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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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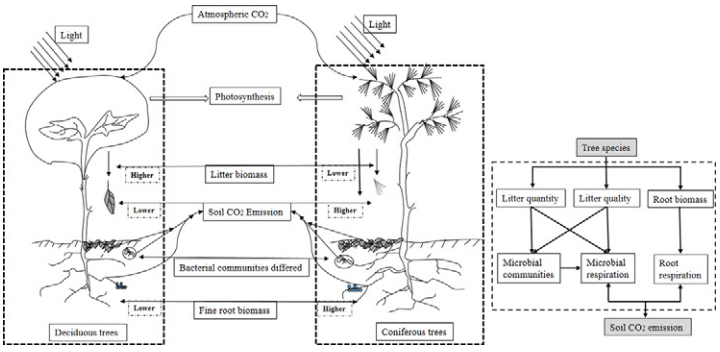
HIGHLIGHTS

- 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