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Mycorrhizal associations differentiate soil respiration in five temperate monocultures in Northeast China

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ABSTRACT

Tree species associated with different mycorrhizal fungi play a crucial role in the carbon (C) cycling of forest ecosystems, while their effects on soil respiration (R_S) and the underlying mechanisms remain uncertain. In this study, we used a common garden experiment that included five monocultures (two arbuscular mycorrhizal – (AM) and three ectomycorrhizal-associated (ECM) temperate tree species) to explore the effects of mycorrhizal associations on the R_S and the driving factors. Our specific objectives were to (1) compare the R_S between the AM and ECM stands, and (2) explore the driving factors of the R_S. We found that the R_S in the AM stands was significantly greater (34.3%) than that in the ECM stands. The R_S was significantly and positively correlated with microbial biomass C (C_{mic}), fine roots biomass (B_{root}), or soil water content (W_5), but negatively with forest floor mass (F_{mass}) or soil dissolved organic C content (C_{dis}). The best-fitted models of R_S explained 46.3%, 38.3%, and 45.4% of the variations in the R_S for the AM stands, the ECM stands, and the combined dataset, respectively. However, the factors contributing to the R_S varied with mycorrhizal groups. The R_S of the AM stands was mainly influenced by C_{mic}, B_{root}, root C/N ratio, F_{mass}, and C_{dis}, whereas the R_S of the ECM stands was mainly affected by litter C/N ratio, C_{dis}, soil dissolved nitrogen content, soil temperature and W_5. These findings highlight the significance of shifts in AM or ECM tree abundance due to forest management and global change in forest C cycling.

1. Introduction

Soil respiration (R_S), the dominant carbon (C) flux to the atmosphere in terrestrial ecosystems, is estimated to be ten times greater than the annual CO_2 emission from fossil fuel combustion (Raich et al., 2002; Bond-Lamberty and Thompson, 2010). Small changes in R_S, therefore, may substantially influence the atmospheric CO_2 concentration, and in turn global changes (Luo et al., 2001; Raich et al., 2002; Wang et al., 2010). In forest ecosystems, tree species can directly and/or indirectly influence the R_S, and thus the C cycling process (Reich et al., 2005; Vesterdal et al., 2012; Yu et al., 2017). Recent evidence suggests that tree species associating with arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi alter the soil C and nitrogen (N) cycling in distinct ways (Phillips et al., 2013; Cheeke et al., 2017; Lin et al., 2017, 2018; Craig et al., 2018), and also change responses of forest production to global changes (Terrer et al., 2016, 2018). Therefore, it is crucial to investigating impacts of plant-microbe interactions on R_S for understanding the biogeochemical cycling of forest ecosystems under global change scenarios.

Previous studies show divergent directions and magnitudes of the effects of mycorrhizal associations of trees on R_S (Reich et al., 2005; Jia et al., 2010; Vesterdal et al., 2012; Lin et al., 2017; Yu et al., 2017), and the underlying mechanisms remain uncertain. AM- and ECM-associated tree species can influence the heterotrophic (R_H) and autotrophic respiration (R_A) – the two main components (Bond-Lamberty et al., 2004) in different ways. AM and ECM stands are likely to have different allocations of the photosynthates to the roots, and thus alter the R_A (Högberg et al., 2001, 2002; Withington et al., 2006; Jia et al., 2010; Yu et al., 2017). For example, the root production of AM forests is 3.5 times greater than that of ECM forests (Withington et al., 2006), which may lead to a stronger metabolic activity of roots and thus a greater R_A and R_S in AM forests. Meanwhile, AM and ECM stands produce different amounts and quality of litter for soil microorganisms (Cornelissen et al., 2001; Veresoglou et al., 2012; Phillips et al., 2013; Craig et al., 2018; Jacobs et al., 2018), which will affect growth and metabolism of microbes and plants (Jia et al., 2010; Vesterdal et al., 2012; Phillips et al., 2013; Cheeke et al., 2017; Lin et al., 2017), and thus both R_H and R_A. Nevertheless, the underlying mechanisms are rarely explored in field experiments (Reich et al., 2005; Vesterdal et al., 2012), but likely vary with mycorrhizal associations, because AM and ECM stands have

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different effects on substrates and soil properties (e.g., nutrients, temperature, moisture; Reich et al., 2005; Vesterdal et al., 2012; Yu et al., 2017). It is documented that ECM fungi produce extracellular enzymes that can access organic N directly from soil organic matter (Van Der Heijden et al., 2015; Fernandez and Kennedy, 2016), which may compete for the limited N with free-living microbes and consequently constrain their metabolic activity and the R_H. Conversely, AM stands lack such enzymatic capacities, and often have greater nutrient availability due to their higher litter quality (Reich et al., 2005; Phillips et al., 2013; Lin et al., 2017; Craig et al., 2018), and thus stimulate the litter decomposition and the R_S. To date, however, most studies have been conducted in ECM stands (Wiseman and Seiler, 2004; Olsson et al., 2005; Cheng et al., 2015; Zeng and Wang, 2015; Yin et al., 2016), and have seldom investigated potentially different drivers of the R_S between AM and ECM stands (Vesterdal et al., 2012).

Quantifying effects of tree mycorrhizal-associations on ecosystem processes is challenging in natural settings mainly due to many confounding factors (Reich et al., 2005; Binkley and Menyailo, 2006; Vesterdal et al., 2013). Most previous studies addressed this issue in mixed stands (e.g., Brzostek et al., 2015; Craig et al., 2018; Lin et al., 2018), even from disparate biomes (Smith and Read, 2008), which may fail to discern the effects of specific mycorrhizal association on the biogeochemical cycling because of the confounding effects of other site-related factors (e.g., climate, soil matrix, topography, and interactions among tree species; Phillips et al., 2013; Lin et al., 2017). One effective approach to unravel the effect of tree species with different mycorrhizal associations is conducting a common garden experiment where different monocultures are planted at the same site conditions (Reich et al., 2005; Vesterdal et al., 2012, 2013). In this study, we used a common garden experiment to explore the effects of tree species with AM and ECM associations on the R_S and the underlying mechanisms. The experiment was established in 2004 with a completely randomized design that included five 11-year-old monocultures: two AM-associated tree species (*Fraxinus mandshurica*, *Juglans mandshurica*) and three ECM-associated tree species (*Betula platyphylla*, *Larix gmelinii*, *Pinus sylvestris* var. *mongolica*). Our objectives were to (1) compare the R_S between the AM and ECM stands, and (2) explore the driving factors of the R_S. Specially, we test the hypotheses: (1) the R_S in the AM stands is greater than that in the ECM stands because the AM stands have higher litter quality and substrate availability (Withington et al., 2006; Phillips et al., 2013; Lin et al., 2017); (2) the factors influencing the R_S vary between the AM and ECM stands because they influence the substrates, soil environmental and microbial properties in different ways (Lee and Jose, 2003; Vesterdal et al., 2012; Lin et al., 2017; Yu et al., 2017).

2. Materials and methods

2.1. Site description and experimental design

This study was conducted at the Maoershan Forest Ecosystem Research Station of Northeast Forestry University in Northeast China (45°20′N, 127°30′E, 400 m a.s.l.). The mean annual precipitation is 629 mm; the mean annual temperature is 3.1 °C; the parent material is granite bedrock. The primary vegetation is a temperate mixed forest representative in Northeast China (Wang et al., 2013).

The common garden experiment was established at a flat abandoned agricultural field with a relatively uniform soil. The experimental design was a completely randomized design that included five tree species monoculture plantations, three replicated plots (25 m × 25 m) each monoculture. The tree species included two AM-associated tree species (*F. mandshurica*, *J. mandshurica*) and three ECM-associated tree species (*B. platyphylla*, *L. gmelinii*, *P. sylvestris* var. *mongolica*). The 2-year-old seedlings were planted at a 1 m × 1 m spacing (625 individuals per plot) in the spring of 2004. The stand inventory and plant traits survey were conducted in October 2013 and 2015, respectively. The understory was dominated by *Carex meyeriana*, *Viola verecunda*, *Urtica fissa* E. Pritz., and *Sorbaria sorbifolia*, except for the *L. gmelinii* stand where there was little understory. The understory may affect the soil properties and add noise to our analysis; however, it is closely associated with the overstory trees and contributes only 3–6% of the soil organic matter (Binkley and Menyailo, 2006). Therefore, the understory composition may not introduce much uncertainty in our analysis.

It should be noted that the canopy of the monocultures was closed about five years before the investigation because of the narrow spacing and fast growth due to the synchronization of temperature and precipitation during the growing season in this region. Realizing that the stands were relatively young and mycorrhizal-fungi and plant inputs mostly exerted influences on the topsoil (Craig et al., 2018), we focused our measurements on the variables related to topsoil (0–10 cm) and plant traits.

2.2. Measurements of soil respiration and related factors

In early April 2014, five PVC collars (10.2 cm in diameter and 5 cm in height) were randomly installed at each plot. The collars were inserted into 3 cm depth of soil from the ground surface and left at the same locations throughout the study for continuity (Wang et al., 2006). Soil respiration (R_S, μmol CO_2-C m^{-2} s^{-1}) was measured with an LI-840 portable CO_2 infrared gas analyzer (LI-COR Inc, Lincoln, USA) equipped with a customized chamber. The R_S was measured between 09:00 and 14:00 local time, twice a month from early June to late August. Meanwhile, the soil temperature (T_5) and volumetric water content at the 5 cm depth (W_5) were measured adjacent to each collar with digital temperature and moisture probes, respectively (Spectrum Technologies, USA).

The leaf litter and fine roots (< 2 mm diameter) traits were measured in 2015. The leaf litter was collected using litterfall traps to determine the litter C/N ratio (C/N_{litter}) in October 2015. Forest floor was sampled from three 30 cm × 30 cm subplots per plot in July 2015; and the samples were oven-dried at 65 °C to a constant mass to determine the litter mass (F_{mass}, kg m^{-2}). Eight soil cores (an area of 29.2 cm^2) per plot were taken randomly down to 10 cm depth of the mineral soil at the end of July 2015 for determining the fine root biomass (B_{root}, g m^{-2}). The fine roots in the soil cores were manually separated, oven-dried at 65 °C to a constant mass, and weighed to the nearest 0.001 g. After that, the fine root samples were combined by plot as a composite sample for determining the C/N ratio of the fine roots (C/N_{root}). The C concentrations of the litter and fine roots were determined using the dry combustion method with a Multi N/C 2100 analyzer (Analytik Jena AG, Germany), while the N concentrations were determined with a Kjeldahl analyzer (Kjeltec 8400, Foss, Hillerød, Danmark) since the Multi N/C analyzer in the laboratory was not equipped with modules for solid N analysis. We realized that these measurements were asynchronized with the measurements of soil properties but may be still feasible for exploring relationships between the R_S and plant traits, because plant traits may not change significantly within the 1-year period (Mueller et al., 2015).

Three replicate topsoil (0–10 cm) samples per plot were randomly taken within the central 20 m × 20 m of each plot (i.e., leaving 5 m buffer in each side) once a month from June to August. The fresh samples were carefully mixed and sieved through a 2 mm mesh to remove all plant material and rocks, and then stored at ~4 °C until further microbial processing within one week. Some subsamples were air-dried for determining soil pH with 1.0 M KCl and a Mettler Toledo pH meter (Mettler Toledo, Columbus, Ohio, USA).

Soil microbial biomass C (C_{mic}) and N contents (N_{mic}) were measured using the chloroform fumigation extraction method (Vance et al., 1987). A fresh subsample (10.0 g) was fumigated with ethanol-free chloroform in desiccators for 24 h, and subsequently extracted with 25 mL 0.5 M K_2SO_4. Another subsample was nonfumigated and extracted as done for the fumigated soil. Soil dissolved organic C (C_{dis}) and total N (N_{dis}) were estimated from the nonfumigated K_2SO_4