, and ash, interspersed with larch (*Larix olgensis var.*), mono maple (*Acer mono*), and other deciduous woody species. The mean canopy height is about 27.0 m, the stand density is 560 stems ha^{-1} (stem diameter > 8 cm), and the maximum leaf area index is up to 6.0 (Wu et al., 2012). The soil is montane dark brown soil developed from volcanic ash (Albi-Boric Argosols).

To minimize the disturbance of other species, tree clusters, defined as three adjacent mature trees (one species) that were standing in a triangle to each other, were chosen for investigation. The three trees have similar diameter at breast height (DBH), and a mean distance from their cluster center of 2.5 m, ranging from 1.5 to 5 m. The center did not have other trees and is less influenced by other species. Three replicate clusters were selected for each tree species (Korean pine, oak or ash). The experimental setup followed Langenbruch et al. (2012).

2.2. Soil respiration measurement

Five cylindrical PVC collars, 10.4 cm in diameter and 7 cm in height, were randomly placed at each cluster (the distance from tree > 1.5 m). The PVC collars were inserted into soil to a depth of 3 cm two months before the first CO_2 measurements, and remained in the soil for the duration of the experiment. Soil CO_2 efflux was measured by using a Li-6400 XT portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) with a Li-6400-09 soil chamber. Measurements of in situ soil respiration rate (SR) in each cluster were performed about once a week in sunny day in growing seasons during late August 2013 to the end of October 2014. Measurements were consecutively replicated three times at each collar and conducted from 09:00 to 14:00 local time. The soil volumetric water content and temperature were measured at depths of 10 cm at the same time using a HydroSense soil moisture probe (Campbell Scientific, Logan, UT) and a penetration probe inserted into the soil in the vicinity of the collar, respectively.

2.3. Sampling of litterfall, roots and soil

Three litter collectors (50 × 50 cm) were installed at the center of each cluster. The litterfall was sampled at monthly intervals. The collected litter was picked up manually according to tree species in each cluster, then dried at 70 °C for 72 h. The sum of dry weight from all sampling dates represented the annual litterfall biomass.

At the end of September 2014, three soil cores of 5 cm diameter (0–20 cm depth) were obtained from each cluster. The roots were washed free of soil over a 0.5 mm sieve, and manually separated into fine roots (diameter < 2 mm) and coarse roots (diameter > 2 mm) using tweezers. Living and dead roots were separated according to root color, i.e., black roots were assumed to be dead roots (Majdi and Andersson, 2005; Vance et al., 1987). The fine roots were dried at 70 °C for >48 h and weighted. The fine root biomasses (g m^{-2}) were calculated as the dry weight of fine roots.

Five soil cores of 5 cm diameter were taken from each cluster to a depth of 10 cm and were combined into one composite sample for each cluster, and then transported at 4 °C to the Institute of Applied Ecology, Chinese Academy of Sciences at Shenyang, China. Soil samples

were sieved through a 2 mm mesh and remove plant detritus, roots and stones. A portion of each soil sample was stored at −20 °C until DNA extraction. The remaining soils were used to determine total soil C and N concentrations, organic C, natural abundance of $\delta^{13}C$, soil microbial biomass carbon content (MBC) and soil physiochemical.

2.4. Laboratory analyses

Total C and N concentrations, and natural abundance of $\delta^{13}C$ were determined from litter, fine root and soil samples. The total C and N concentrations were measured with an elemental analyzer Vario EL (Elementar Analysensysteme GmbH, Germany), and the natural abundance of $\delta^{13}C$ was determined from stable isotope-ratio mass spectrometers (Thermo Fisher MAT 253, America). The soil organic carbon was determined by potassium dichromate oxidation-ferrous sulfate titrimetry. The pH value was determined by a soil acidity meter (PHSJ-3F, China) using water extraction method (10 g fresh soil extracted with 50 ml deionized water). The nutrient and exchangeable cations (phosphorus [P], available phosphorus [AP], potassium [K], sodium [Na], calcium [Ca], and magnesium [Mg]) were determined using an inductively coupled plasma atomic emission spectrometer (ICPS-7510; Shimadzu, Kyoto, Japan). Microbial biomass C was determined via the chloroform fumigation-extraction (Vance et al., 1987) using a total organic carbon analyzer (Shimadzu, Columbia, MD).

Before the microbial community analysis, subsamples of three clusters from each tree species were pooled into one sample. Soil DNA was extracted from 0.25 g freeze-dried soil after sampling by using a Mobio PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA). The DNA was eluted by 100 μl Tris buffer (10 mM), then quantified by spectrophotometer (at 260 nm), and stored at −20 °C until use. Soil DNA samples were sent to Novogene Company (Beijing, China) for high-throughput sequencing, and the detailed methods were described by Xia et al. (2016).

2.5. Data analyses

For simplicity of calculation, monthly measurements of soil respiration, temperature and moisture for each cluster were interpreted as repeated measurements of the same experimental unit. Effects of tree species on soil respiration were consequently analyzed by repeated measures ANOVA. Effects of tree species on litter quality and quantity and all soil properties were also analyzed by ANOVA.

The exponential equation of van't Hoff type (Davidson et al., 2006a) was used to describe the temperature dependence of soil respiration: $SR = ae^{bT}$, where SR is soil respiration rate, a and b are fitted parameters, and T is measured soil temperature. The Q_{10}, known as temperature sensitivity of respiration can be calculated as follows: $Q_{10} = e^{b10}$.

The relationships between soil respiration rates and soil moisture were examined by linear regression analyses. Statistical analyses were performed using R 3.1.0.

A principal component analysis (PCA) was carried out to analyze overall effects of tree species (pine, oak and ash) on fine-scale environmental traits. The data comprised soil parameters, root parameters, litter parameters and soil respiration rates. The PCA was applied using the vegan package for R 3.1.0.

3. Results

3.1. Soil respiration and microclimate under three tree species

Soil respiration showed a typical seasonal pattern following soil temperature with the maximum occurred in July and minimum appeared in April for all three tree species (Fig. 1). Generally, the mean soil temperature at 10 cm depth did not significantly differ among ash (12.33 °C), oak (12.27 °C), and pine (12.18 °C, $P = 0.31$), and the statistically significant difference (increasing in the order of pine < oak < ash) only exhibited in September and October of 2013, and July, August and September of 2014. The soil moisture at 10 cm depth increased in the order of pine < ash < oak, although these differences were only significant in May and June in 2014 (Fig. 1).

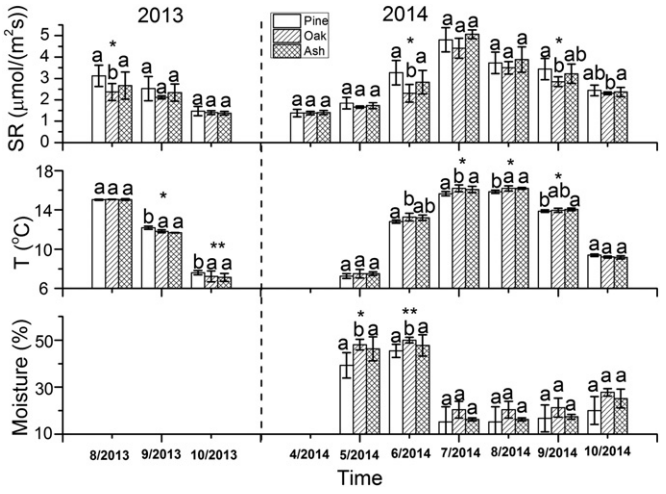

Fig. 1. Monthly mean of soil respiration rate (SR), soil temperature (T) and soil moisture below the canopy of Pine, Oak and Ash from August 2013 to October 2014. Significantly different mean values are indicated by different letters and bars represent ±SD. $^{*}P < 0.05$, $^{**}P < 0.01$.

Mean respiration rates increased in the order of oak (2.46 μmol m^{-2} s^{-1}) < ash (2.68 μmol m^{-2} s^{-1}) < pine (2.80 μmol m^{-2} s^{-1}), although these differences were not statistically significant. However, soil respiration rates among tree species differed significantly in August of 2013, June and September of 2014 (Fig. 1).

Soil respiration rates from each tree species were significantly correlated with soil temperatures (Table 1, $P < 0.001$). The exponential model showed that soil temperature could explain 76%, 68% and 75% of the temporal variation in soil respiration rates under the canopy of pine, oak, and ash, respectively. Q_{10} value from each tree species, calculated for the temperature range of 3.6–18.3 °C, was higher in pine (4.22), followed by ash (3.60) and oak (3.53).

Soil respiration rates from each species exhibited linear relationships with soil moisture over the study period (Table 2). Soil respiration rate under the canopy of pine, oak, and ash increased with soil moisture before it reached 24.9%, 37.5%, and 27.4%, respectively, and thereafter declined with further increase of soil moisture.

3.2. Microbial community under three tree species

The bacterial communities were sharply different among tree species, while the fungal communities were nearly consistent among tree species (Fig. 2). The dominant bacterial phyla abundance decreased in the order of *Acidobacteria* < *Chloroflexi* < *Proteobacteria* < *Actinobacteria* < *Verrucomicrobia* < *Planctomycetes* < *Gemmatimonadetes* under pine, while decreased in the order of *Proteobacteria* < *Actinobacteria* < *Acidobacteria* < *Gemmatimonadetes* < *Chloroflexi* < *Planctomycetes* < *Verrucomicrobia* under oak, and decreased in the order of *Proteobacteria* < *Acidobacteria* < *Actinobacteria* < *Verrucomicrobia* < *Planctomycetes* < *Chloroflexi* < *Gemmatimonadetes* under ash. In addition,

Table 1
Best-fit exponential models of soil respiration rates (μmol m^{-2} s^{-1}) as a function of soil temperature (°C) at 10 cm depth during all measured date.

Species	Function	R^2	P	Q_{10}
Pine	$SR = 0.39\ e^{0.144T}$	0.76	<0.001	4.22
Oak	$SR = 0.59\ e^{0.126T}$	0.68	<0.001	3.53
Ash	$SR = 0.61\ e^{0.128T}$	0.75	<0.001	3.60

Table 2
Best-fit linear mixed models of soil respiration rates (μmol m^{-2} s^{-1}) as a function of soil moisture (%) at 10 cm depth during all measured date. Soil respiration rates were positively correlated with soil moisture before it reached split point, and thereafter declined with further increase of soil moisture.

Species	Positive correlation			Negative correlation			Split point (%)
	Function	R^2	P	Function	R^2	P	
Pine	SR = 0.103x + 2.285	0.126	0.027	SR = −0.090x + 7.059	0.28	<0.001	24.9
Oak	SR = 0.103x + 1.382	0.388	<0.001	SR = −0.220x + 13.475	0.454	<0.001	37.5
Ash	SR = 0.143x + 1.835	0.286	<0.001	SR = −0.179x + 10.624	0.562	<0.001	27.4

the bacterial phyla of *Verrucomicrobia* was minor in oak, while *Chloroflexi* was minor in both oak and ash. The dominant fungal phyla across all soil samples were *Basidiomycota*, *Ascomycota* and *Zygomycota*, accounting for >90% of the fungal sequences from each of the soil sample.

3.3. Fine-scale environmental heterogeneity among tree species

Soil pH was lower under pine than ash (Table 3). Soil total phosphorus and available phosphorus were higher under pine and oak than ash. There was no difference in soil bulk density among tree species. Soil Ca^{2+} and Mg^{2+} concentrations were higher under pine and oak than ash, while soil K^+ content was higher under oak and ash than pine. Soil Na^+ content and microbial biomass C were higher under oak than ash. Soil organic C was significantly lower under pine than oak.

The annual litterfall biomass of pine was 350.3 g m^{-2}, which was significantly lower than oak (530.0 g m^{-2}) and ash (488.7 g m^{-2}), while fine root biomass was significantly higher in pine (459.4 g m^{-2}), followed by ash (408.2 g m^{-2}) and oak (384.2 g m^{-2}, Table 4). Litter chemistry properties were significantly variable between ash and oak (deciduous trees) and pine (coniferous trees, Table 4). Compared to ash and oak, litter N content of pine was lowest while its C content was highest, hence the highest C/N ratio. Whereas, the C/N ratio of fine roots was higher in ash, followed by pine and oak. For both litter and fine roots, oak more enriched $\delta^{13}C$ signatures than pine and ash.

Two main gradients in fine-scale environmental traits emerged from the PCA. The first axis (58.3% of the total inertia) was defined by an opposition between on the one hand C content and C/N ratio of litter, and on the other hand variables that describe the compaction and chemistry traits (i.e. soil density, soil N & C contents and soil C/N ratio) and litter N content (Fig. 3). The second axis (25.3% of the total inertia) opposed the SR, fine root C/N and C content and DBH to litter biomass, fine root biomass, fine root N, and microbial biomass carbon. In addition, pine, oak and ash were somewhat different overall in fine-scale environmental traits (Fig. 3).

4. Discussion

4.1. Soil heterogeneity among tree species

Properties of soil, litter and fine roots strongly differed among tree species (Fig. 3). Litter N concentration of pine was lowest while C concentration was highest compared with ash and oak, hence the highest C/N ratio. This result is consistent with previous litter quality estimations by Ayres et al. (2009) and Stump and Binkley (1993), which indicated that C/N ratio of litter was higher in coniferous trees than in deciduous trees. Previous synthesis results of Berg (2000) demonstrated that litter decomposition rates are positively correlated with nitrogen concentrations at earlier decomposition stage, while negatively correlated in the late stages. Pérez-Harguindeguy et al. (2000) proposed that higher C/N ratio could reduce the litter decomposition rate. The lower N content and higher C/N ratio of pine than ash and oak might result in a generally higher recalcitrance and slower rate of decomposition at earlier decomposition, hence elevate carbon retention in litter. This is similar to the previous findings of Vesterdal et al. (2008), which reported that litter decay from deciduous plants was faster than that from conifers. In addition, this study suggests that C/N ratio of fine roots was higher in ash, followed by pine and oak, while nitrogen content of fine roots did not significantly differ among tree species (Table 4). Li et al. (2015) conducted a meta-analysis and suggested that lower C: N ratio and higher nitrogen content of fine roots could delay their decomposition. Combined our results of fine root's C and N content, we deduce that fine roots of ash likely have highest decomposition rate, followed by pine and oak.

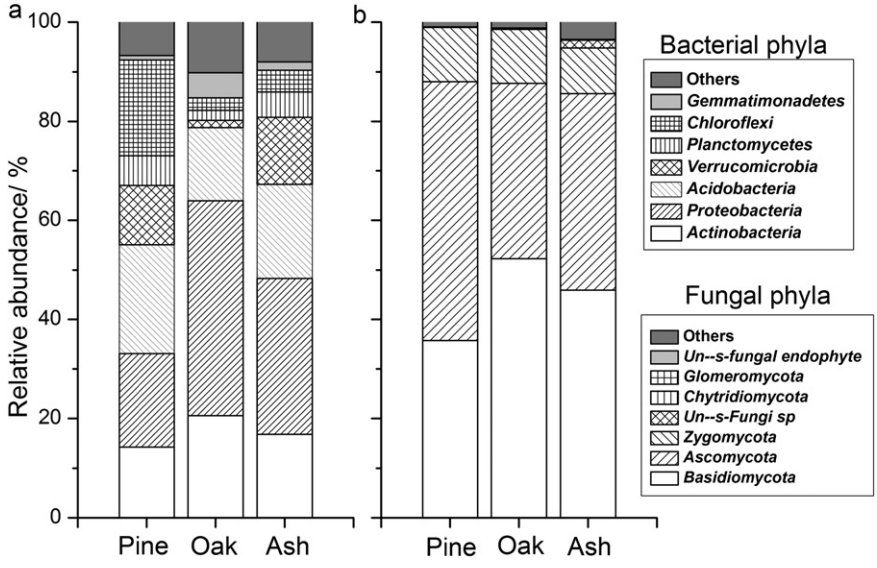

Fig. 2. Relative abundances of the dominant bacterial (a) and fungal (b) phyla in soils separated according to tree species. Relative abundances are based on the proportional frequencies of those DNA sequences that could be classified at the phylum level.

Table 3
Soil characteristics (0–10 cm) at different tree species (mean value (±SD, $n = 3$)). (TP: total phosphorus, AP: available phosphorus, MBC: microbial biomass). Significantly different mean values are indicated by different letters ($P < 0.05$).

Species	Bulk density (g/cm^3)	pH	TP (g/kg)	AP (mg/kg)	K (mmol/kg)	Na (mmol/kg)	Ca (mmol/kg)	Mg (mmol/kg)	Organic C (%)	MBC (g/kg)
Pine	0.33(0.08)a	5.21(0.18)a	1.13(0.45)b	6.11(0.85)b	4.70(0.50)a	1.68(0.26)ab	138.84(29.44)b	34.35(7.01)b	9.78(2.3)a	1.25 (0.28)ab
Oak	0.42(0.08)a	5.29(0.10)ab	1.57(0.12)b	6.04(0.53)b	5.65(0.60)b	2.01(0.33)b	158.63(33.63)b	39.75(8.12)b	14.64(2.6)b	1.48(0.32)b
Ash	0.45(0.13)a	5.38(0.21)b	0.607(0.26)a	4.15(0.48)a	5.70(0.60)b	1.29(0.18)a	102.82(21.80)a	26.19(5.35)a	12.58(2.9)b	0.94(0.20)a

Previous studies concluded that soil surface nutrient status was influenced by the ability of different tree species to improve or maintain soil productivity via nutrient uptake and redistribution (Langenbruch et al., 2012; Neirynck et al., 2000). In this study, soil pH was significantly higher under ash than pine, while soil P, Ca^{2+} and Mg^{2+} contents were significantly lower under ash than pine and oak, which strongly contributed by tree species litter nutrient, Ca and Mg concentration (Noble and Randall, 1999; Reich et al., 2005). Microbial biomass C was generally described as a living or active pool which indicates potential rate of C flux (Franzluebbers et al., 1999), and was used to simulate soil organic C turnover in model (Coleman and Jenkinson, 1996). However, this study indicates that microbial biomass C was higher under oak than ash, which is different from the pattern of soil respiration. The mechanism of this discrepancy result is still unclear, while one of potential causes was the different MBC measure method because the correlation between soil respiration and MBC was strongly depend on the measure method (Wang et al., 2003). In addition, we found significantly lower stocks of soil organic C under pine than oak, presumably because the slower turnover rate of pine litterfall delayed carbon and nutrient return to the soil (Jacob et al., 2009; Oostra et al., 2006).

Soil fungi and bacteria are dominant players in microbial heterotrophic respiration for decomposing the dead organic matter via metabolism (Couteaux et al., 1995; Harmon et al., 2011). Here we observed that soil bacterial diversity exhibits more apparent difference among selected tree species compared to soil fungal diversity. These results are similar to the conclusion of Chu et al. (2011) that bacterial communities differed significantly and consistently according to vegetation type, while the fungal communities of all vegetation types were dominated by two common phylotypes in Arctic tundra soil. The main reason likely was that fungi could better adapt to abiotic environmental factors than bacteria (Swift et al., 1979). However, Nielsen et al. (2010) observed that soil fungi community composition was directly associated with plants, whereas soil bacterial community composition did not directly associate with plants but depended on soil properties (e.g. pH and C/N ratio). These results are consistent with the findings of Shen et al. (2013), who observed that soil bacterial diversity and community composition in Changbai Mountain can largely be predicted by soil pH. In addition, Chu et al. (2010) observed that soil TOC, N, and C/N ratio were also important factors for predicting soil bacterial diversity. In this study, soil microbial communities, litter quality and soil properties differed among selected tree species. Thus, we infer that tree species might indirectly regulate microbial distribution by different litter quality and soil properties.

4.2. Tree species distribution and soil respiration heterogeneity

Soil respiration rates were quite variable during the growing season and differed among tree species. Based on measurements over two growing seasons, the highest and lowest mean respiration rates were found under the canopy of pine (conifers) and oak (deciduous trees), respectively. The other deciduous tree, ash, was intermediate in respiration rate. Previous studies indicated that root respiration contributed up to 65% of total soil respiration in boreal pine forest (Nordgren et al., 2003), and contributed up to 39–41% of total soil respiration in oak forest (Tang and Baldocchi, 2005). In this study, the higher fine root biomass under pine than oak and ash could lead to higher autotrophic respiration. In addition, the higher decomposable litter biomass (higher N content and lower C/N ratio) under ash and oak accelerated the decomposition and nutrient cycling compared to pine (Olsson et al., 2012; Reich et al., 2005), and thus could increase heterotrophic respiration. Similar to our findings, Vesterdal et al. (2012) suggested higher soil respiration in an ash stand than in an oak stand. However, some of previous results indicated that no general difference in soil respiration between pure coniferous and deciduous trees (Borken et al., 2002; Ladegaard-Pedersen et al., 2005). These discrepancy results presumably contributed by the forest type because previous studies indicated that mixed forest have both higher root respiration and higher decomposition rate than pure forest (Berger et al., 2010; Gartner and Cardon, 2004).

4.3. Effects of soil properties on respiration among tree species

In this study, soil respiration rate was higher under canopy of pine (coniferous trees) compared to oak and ash (deciduous trees), whereas soil temperature was lower, suggesting that soil temperature was not the main regulator to soil respiration spatial variation among different tree species. The temperature sensitivity (Q_{10}) differed among pine (4.22), oak (3.53) and ash (3.60, Table 1), and all of them were higher than the median value of 2.4 from various soils (Raich and Schlesinger, 1992), but were consistent with other studies from temperate forests. Davidson et al. (1998) reported Q_{10} values are 3.4–5.6 for different soil water content at the Harvard forest. Lower Q_{10} values in the

Table 4
Physical and chemical properties of litterfall, fine roots and soil in three species (mean value (± SD, $n = 3$)). Significantly different mean values are indicated by different letters ($P < 0.05$).

Species	$\delta^{13}C$ (‰)	N (%)	C (%)	C/N	Biomass (inputs, g/m^2)
Litter					
Pine	−28.96(0.429)ab	0.49(0.087)a	51.56(0.221)b	108.64(21.436)b	350.3(44.6)a
Oak	−28.62(0.262)b	1.30(0.229)b	45.61(0.627)a	35.89(6.400)a	530.0(37.0)b
Ash	−29.00(0.166)a	1.02(0.164)b	45.00(1.869)a	44.89(8.276)a	488.7(84.1)b
Fine roots					
Pine	−28.81(0.939)b	1.68(0.125)a	36.91(1.566)a	22.35(3.267)a	459.4(18.7)b
Oak	−28.45(0.612)ab	1.82(0.008)a	38.67(0.340)ab	21.25(0.186)a	384.2(9.0)a
Ash	−30.22(0.923)a	1.45(0.082)a	39.74(2.908)b	27.38(0.469)b	408.2(61.9)a
Soil					
Pine	−24.44(2.948)a	0.86(0.169)a	9.21(1.860)a	10.77(0.467)a	809.7(48.4)#
Oak	−25.16(2.683)a	1.22(0.172)b	14.01(2.924)b	11.41(0.767)b	914.2(38.1)#
Ash	−25.07(2.841)a	0.93(0.113)ab	11.81(2.350)ab	12.61(1.318)b	896.9(104.4)#

The soil carbon inputs are the sum of the litter and fine root biomass.

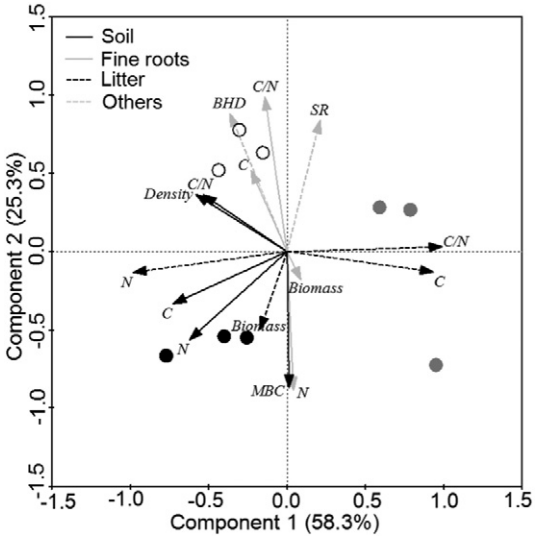

Fig. 3. Principle component analysis of site properties. Score plot of nine cluster during principal component analysis of site properties, including the C, N content and C/N ratio of soil, litter and fine roots, litter and fine root biomasses, soil bulk density, diameter at breast height (DBH), microbial biomass carbon (MBC), and annual soil respiration rate (SR). The points represent the clusters of Pine (gray), Oak (black) and Ash (hollow).

range of 3.1–3.8 were calculated with different forest site in European (Borken et al., 2002). Previous studies suggested that the large range of Q_{10} values were contributed by the differences of stand age (Buchmann, 2000) and soil depth of measured temperature (Borken et al., 2002). In this study, we have used 10 cm depth temperature to calculate the Q_{10} values in order to reduce errors, and we induce that the difference of Q_{10} values among tree species were mainly produced by the thickness of O-horizons because it strongly affect the heat conductivity (litter biomass were lower under pine compared to oak and ash (Table 3)) (Borken et al., 2002). Alternatively, Boone et al. (1998) calculated the Q_{10} for total soil respiration (4.6) and root respiration (2.5), and demonstrated that the Q_{10} for autotrophic respiration is relatively higher than heterotrophic respiration. Fine root biomass was significantly higher under pine than oak and ash in this study, which potentially was the main contributor to the higher Q_{10} value under pine than oak and ash.

Soil CO_2 efflux and soil moisture were positively correlated at low soil moisture contents (lower than 24.9%, 37.5%, and 27.4% under the canopy of pine, oak, and ash, respectively) and negatively correlated at high soil moisture (Table 2). Similar to our result, the splitting points of 19% and 12% were proposed in a subtropical young ponderosa pine forest (Xu and Qi, 2001) and a mixed temperate forest (Davidson et al., 1998), respectively. At high soil moisture contents, the negative correlation between soil respiration rates and soil moisture might be caused by the confounding of soil temperature (Xu and Qi, 2001). The difference of splitting point among tree species may be contributed by two factors. First, the availability of O_2 in the soil pore space, which could affect microbial activity (Linn and Doran, 1984). Second, the different water demand among tree species. In this study, the $\delta^{13}C$ values of both litter and fine roots were highest in oak, which suggests that oak was in the water shortage condition in our study area (Rundel et al., 2012), and thus the oak have a higher potential water demand with higher splitting point.

Tree species can regulate soil respiration through variety mechanisms, essentially by controlling quantity and quality of input litter, and root-derived respiration (i.e. root respiration and root exudates) (Brechet et al., 2009). Our result showed that the litterfall biomass was significantly higher under oak and ash than pine, combined with the more decomposable traits of litter under oak and ash than pine (Olsson et al., 2012; Reich et al., 2005), which lead to the higher soil heterotrophic respiration. By contrast, fine root biomass was significantly higher under pine than oak and ash (Table 4), which could induce higher soil autotrophic respiration. More works are necessary to determine the contribution of these components (heterotrophic and autotrophic respiration) to total soil respiration across tree species in our further research. The principle component analysis indicated that fine roots and litter C/N ratio significantly affect soil respiration, which is consistent with the result of Makita and Fujii (2015), that microbial respiration among tree species were related to both chemical and morphological traits of leaf and fine root litter. In addition, this study showed that soil carbon inputs through litter and fine roots were higher under oak, followed by ash and pine, while the litter decomposition from oak and ash was faster than that from pine (Vesterdal et al., 2008). These results suggest that more efficient nutrition return to soil existed under oak and ash compared to pine.

5. Conclusions

This study explored the effects of tree species on small scale spatial heterogeneity of soil respiration and microbial community in a temperate mixed forest in Northeast China. Soil respiration rates were higher under pine followed by ash and oak, and these differences were not caused by soil temperature. The lower N concentration and higher C/N ratio of pine litter than oak and ash likely resulted in a generally higher recalcitrance and slower rate of decomposition under pine than oak and ash. Our findings suggested that autotrophic respiration dominated the total soil respiration under the canopy of pine, while the heterotrophic respiration dominated the total soil respiration under the canopy of oak and ash. In addition, the lower soil organic C stocks under pine also suggested that C turnover rate was slower compared to oak and ash, which elevates carbon and nutrition retention in litterfall. Moreover, the tree species strongly affected bacterial communities through regulating litter and soil properties, while had little influence on the fungal communities.

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